A comparative analysis of play behaviour in primates and carnivores

Lewis, Kerrie Patricia

A Comparative Analysis of Play Behaviour in Primates and Carnivores

Kerrie Patricia Lewis

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Abstract

This thesis considers the evolution of play behaviour, focusing on comparative analyses of extant primates and carnivores from various perspectives, including intra-specific analyses, life-history, socio-ecology, and brain anatomy, taking data from the existing literature, and using phylogenetic comparative techniques.

Phylogenetic reconstructions suggest that each play category represents its own evolutionary trajectory, and support previous findings that social play, being the most ancient form of play in primates, may represent a distinct category of behaviour.

Analyses of intra-specific play patterns proved difficult due to a lack of available data in the literature, but point to the importance of controlling for variables that differ between populations of the same species, such as group composition, and research effort.

Comparative analyses of life-history variables and play demonstrate that precocial species play more than altricial species. Precocial species have a relatively shorter developmental period of postnatal brain development, and may therefore require the neurological and physiological benefits afforded by play behaviour in order to hone brain development prior to adulthood.

Comparative analyses of socio-ecology and play suggest that larger groups require increased play time budgets, possibly because of a need to fulfil the social skills required to maintain group cohesion. Social networks of the population (clique size and network size) predict social play frequency in primates. Contrary to previous findings, I found no evidence that diet is a good indicator of time spent in play, although basal metabolic rate does correlate with play, suggesting that other socio-ecological factors contribute to the performance of play.

Comparative analyses of brain components and play indicate that brain correlates are selective and do not apply to all regions. There are strong correlations between socio-cognitive, motor, emotional, and also visual areas of the brain and social play in primates, namely the neocortex, cerebellum, visual cortex and LGN, vestibular complex, striatum, medulla, amygdala, and hypothalamus.

Although play is a difficult ethological topic, it appears to be vital to development and life in social groups.

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Declaration:

I declare that no material contained within this thesis has been previously submitted for a degree in this, or any other university.

Statement of copyright:

For my parents

Chapter 1:

Introduction

This thesis deals with the evolution of play behaviour, focusing on comparative analyses of extant primates and carnivores. Play behaviour is assessed from various perspectives, including brain anatomy and cognition; socio-ecological variables such as social organisation and foraging ecology; life-history variables such as gestation, and lifespan; and behavioural ontogeny. Comparative data on primates and carnivores are analysed using phylogenetic methods.

Before dealing with each broad category in detail, it is necessary to present some background on the nature of play, and the factors that have been proposed to affect and shape it.

1.0 Background

1.1 The Problem of Play

Play is a behaviour that is often ignored by evolutionary ethologists. It is a category frequently dismissed as non-essential, trivial, or unimportant in the behaviour and development of animals (Fagen 1981; Burghardt 1998a), and disparaged as the harridan or "*hobgoblin of animal behavior*" (Mitchell 1990: 197). Yet, play is commonly identified in the behavioural repertoires of many animals, and it is assumed that the young of most mammals and some bird and reptile species exhibit some form of play behaviour (Ficken 1977; Fagen 1981; Ortega & Bekoff 1987; Fagen 1995; Burghardt et al. 1996; Kramer & Burghardt 1998; Burghardt 1998a; Heinrich & Smolker 1998; Gamble & Cristol 2002). Remarkably however, there is still a lack of data regarding the species that do in fact play (Burghardt 1984; Bekoff & Byers 1998: xiv). Play seems to pose a particular problem to ethologists in that structurally, the behaviour can vary widely between species, and there remains conflict and confusion in attempting to define it functionally (Bekoff & Byers 1985).

1.2 Patterns of Play

1.2.1 Recognising Play

It is frequently claimed that although play behaviour is easily recognised (e.g. Poole & Fish 1975; Bekoff & Byers 1985; Martin & Caro 1985; Fagen 1995), it is difficult to define and to quantify (Fagen 1981; Bekoff & Byers 1998). So much so in fact, that some researchers have suggested that it is impossible even to ask theoretical questions about play, never mind attempting to answer them (Marler & Hamilton 1966). Fortunately, further analyses of this behaviour have superseded this pessimistic view (see Fagen 1981; Smith 1984; Bekoff & Byers 1998 for reviews). It is often said of play, that it is defined by what it is not, and that play all too often becomes a default explanation for a behaviour that appears functionless (Martin & Caro 1985; Gamble & Cristol 2002). Indeed, there has been much dispute in the literature as to what constitutes play and the difficulty in defining it (Fagen 1981; Allen & Bekoff 1997). I will not attempt to become embroiled in the ensuing semantics of this debate, and instead refer to Bekoff & Byers' (1981: 301) now widely-cited definition that provides an excellent basis by which to understand play:

> *"Play is all locomotor activity performed postnatally which appears to an observer to have no obvious immediate benefits for the player, in which motor patterns resembling those used in serious functional contexts may be used in modified terms. The motor acts constituting play have some or all of the following structural features: exaggeration of movements, repetition of motor acts, and fragmentation or disordering of sequences of motor acts."*

In spite of play sequences "borrowing" their appearance from "serious" behavioural patterns, it might be fair to suggest that a continuum exists between play behaviour and more "serious" behaviours, especially given that in older juveniles and adults (in species that exhibit adult play) it often becomes difficult to differentiate a play type such as play-fighting from actual aggression, and that play-fights often end antagonistically (e.g. Poole & Fish 1975; Beckel 1991). More recently, a set of five criteria have made it possible to recognise play as a distinct behaviour in many species (Burghardt 1999, 2001, in press), enabling play to be identified in not only many mammals and birds, but also turtles, lizards, and fish (Burghardt 1998a; Kramer & Burghardt 1998; Burghardt et al., in press). In brief, these criteria can be explained thus (Burghardt 2001: 332):

> *"Play is repeated incompletely functional behavior differing from more functional versions structurally, contextually, or ontogenetically, and occurring voluntarily when the animal is in a relaxed or unstressed setting".*

To date, most studies of animal play divide this heterogeneous category of behaviour into one of three types: locomotor-rotational, object-manipulation, and social (chasing, wrestling) play (e.g. Bekoff & Byers 1981; Miller & Byers 1998), whilst in humans other kinds are frequently identified, including pretence, socio-dramatic play, language play, and others (Johnson et al. 1999). Other forms of play, such as sexual play, which usually takes the form of mounting (Vankova & Bartos 2002), and play-mothering (Lancaster 1971), might also occur. Although these broad categories are specified, they are not necessarily distinct (Burghardt 2001) and are often subdivided further; for example, by distinguishing rough-and-tumble play from other forms of social play (e.g. Aldis 1975). Table 1.1 details example characteristics of play types with example species observed to exhibit each behaviour; the list is not exhaustive in either case, but gives an overview of the behavioural elements of play. Although such studies provide some evidence to support the theories as to why animals play, many fail to look at the broader comparative (see Burghardt 1998a); perhaps this is why the functions of play behaviour are still poorly understood and disputed (Martin & Caro

Table 1.1. Ethogram of play type characteristics and example species of primates and carnivores observed to engage in specific play behaviours.

Play Category	Characteristics	Example species	Source
Solitary/ Locomotor-rotational	Hop; leap; roll; somersault; spin; flip; jump; bounce; headshake; roll; porpoise; spin; galumph; dig.	*Presbytis entellus*; *Cercopithecus aethiops*; *Phoca vitulina; Haliochoerus grypus.*	Sommer & Mendoza- Granados 1995; Fedigan 1972; Renouf & Lawson 1986; Wilson 1974.
Object	**Play directed towards inanimate objects:** chew; mouth; manipulate; shake; bat; paw & bite; carry; toss; pick-up-drop.	*Macaca nemestrina*; *Pan troglodytes*; *Colobus badius*; *Anonyx cinera*; *Cerdocyon thous*; *Speothos venaticus*; *Felis silvestris*.	Kirkevold et al. 1982; Mendoza-Granados & Sommer 1995; Clutton-Brock 1974; Pellis 1991; Biben 1982; Martin 1984a.
Social/ Play-fighting	**Aggressive movement patterns without threat gestures:** chase; wrestle; slap; jump at; play bite; cuff; pull tail; rough-and-tumble; run towards; kick; splash; porpoise; sniff.	*Macaca fuscata*; *Papio* spp; *Theropithecus gelada*; *Presbytis entellus*; *Gorilla gorilla*; *Pan troglodytes*; *Callithrix jacchus*; *Panthera leo*; *Phoca vitulina*; *Haliochoerus grypus*; *Ailuropoda melanoleuca*.	Koyama 1985; Young et al. 1982; Barrett et al. 1992; Sommer & Mendoza-Granados 1995; Fischer & Nadler 1978; Hayaki 1985; Voland 1977; Schaller 1972; Renouf & Lawson 1986; Wilson 1974;Wilson & Kleiman 1974.
Adult	**Usually rare:** tickling; gentle wrestling; non-aggressive biting; grapple.	*Macaca fuscata*; *Macaca radiata*; *Pongo pygmaeus*; *Ursus maritimus*.	Koyama 1985; Caine & Mitchell 1979; Zucker et al. 1978; Latour 1981.
Sexual	Mounting.	*Papio* spp; *Cercopithecus aethiops*; *Phoca vitulina*.	Young et al. 1982; Fedigan 1972; Wilson 1974.

1985). For this reason, a clearer differentiation of Tinbergen's Four Whys of function, evolution, development, and causation is required (Tinbergen 1963; Burghardt 1998a).

1.3 Functions of Play

1.3.1 Is play functional?

The functions of play are often not obvious. One of the overwhelming difficulties in defining play function is that play behaviour has often been described as "functionless" (Bekoff & Allen 1998) or "*incompletely functional*" (Burghardt 2001). This is perhaps because the adaptive significance of play behaviour is less well understood than other categories of behaviour such as sex or fighting (Fagen 1981; Krebs & Davies 1993). If there is no function in playing however, it might be assumed that any costs incurred through playful activity would lead to selection *against* it (Martin & Caro 1985). There do however appear to be several areas of proposed functions of play behaviour: to maximise physical benefits of exercise and activity, in honing both social and non-social skills, the contribution of play to the development of the central nervous system (CNS), and the exhibition of novel behaviours and innovation (Burghardt 1988). Typically, for example, social play behaviour has long been considered to be one vital aspect in the learning and development of skills that are later fully utilised in adulthood, possibly contributing to facilitating the learning and maintenance of some adult social relationships (Bekoff 1978; Lee 1983; Martin & Caro 1985; Mendoza-Granados & Sommer 1995), which are developed through social interactions with conspecifics (e.g. Rowell & Chism 1986; Govindarajulu et al. 1993; Smith et al. 1998). As play generally does not persist into adulthood, it is also believed that play may function as preparation for certain other skills of adult life, by promoting the learning of adult motor, social, communicative, and cognitive skills, as well as sex, dominance and aggression (Doyle 1979; Jolly 1985: 401; Baldwin 1986; Harcourt 1991; Fagen 1993). The mounting behaviour of sexual play forms part of the play repertoire of some mammals, and is typically thought to promote locomotor and social skills, and also arguably, to gain sexual experience (Vankova & Bartos 2002); as juveniles typically cannot reproduce, this behaviour is sometimes referred to as "pseudo-sexual play" (Bon & Campan 1996; Yamane 1999). Socially deprived male rats still respond normally when introduced to sexually mature females in laboratory situations, although it has been reported that male rats of the same age who have been allowed access to play mates are more likely to be successful in fighting off other male competitors (Panksepp 1998). Many theories have been proffered as to what an animal has to gain by playing, yet it is not always apparent what the functions of play might be (Bekoff & Allen 1998). Perhaps play might not so much practice skills as be a means of activating the animal to engage in vigorous complex actions that give its sense organs, brain, and muscles experiences in working together and responding to varying, often unpredictable, conditions (Burghardt 2001; Špinka et al. 2001). Thus, play may assist or contribute to the development of permanent effects on physical, neural, and mental processes. Table 1.2 details examples of the proposed functions of different aspects of play.

1.3.2 Play as practice?

From the earliest discourse on play behaviour, the idea that play occurs in juvenile animals as practice for adult life has been central to the study of play in animals (Groos 1898) and humans (Groos 1901). In fact, this theory has remained a key factor in play research to date (e.g. Govindarajulu et al. 1993; Byers & Walker 1995). The theories as to why animals play tend to concentrate on different aspects of these adult skills, such as fighting (Pellis & Pellis 1996), social skills (Bekoff 1995), object manipulation (Takeshita & Walraven 1996) and locomotor skills (Byers & Walker 1995). Enthusiasm for such theories has to be tempered by the fact that mammals deprived of the opportunity to play still develop these adult skills (Baldwin & Baldwin 1973). However, the relationship between juvenile play and the level of competence in these skills has not been fully assessed, so whilst animals may still develop adult skills, they may not be as competent in such skills in comparison with those individuals who engaged in play as juveniles (Hol et al. 1999). Despite this, not all learning occurs through play (Martin & Caro 1985). The performance of play behaviour in general however, may serve to enhance and promote adult skills

Table 1.2. Proposed functions of play behaviours

Play type/ behaviour	Possible function	Source
General functions: all play	To develop adaptive responses to unexpected events	Špinka et al. 2001
	To develop awareness of the environment	Meaney et al. 1985
	To rid of excess energy	Barber 1991
	Self-assessment in task-performance	Thompson 1998
	To modify the CNS during early postnatal development	Fairbanks 2000; Burghardt 2001
Solitary/locomotor-rotational play	Motor training (see section 1.3.3)	Byers 1998b
	To hone skeletal muscle fibre	Byers & Walker 1995
	To practice predator avoidance and agility	Špinka et al. 2001
Object play	To practice hunting/foraging behaviour	Martin 1984a
	To train hand-eye co-ordination	Takeshita & Walraven 1996
Social play	For cognitive enhancements for social interactions & in "reading" unpredictable social situations	Špinka et al. 2001
	To relieve group tensions	Enomoto 1990
Social play signals	To demonstrate or practice intent	Bekoff 1975; 1977; 2001b

Play type/ behaviour	Possible function	Source
Social play (continued)		
Play-fighting	To practice dominance and aggression/ test strength/ mate-defence	Bramblett 1976; Fagen 1981; Pellis & Pellis 1996
	To develop communicative abilities, especially during agonistic situations	Dolhinow 1971
	To demonstrate behavioural and physical competency	Chiszar 1985
	Learn co-operation/trust/"fair play"	Bekoff 2001a, b
Self-handicapping	To create practice for the "unexpected"	Špinka et al. 2001
Play-mothering	To develop/practice maternal behaviour	Lancaster 1971; Meaney et al. 1985

(Chalmers 1984) through the permanent effects on the developing nervous system during the juvenile period (Fairbanks 2000).

1.3.3 Motor training

The term "motor-training" refers to juvenile activity that improves physical performance (Bekoff & Byers 1981). The motor-training hypothesis proposes that animals play for physical exercise or to develop and maintain physical skills, and that the adaptive function of play in this context is to modify the developing neuromuscular system (Brownlee 1954; Bekoff & Byers 1981; Byers & Walker 1995). The type of play considered in this hypothesis, are the energetic locomotor patterns seen in most mammals that are known to play. The patterns mimic other behaviour patterns connected with survival and reproduction, such as intra-specific fighting, capturing prey, or escaping from predators (Govindarajulu et al. 1993; Byers & Walker 1995). Indeed, enhancing and maintaining physical ability, strength, and agility through energetic play may be beneficial in terms of these "serious" behaviour patterns (Brownlee 1954; Symons 1978; Fagen 1981). However, developing strength through this type of play might also be costly to an animal if it means the animal spends less time in search of food, detecting danger or risks physical injury. An animal may take considerable risks whilst playing, not least in terms of sustaining injuries either through collision or a fall, or by falling prey to predators (Byers 1977; Berger 1979, 1980; Harcourt 1991). There is considerable evidence that early play serves to enhance physical fitness, and develop motor co-ordination and fighting skills, so as to minimise the risk of injury (Renouf & Lawson 1986; Govindarajulu et al. 1993). Thus, the ability to modify physical skills should be adaptive as, in short, there is no point in maintaining physical skills that are not, or cannot be, used by the individual (Fagen 1981; Byers & Walker 1995).

1.3.4 Play as training

Not all physical and neural responses are permanent; physical training may improve physical skills at any age (Stamford 1988), but these increments may be lost as training ceases. Byers & Walker (1995) maintain that it is important to consider how much an animal plays in comparison with how much exercise it needs to take to increase strength and endurance. Byers (1998b) states that it is often the case that the duration of play, and the amount of exercise gained through play, is much lower than would be needed to maintain physical skills, thus rejecting the theory that play serves as "getting into shape". This might show a temporary benefit of play, but not a long term one. Indeed, any behaviour (e.g. foraging), will contribute towards the physical fitness of an individual in terms of muscle tone and general mobility and activity. If play were solely for the purpose of gaining and maintaining physical fitness, then it would have to be shown that play provides enough exercise to facilitate aerobic or anaerobic physiological training responses (Bekoff 1989a). Byers (1998b) predicts that play alone will not meet the necessary criteria. Indeed, the benefits of exercise might not be achieved through play due to the varying functional constraints of play and exercise (Burghardt 1984). This might not be the case in all species however. The locomotor play of some ungulate species, for example, seems to show marked physical endurance training (e.g. Berger 1980; Miller & Byers 1991).

It was previously thought that because locomotor play behaviour can be physical exercise, for example, the energetic gambolling of lambs (*Ovis canadensis*, Bonnett & Fewell 1987), or the running of pronghorn fawns (*Capra americana*, Miller & Byers 1991), the function of play is purely for physical fitness or physical training. It may be said that physical fitness is a consequence of locomotor play, but this does not necessarily mean it is the reason it evolves (Byers 1998b). Indeed, it is often the case that a playing animal does not engage in enough locomotor play to be of any substantial benefit to its physical fitness (Byers & Walker 1995). As play behaviour typically occurs only in juvenile animals (Fagen 1981), it seems extremely unlikely that play occurs only to facilitate physical exercise (Byers 1998b); this is because many physical training responses are only transitory and are not limited by age (Heath et al. 1981). If play did occur for physical exercise, it would be expected that adults would play more than juveniles, as the age-category with the most need for fighting ability.

1.3.5 Adult play

Play behaviour is usually concerned only with the young, yet in some species it progresses beyond the juvenile phase, and into adulthood. Adult play occurs in some species of primate, carnivore, and rodent, yet the rate at which adults play is far lower than that of juveniles, and is often negligible (Caine & Mitchell 1979; Enomoto 1990; Beckel 1991; Walker & Byers 1991; Pellis et al. 1992; Fedigan 1993; Hall et al. 1998). Adult play appears in various forms: solitary adult play, adult-adult play and adult-juvenile play, and occurs in many mammalian species (e.g. *Marmota flaviventris*, Armitage 1962; *Gorilla gorilla gorilla*, Fischer & Nadler 1978; *Phoca vitulina*, Renouf & Lawson 1986; *Orcinus orca*, Guinet 1990). Adults may play with their offspring or with other juveniles within the group. Indeed mother-infant play is relatively common in many species (e.g. Byrne et al. 1983; Watson 1993), yet in harbour seals (*Phoca vitulina*) for example, adult play may account for 17.6% of all play behaviour recorded, but mother-pup play is rare at only 1.4% (Renouf & Lawson 1986). Although play is relatively common between a mother and her offspring (e.g. *Macaca arctoides*, Rhine & Hendy-Neeley 1978; *Macaca fuscata*, Glick et al. 1986a; *Macropus rufogriseus banksianus*, Watson 1993), it is often the case that other adult members of the group might also engage in playful activity with youngsters (e.g. *Cercopithecus aethiops*, Lancaster 1971; *Pongo pygmaeus*, Zucker et al. 1978; *Pan paniscus*, Enomoto 1990; *Pan troglodytes*, Pruetz & Bloomsmith 1995).

Most discussions of adult play deal with social play behaviour (e.g. Pellis & Iwaniuk 1999b). However, object play in adults is known to occur in some species, notably domestic or captive carnivores (Hall 1998). This type of play is generally associated with behaviour patterns usually seen in predatory and hunting behaviour (Martin 1984a, b), and the two types of behaviour are often difficult to distinguish in adults. This is contrary to aggressive behaviour, whereby at any point in life-history, play is distinct from aggression, and both are clearly recognisable (Thompson 1998). Adult play is also distinct from juvenile play in that patterns from different categories of behaviour are not mixed, they are non-random, and may be strikingly similar to the "serious" pattern of behaviour that the play resembles (Hall 1998). In some domestic carnivores, the structure and motivation for adult play is identical to that of predatory behaviour, and the only distinction between them is the absence of a kill bite during play (Sen-Gupta 1988). It seems likely that there is a strong motivational association between object play and hunting behaviour, in carnivores at least (Biben 1979).

Adult play is often considered to be unnecessary "behavioural fat" and that a playing adult is being rather indulgent by devoting time and energy to play (Müller-Schwarze 1978; Symons 1978; Müller-Schwarze et al. 1982; Martin 1984; Hall 1998). However, adult play may have certain benefits in terms of assisting the development of their offspring and maintaining aspects of their own social relationships (Fagen 1981). In fact, if play does in part facilitate the practice of skills used later in life, then an adult's play with its offspring may be a form of parental investment (Zahavi 1977; Fagen 1981). Moreover, it has even been suggested that the exhibition of play behaviour offers a means by which parents can assess the behavioural and physical competence of their offspring (Chiszar 1985), and indeed rough-and-tumble play may function to perfect social competence and affect the transition from juvenile to adolescent (*Homo sapiens*, Pellegrini 1995 a, b). The degree of relatedness between players certainly seems to be important within adult play behaviour. It is more likely that an adult's play partners, regardless of age, will be close kin (e.g. *Panthera leo*, Schaller 1972; *Macaca mulatta*, Symons 1978). Indeed, relatedness is important for juvenile players also, in that play partners are often selected on the basis of the social relationships of the player's mother (e.g. *Macaca fuscata*, Koyama 1985; Glick et al. 1986; *Pan troglodytes*, Tomasello et al. 1990).

It is suggested (Fagen 1981) that parental play is more likely to occur in species where both parents assist in the rearing of offspring, as there is a greater likelihood of paternity; if play can be adaptive, then playing offspring might benefit the parent in terms of gene persistence. Adult males in promiscuous species such as chimpanzees may also engage in play with infants. It might be expected that adult males should only participate in play interactions with infants that they can be *relatively* sure are their own offspring (unless they actually want to harm them), if it is assumed that the function is to assist the physical and behavioural development of its own offspring (Fagen 1981). Moreover, adult males who can be comparatively sure of their paternity are more likely than other males to protect and care for infants in any sense (Hrdy 1976). However, in captivity at least, it has been shown that there are no significant differences between the play of adult males and their *likely* offspring, and play between adult males and other-sired offspring (see Pruetz & Bloomsmith 1995). Captive adult orang-utan males may play with their offspring, although this is rarely observed in their wild counterparts (Zucker et al. 1978).

Playing with an infant may grant some level of status to an adult, whilst simultaneously demonstrating a "goodwill gesture" to the infant's mother. Such signals may be open to falsification should the adult [male] then commit infanticide. Although adult-immature play may distance a mother from her infant, play does not seem to precede infanticide (Fagen 1981). Van Schaik et al. (1999) state that in primates at least, adult males do not commit infanticide in species where there is a stable system of communal care of infants. It seems plausible that this might include aspects of allo-mothering and incidences of adult-infant play behaviour.

Adult-adult play usually occurs between males and females as courtship behaviour (Fagen 1981; Pellis & Iwaniuk 1999a, 2000b), but may also occur between same-sex individuals (e.g. Fischer & Nadler 1978). Play fighting occurs in adults both with juveniles, as well as with other adults, but the most common form between adults is as a prelude to courtship (e.g. *Phoca vitulina*, Wilson 1974). It is supposed that this behaviour functions to dilute possible aggression between unfamiliar potential partners (Pellis & Iwaniuk 1999a). Alternatively, adult play-fighting may provide a means by which to assess potential mates and may serve as an honest signal of fitness (Fagen 1981; Kramer & Burghardt 1998; Pellis & Iwaniuk 1999a, 2000b). Other forms of play might also be indicative of biological fitness; adult hunting dogs (*Lycaon pictus*), timber wolves (*Canis lupus*), and choz-choz (*Octodontomys gliroides*) are species that play socially before hunting (Estes & Goddard 1967; Mech 1970; Wilson & Kleiman 1974) perhaps in order to warm up physically, and possibly also as a sort of "*pep rally*" (Estes & Goddard 1967). This too may serve as honest signalling to other members of the pack to show which individuals are healthy for the hunt (see Fagen 1981: 441). Clearly, play does not have to occur for physical warming up of muscles to take place, but in tandem with any physical warm up, playing before hunting may be beneficial as a social signal to show willingness to engage in social activities, in this case, foraging or hunting (Fagen 1981). Using play as a warm up also appears to occur in other adult animals, such as the mountain hare (*Lepus timidus*) (Flux 1970), and flying squirrel (*Petinomys fuscocapillus*) (Krishnan

1972) before foraging. It might be expected to find social play incorporated in these "pep rallies" in species that hunt co-operatively, such as social carnivores (Fagen 1981).

There are various theories as to the functions of adult play, and it may be that these differ in different taxa. Adult play might allow the maintenance of some predatory skills (Hall 1998); competence gained through object play may permit a reduction in time required in actual predatory behaviour (Russell 1990). Object play may allow for further exploratory and learning skills about novelty and tool use (Rumbaugh et al. 1972; Tayler & Saayman 1973; Tomasello et al. 1989; Visalberghi & Guidi 1998). In other species, it may be so that social play amongst adults serves to relieve group tensions (*Pan troglodytes*, Enomoto 1990). It seems likely that adult social play certainly serves to strengthen social relationships within the group (Bekoff 1974; Renouf & Lawson 1986).

1.3.6 Exploration & inquisitiveness

Play and exploration may be closely related behaviours, and because play appears to develop from exploration, it has been argued that play exists as a learning mechanism, to aid the acquisition of experience about the environment (Baldwin & Baldwin 1978; Baldwin 1986). For example, juveniles often exhibit much age-specific curiosity about the types of food adults may eat, and as such "play-feeding" can occur, which may serve as part of the learning process about which foods are edible (Janson & Van Schaik 1993; Nash 1993). Play may be linked to diet through inquisitiveness. Herbivores are less inquisitive than omnivores (Baldwin 1986); this may be because certain skills of exploration are required to find food with an increased nutritional value. Thus, if exploration and play are intrinsically linked, play may be selected for if inquisitiveness is required for foraging (Baldwin 1986). It might rather be the case, as in felids, that predators exhibit certain types of play behaviour more readily as practice for hunting skills (Martin 1984a; Hall 1998). In spite of these theories, it is important to bear in mind that the function of exploration is to gather information about the environment, whereas play does not appear to have an immediate function, and it is not the case that animals *must* and *do* learn and practice all skills through play (Burghardt 1984). So although play may borrow certain aspects of exploratory behaviour, especially with regard to novel stimuli, play and exploration are typically considered discrete behaviours.

1.3.7 Costs and benefits

One of the principal assumptions about play behaviour, like all other behavioural patterns, is that it has both costs and benefits (Fagen 1981). It is argued that play should have immediate costs with delayed benefits, and that these long-term benefits should outweigh whatever costs may be incurred in the process (Fagen 1981; Chalmers 1984; Caro 1995). Table 1.3 details examples of immediate costs with associated long-term benefits to play.

Table 1.3. Immediate costs with associated delayed benefits to playing

Immediate cost		**Delayed benefit**
(Risk of) injury	►	Resilience through play
(Risk of) predation	►	Agility and behavioural boldness
Reduction in food	►	Environmental familiarity

There are many potential risks associated with playing, largely due to lack of control, exuberance, or simply failing to notice dangers whilst engrossed in the act of play (Fagen 1981). Classic examples of the costs of play might include the risk of a fall whilst playing in trees, or in other unstable terrain (e.g. Jolly 1966, 1985; van Lawick-Goodall 1967; Byers 1977); the risk of becoming separated from primary caregivers or otherwise becoming a potential lone target of predators (e.g. Sugiyama 1971; Hausfater 1976), or conversely, startling the potential prey of one's own group (Wrogemann 1975); the risk of being too exuberant during play-fighting, or misjudging playful intention resulting in aggressive injury (e.g. Angst & Thommen 1977; Kurland 1977); or becoming at risk from environmental dangers (becoming trapped in rocks; falling rocks; collisions; falling against cacti etc.; Kummer 1968; Douglas-Hamilton & Douglas-Hamilton 1975; Berger 1980).

The age-distribution of play has been cited as evidence that play behaviour must have delayed benefits (Fagen 1977, 1981; Smith 1982), but others state that play could also have immediate benefits (Bekoff & Byers 1981). Play remains widely regarded as a costly activity, in terms of time, energy, risk of injury, and risk of predation (Zimmermann et al. 1975; Berger 1980; Fagen 1981; Martin & Caro 1985). Due to this, it is believed that there must be significant benefits to play, or individuals would not be selected to perform such behaviour. Indeed, the fact that play incurs costs is *"often the only argument for its benefits"* (Martin & Caro 1985: 79-80). Martin & Caro (1985) argue that as play occurs, it must be adaptive. However, Gould & Lewontin (1979) have criticised this kind of statement as lacking scientific credibility. The notion that all traits are adaptive (relative to the viable alternatives) as a result of natural selection has been termed the "adaptationist programme". Gould & Lewontin's (1979) general criticism of this is that it fails to distinguish the current utility of a trait from its origin and the evolutionary reasons for it. Insofar as play behaviour is concerned, it is clear that the functions of play must be better understood relative to its evolution.

However, in spite of the wide variety of risks and setbacks that play may incur, there appears to be a strong motivation for young animals to engage in play (Fagen 1977); they will often self-handicap in order to play, even with ill-matched partners (Bekoff 1978; Fagen 1981), and attempt to play regardless of parental discipline and physical risks (Bekoff 1978). It thus seems likely that play does have important functions, perhaps both proximally and ultimately, for it not to be selected against (Martin & Caro 1985). However, play is not always so robust, diminishing under severe adversity (Burghardt 1984). It seems thus plausible that playing as a juvenile offers significant advantages to those that are able to engage in play, as opposed to individuals that do not, both in terms of immediate and delayed benefits, although not necessarily in equal measure. In terms of immediate benefits, social and physical "enjoyment" (Fagen 1992), immediate social bonds (Špinka et al. 2001), and immediate learning enhancement, may be key to a juvenile's current situation, which may in turn affect ultimate individual fitness. In terms of delayed benefits, crucially that of honing the CNS at the period of juvenile plasticity (Byers & Walker 1995; Fairbanks 2000) is likely to be the most important factor to a playing juvenile, although experience of physical agility in the surrounding environment, and social and co-operative interactions (Bekoff 1978; 2001b; Meaney et al. 1985; Špinka et al. 2001) are also vital in terms of actual and social survival, especially for primates and carnivores. Thus overall, there is likely to be some overlap in the immediate and delayed benefits of play as both almost certainly occur. Delayed benefits may be argued to contribute most significantly to individual fitness; however, if play significantly reduces juvenile mortality as a direct result of enhanced social integration, then both immediate and delayed benefits are important facets in play's behavioural evolution.

1.4 Play and Evolution

The origins of play and the evolution of playfulness are largely ignored in the literature through focus on proximate causes and functions (Burghardt 1998a; Pellis & Iwaniuk 1999a,b, 2000b), and few comparative studies have addressed play behaviour. There has often been very little overlap between the structural and the functional approach to play (Burghardt 1998a), yet neither approach on its own fully informs us as to the origin of play, since there are problems distinguishing origin and phylogeny from function or current adaptiveness (Burghardt 1998a; Pellis & Pellis 1998).

1.4.1 The roots of play

Given that play behaviour appears to occur in most mammals, it seems reasonable to suppose that play occurred in the earliest mammals. Consequently, researchers such as Burghardt are strong proponents of the idea that in order to answer questions about the evolutionary patterns of play, it is imperative to study play in those taxonomic groups that are ancestral to birds and mammals: reptiles (Burghardt 1984, 1988, 1998a, b, 1999, 2001, Burghardt et al. 1996, in press, Kramer & Burghardt 1998). Reptilian play is seldom reported, and thus considered to be a rare occurrence; thus this thesis will not deal directly with the play of reptiles, but it is important to refer to reptiles with reference to the evolutionary context of play behaviour. The term "reptile" is itself however, rather misleading: *Reptilia* is a paraphyletic group in that shared traits are found in some, but not all of the descendant species pertaining to the common ancestor (Ridley 1996). Forms such as crocodiles have changed very little from the ancestral state, but birds represent the excluded species, descended from the same common ancestor, but that have undergone extreme phenotypic change (Futuyma 1986; Ridley 1996). Crocodiles are more closely related to birds than any other non-avian reptile group, and as such they share several behavioural elements in common (Burghardt 1998). Arguably, the most important of these insofar as play is concerned, is postnatal parental care (Herzog & Burghardt 1977), and longevity (Burghardt 1984). However, despite an extended period of parental care in relation to some other reptiles, crocodiles have not been observed to engage in social play; the same is true of iguanas (*Iguana iguana*) (Burghardt 1977, 1984) although object play may sometimes occur in both species (Burghardt 1998a).

Traditionally, it has been claimed that fish, reptiles, and amphibians (ectotherms) generally do not play (Burghardt 1984, 1988), but recent studies are beginning to change this view (Burghardt et al. 1996; Kramer & Burghardt 1998; Mather & Anderson 1999; Burghardt in press). Although play is generally considered to be the domain only of mammals and some birds, especially if related to neocortical wiring (see Chapter 7), there are some reports of other animals, especially some non-avian reptiles, engaging in play-like activities. Reptiles are generally believed to be rather limited in the behaviours they exhibit through play. There are however, various reports in the captive literature about object play in different species, such as komodo dragons (*Varanus komodoensis,* Hill 1946; Burghardt et al. in press), alligators (*Alligator mississippiensis,* Lazell & Spitzer 1977), iguanas (*Iguana iguana*, Hatfield 1996), and turtles (*Trionyx triunguis,* Burghardt et al. 1996; Burghardt 1998a), and usually involve some form of aquatic-object play, such as nudging objects around a pool or "playfully" snapping at water jets (Burghardt 1998a), arguably suggesting that reptilian forms of play-like behaviour are rooted in exploration. Within captive settings, objects may be used for environmental enrichment with both juvenile and adult animals. Indeed, it is interesting to note that object play is often reported in species that typically are not deemed to be playful (Burghardt in press), such as reptiles. Beyond reptiles, play has even been reported in cephalopods (*Octopus defleini*, Mather & Anderson 1999). However, these reports are limited in number and are often anecdotal in form.

Some reptiles do however exhibit exploratory behaviour (Rand et al. 1975; Drummond & Burghardt 1982; Burghardt 1984). It is known that there is a behavioural link between on the onset and development of exploratory behaviour and play (Baldwin & Baldwin 1977), and that exploration often precedes play in many species, including humans (Smith et al. 1998). Indeed, advanced play and exploratory activities in animals are generally accepted as evidence of advanced evolutionary development (Tayler & Saayman 1973). "Playful" exploration of objects during play, might suggest that the ecology of the species is more important than its phylogenetic position (Aldis 1975). This might be especially important in species such as pigs, *Sus scrofa*, that are opportunistic and typically curious; thus the practice of exploratory behaviour seems to be highly important (Stolba & Wood-Gush 1989; Wood-Gush & Vestergaard 1991). Play behaviour might represent the origin of curiosity and also the novel behaviour patterns that are seen in so many mammals (Burghardt 1998a).

1.4.2 The ancestral form of mammalian play

Mammals evolved from reptiles 150 million years ago (Jerison 1973; Eisenberg 1981). If play occurs in most mammals as is predicted, then it is likely that mammalian play behaviour, or an approximation thereof, arose during the Cretaceous period (144 - 65 mya [Futuyma 1986]), before the separation of different taxonomic lineages leading to modern taxonomic groups (Byers 1984, 1998b). Play behaviour is recognised as having various forms and functions in modern mammals, but it seems highly unlikely that play was so heterogeneous in its earliest form. It is possible, although unlikely, that play arose either through parallel evolution or convergence, after modern taxonomic lineages arose, whereby there was a similarity of playful behaviour in independent lineages (rather than a common ancestor). Byers (1984) however, states that the most likely path of play evolution is from an ancestral form and function of play in mammals, which has been largely retained but with modification in form, in response to changing selection pressures and adaptive radiation.

If a common form of play can be recognised across extant species, it might give some indication as to the primitive form and function of play. Byers (1984) thus strongly advocates that the ancestral form and function of mammalian play behaviour (as opposed to the reptilian "play-like" behaviour) is that of motor training, for the reason that it remains a primary function of play in mammals (see also Bekoff & Byers 1981; Byers & Walker 1995) and can occur without specialised encephalisation or social organisation being present. It is improbable that natural selection would have acted uniformly to select for social cohesion across taxa, that is, as sociality is not a primitive condition in mammalian evolution, it seems unlikely that social play represents the primitive condition for play (Byers 1984). Byers (1984) states that play patterns that resemble the serious behavioural components of the flight response are those most likely to have evolved first, thus solitary locomotor-rotational play behaviour is the most likely representation of the earliest form of play, followed by play that mimics adult agonistic competition (social play).

Support for the motor-training hypothesis comes from the long-held assumption that a primitive function of play was to enable the development of neuro-muscular systems (Bekoff & Byers 1981). As endothermy evolved, the onus on the biological necessity to conserve energy increased. The musculo-skeletal systems of endotherms became increasingly responsive to the use of specific bones and muscles, which became honed and trained through use, and specifically fine-tuned to be more energy efficient (Bekoff & Byers 1985; Byers 1985). Moreover, musculo-skeletal systems that are use-dependent enable an individual to practice motor skills associated with survival skills: thus the increased likelihood for motor training being representative of the ancestral form of play behaviour. As play may be connected to endothermy and metabolism (Burghardt 1988), it is likely that these specialisations were in place at the emergence of play behaviour. Play is less prominent in species with a low basal metabolic rate, such as reptiles, and some mammals such as anteaters and sloths (Fagen 1981; Burghardt 1984). Play, and other vigorous behavioural activities, might actually be detrimental to some reptiles as they are less likely than mammals to maintain the homeostasis and metabolism that permit such behaviours in mammals (Burghardt 1988). Similarly, most reptiles do not exhibit a juvenile period during which social, locomotor, avoidance, and feeding skills are honed: the key play period in mammals (Burghardt 1984, 1988). Future research should aim to focus on reptiles, especially those such as varanid [*Varanoidea*: monitor] lizards that exhibit a relatively high metabolic rate (overlapping with the rate of some mammals). It might be possible to glean further knowledge as to the importance of endothermy to the evolution of play behaviour (Burghardt 1984, 1988, in press).

1.4.3 Evolution & social complexity

Endothermy however, might not be the sole driving force in the evolution of play. Given that the neocortex is a mammalian neural adaptation, which can be used to predict measures of sociality (Dunbar 1992), and that neocortical wiring is critically determined by experience early in life (Quartz & Sejnowski 1997), it seems likely that across mammalian taxa, the evolution of play behaviour may have arisen with neocortical expansion (Lewis 2000). It is widely assumed that play behaviour evolved in association with life in social groups, and also with polygyny, for the purpose of motor training associated with the development of fighting skills, especially amongst males (Smith 1984). The rougher play often seen amongst males is considered to serve as practice for physical skills, used later in adulthood for competition for resources and mates (Lee 1983). It seems likely that although the evolution of endothermy is crucial to the evolution of play, it is neocortical expansion that is associated with the diversity of play from the ancestral motor training functions, to the development of more socially complex play. Thus, with increasing neocortical expansion emerged the specialisation for sociality, which in turn facilitated the divergence from the primitive play condition towards the diversity and complexity of social forms of play. Further studies should seek to demonstrate to what extent this might be the case.

From comparative studies on social play in muroid rodents, Pellis & Iwaniuk (1999b, 2000a) claim that the evolution of play "*is highly idiosyncratic in form and function*" and that play is equally likely to exhibit a reduction in complexity and intensity, as it is to exhibit an increase through common descent. They claim that play should have a positive association with duration of juvenility, thus a greater complexity and frequency of play should be present in species with a greater period of postnatal development (Pellis & Iwaniuk 2000a). The assumption remains that most mammalian species are capable of play, but it should be noted that although rare, play is argued to exist in non-mammalian and non-avian species, and that behavioural differences between the play of these groups may be due to differing ecological and evolutionary functions (Burghardt 1984): play might not physiologically prepare the developing reptile in the same way as the developing mammal, thus the exhibition of mammalian play might be more overt than the play of reptiles (Burghardt 1988).

1.4.4 Play and laughter

As this thesis deals with the play of animals, rather than humans, the phenomenon of humour and laughter is dealt with very limitedly here; there are of course areas of academia that deal with this phenomenon in great detail (e.g. clinical & psychological: Berk et al. 1991, Ramachandran 1998, Shibata et al. 2000, Vejleskov 2001, Rosner 2002; biological bases: Fry 1994; social: Kipper & Todt 2001; sociological: Oshima 2000). Smiling is widely considered to have originated as an ancient mammalian threat display, indicating the potential for harm or self-defence; it may be the case that a simple flash of teeth evolved as a social signal to demonstrate this, requiring no further action (e.g. Andrews 1963). Laughter however, is shown to have a different origin, and may be more keenly founded in the ancestral emergence of play (Panksepp 1998). Laughter may act as a public and social demonstration of victory (e.g. winning a play-fight) or to promote social cohesion (human laughter is "infectious"). Neurologically, the gap between laughing and crying is small. It is hypothesised that the mechanisms that permit the experience of separation-distress, along with those that promote the emotional experience of social bonding, may have been prerequisites for the origin of laughter (Panksepp 1998). If this is the case, it seems intuitive that the mechanisms that allow the experience of social bonding and separation-distress, as well as the propensity to cry and to laugh, may well have been prerequisites in the neural circuitry for the evolution of play. Indeed, as laughter is perhaps synonymous with the play of humans, laughter-like play vocalisations have been reported in some non-human animals (e.g. Marler & Tenaza 1977; Panksepp & Burgdorf 2000; see also section 1.6.2).

1.5 Development and Distribution

Due to the nature and timing of play, it is important to ask developmental questions of play behaviour in order to gain an understanding of its function; if an understanding of play's place in the evolution of animal behaviour is to be reached, it is vital to understand the function of play (Burghardt 1988; Fairbanks 2000). However, development and function are separate questions, and as any population is in part defined by age-structure, it is vital to incorporate the study of development when conducting evolutionary and ecological research (Bekoff & Byers 1985).

1.5.1 Onset and development

Play is a behaviour particularly embedded in infancy; it begins early in postnatal life, reaches a peak during the early juvenile period, and declines with the onset of adolescence and adulthood (Bekoff & Byers 1985; Fagen 1993; Byers & Walker 1995; Fairbanks 2000). In non-human primates, solitary play behaviour is usually the first type of play to emerge (Fairbanks 2000), and in primates can occur within the first two weeks of life (Cheney 1978; Lee 1984; Clarke 1990). Social play soon follows and tends to replace solitary play as the dominant form of play, peaking in frequency around one year of age (e.g. Zucker & Clarke 1992; Govindarajulu et al. 1993). Object play typically begins later than the other forms of play and has its onset during the early juvenile period, declining to adult levels by the end of the juvenile period (Byrne & Suomi 1995, 1996; Fairbanks 2000).

1.5.2 Behavioural patterns within play

Play behaviour is likely to occur and be most prominent in species where speedy motor patterns occur within their normal (non-playful) behavioural patterns, in species that exhibit an extended juvenile period, and species that have the potential to learn quickly (Ewer 1968). For these reasons, play behaviour is most readily recognised and reported in primates, some carnivores, and some ungulates (e.g. Brownlee 1954; Baldwin & Baldwin 1974; Zucker et al. 1978; Berger 1980; Bekoff 1984; Arnold & Trillmich 1985; Martin & Bateson 1985a; Bonnett & Fewell 1987;

Jensen et al. 1998; Kilner 2001). Play behaviour changes with age, and in most cases declines with the onset of adulthood (Chalmers 1980; Panksepp 1981; Fagen 1981; Mendoza-Granados & Sommer 1995; Fairbanks 2000). However, play sequences often consist of behaviours seen in many functional contexts as adults, such as aggression, hunting, and sex, but these lack the consequences of their "serious" behavioural counterparts, such as wounding, killing, or actual copulation (Fagen 1981; Burghardt 1984; Chalmers 1984). It should be noted that play-fighting itself is not a prerequisite for real fighting (Smith 1982). Many of the patterns that appear in the play of felids resemble those used in hunting and catching prey, so for example, felid play might be an example of practice behaviour for adult skills (Martin 1984a; Caro 1995).

1.5.3 Age & sex differences

Data on age-specific rates of play are rare (Byers 1998b). There are however two main hypotheses about play behaviour: that juveniles play more than adults, and that males play more often and more roughly than females (e.g. Cheney 1978; King et al. 1980; Oswald & Lockard 1980; Stevenson & Poole 1982; Lee 1983; Jolly 1985; Brown 1988; Gomendio 1988; Tomasello et al. 1989; Wilkomm 1990; Harcourt 1991; Nash 1993; Watson 1993; Markus & Croft 1995; Mendoza-Granados & Sommer 1995). Play is less common in older adults and it has been suggested that this is due to the fact that motor skills are not required to the same extent in these individuals in comparison with their younger counterparts (Watson 1993). If one type of play behaviour were more risky for females than for males, for example, then it would be expected that female play behaviour would decrease.

As an animal matures and develops, even within relative immaturity, it often becomes harder to distinguish true aggression from boisterous rough-and-tumble play (Martin & Caro 1985). It certainly seems to be the case that an individual primate's capacity for play varies according to its age and sex (Chalmers 1984). It seems that dominant animals are capable of moderating their play behaviour according to relevant asymmetry in strength; if one juvenile plays too roughly with another, it risks alerting the attention of the mother, who may break up the play interaction. As primates mature, they become more aware of intra-troop status, and become more competitive in play (Fagen 1981). Perhaps this is a reason why older male juveniles play more roughly than any other age group (e.g. Owens 1975b; Rowell & Chism 1986; Schåfer & Smith 1996).

It has been documented in many studies that juvenile males in particular become increasingly aggressive with age (e.g. Owens 1975b; Berger 1980; Kraemer et al. 1982; Pusey 1990; Mendoza-Granados & Sommer 1995; Smith et al. 1998). If this is the case, it may also contribute to the understanding of why males of a certain age appear to play more frequently, and also more roughly than their female counterparts. Females in sexually dimorphic mammals mature earlier than males (Baldwin 1986; Smale et al. 1995), which may have some effect on sex-differences in play behaviour. In nongregarious primates, such as nocturnal primates, and also the diurnal orang-utan *(Pongo pygmaeus)*, older juvenile females tend to play less frequently and exhibit less aggressive play than their male counterparts, concentrating more upon interactions with infants and alliances with other females (Nash 1993). Males of the same age, however, do not form alliances in the same way, but concentrate upon rough play with other males, which may, in part at least, serve as a practice of fighting skills (Berger 1980; Rothstein & Griswold 1991; Nash 1993).

Chimpanzees have not been reported to exhibit significant sexual dimorphism in play (Fagen 1981), but sex-differences have been observed in many wild, captive and laboratory studies on play behaviour (e.g. *Saimiri sciureus*, Baldwin & Baldwin 1973; *Ovis aries*, Sachs & Harris 1978; *Cercopithecus diana*, Byrne et al. 1983; Meaney et al. 1985; *Macaca fuscata*, Eaton et al. 1986; *Gorilla gorilla*, Brown 1988, Meder 1990; *Bison bison*, Rothstein & Griswold 1991). Self-handicapping by older or stronger play-partners may often occur to maintain a play bout with a mismatched partner (Pereira & Preisser 1998). However, it has been shown empirically that animals predominantly prefer to choose same-age, same-sex, and same-rank play partners (e.g. *Papio cynocephalus ursinus*, Cheney 1978; *Bison bison*, Rothstein & Griswold 1991; *Cercopithecus aethiops sabaeus*, Govindarajulu et al. 1993; *Ovis canadensis*, Hass & Jenni 1993; *Macropus rufogriseus banksianus*, Watson 1993).

Play behaviour is likely to be connected to life histories, and is associated with slower development, and parental care and longevity (Daly & Wilson 1983; Burghardt 1984).

It is expected that play will appear most frequently within species that exhibit a relatively high metabolic rate, some parental care, and advanced cognitive abilities relative to other species (Ewer 1968; Fagen 1981; Burghardt 1984). In comparison with typically precocial groups such as reptiles, typically altricial mammals display an increased metabolic rate and are not limited by their capacity for aerobic activity (Burghardt 1988); this might affect the exhibition of play behaviour.

1.5.4 Play and the brain

Brains are products of natural selection, and their structure and mechanisms are evolutionary adaptations that fit the animal's behaviour to its environmental and behavioural niche (Barton & Harvey 2000). Behaviour is mediated by the brain and recent trends in the play literature increasingly focus upon the correlation between aspects of neural anatomy and play behaviour (e.g. neocortex, Lewis 2000; cerebellum, Byers & Walker 1995, Pletnikov et al. 1999; localisation, van den Berg et al. 1999; hippocampus, Joseph 1999; amygdala, Pellis & Iwaniuk 2002). Thus, there are many_wide-ranging implications regarding the cognitive and neurological aspects of play behaviour, in addition to the already well-established theories of play.

As stated previously, play is typically thought to have no immediate function, and thus is hard to explain and even study from both proximate (including neural) and evolutionary perspectives (Burghardt 2001). As animals change and develop through different stages in ontogeny, they must maximise and modify physical skills. Byers & Walker (1995) state that skeletal muscle fibre and cerebellar synaptogenesis are the two effects that are permanently affected by postnatal development in mammals; the modification of these structures results in enhanced motor-performance skills, and as such are posited as the true effects of play during the juvenile period (Byers & Walker 1995). Although synaptogenesis continues into adulthood, it is the early postnatal formation of cerebellar synapses that is considered important to the onset of play (Byers & Walker 1995). The cerebellum for example, is fundamental in controlling motor co-ordination, that is, the control of specific motor sequences, and placing them in the context of the motor state of the individual at any given moment (Llinás & Walton 1998); Chapter 7 will deal with this in more detail.

The juvenile period represents an explosion of learning opportunities, developing the body and brain and by extension, the behavior of the individual (Dawson et al. 2000). Yet, which physical, social, and cognitive skills are learned and which mature merely as a consequence of growth is not understood in relation to play. Significant change and growth, both in behaviour and brain, occur during the early stages of life (Dawson et al. 2000), both pre- and post-natally. Indeed, much non-human primate development occurs *in utero*, rendering non-human primates more precocial than their *Homo sapiens* relatives. Soon after an infant is born, the connections between different parts of the brain develop further and strengthen (e.g. Aoki & Siekevitz 1988). The basic organisation of the brain typically does not change after birth, but aspects of its structure and function remain plastic for much of early life (Aoki & Siekevitz 1988), and the juvenile period is a particularly sensitive period during which different experiences can permanently affect the developing brain (Aoki & Siekevitz 1988; Dawson et al. 2000). Genes dictate basic patterns of connections between brain structures, but these are modified by environmental input (Fox et al. 1994).

It is known that in some species play is at its peak when brain development is most active (Panksepp 1981; Byers & Walker 1995). A previous comparative study by Iwaniuk et al. (2001) did not find a relationship between play and overall brain size. The brain is however, a heterogeneous organ and it may be necessary to look at specific brain components during the juvenile period (Lewis 2000). Physiological training responses are also known to occur in connective tissue, bone, the cardiopulmonary system, the endocrine system, and the nervous system (e.g. Rosenzweig 1971; Basset 1972; Tharp & Buuck 1974; Buller & Pope 1977; Fagen 1981; Byers & Walker 1995; Hol et al. 1999). If play can benefit these systems early in ontogeny, it may increase both the physical and Darwinian fitness of the individual later in life.

It has been shown that *some* training responses only occur during the juvenile period (Byers & Walker 1995). Young animals may also respond more quickly and more efficiently to training in comparison with their adult counterparts (e.g. Bekoff 1989a). Certainly, an individual that has experienced physical training from a young age may be more inclined to exhibit a "head start" of increased skills, than an individual that only begins training in adulthood, even if the result is only temporary. Play therefore seems to be an important and prominent behaviour in the formative years of an animal's life (Fagen 1981).

Certain cerebral structures in particular may be adaptively modified by the experience of play and exploration during the juvenile period. Bourgeois et al. (1994) showed that in rhesus macaques (*Macaca mulatta*) there is a high synaptic density during the first stages of postnatal life, when learning experiences are most intense, but that the density decreases via synaptic pruning to become relatively stable during adolescence and puberty. If we apply this to play behaviour, it might give an indication as to the importance of play during this period. In fact, the effects of modification of the cerebellar synaptogenesis and skeletal muscle that influence motor-performance only occur during a very small window of postnatal development. These effects are permanent, as opposed to many other effects of motor-training that can occur at any age. Moreover, the age-distribution of play and the time-frame during which most play occurs, tends to suggest that play characterises a sensitive period whereby motor patterns alter development (Immelmann & Suomi 1981; Byers 1998b). The true effects of play are those that permanently affect the developing CNS during critical or sensitive periods in development, rather than physiological training or exercise responses that can occur at any period during the lifetime of that individual and that tend to be temporary; Byers & Walker (1995) argue that these are the effects of motor-training during the juvenile period. Byers (1999) states that in marsupial play at least, the function of play is to train neural networks. Thus, if the development of neural systems is the main benefit of play, then across taxa, play might be expected to vary more with *relative* brain size, or more likely, the size of relevant brain *structures* (Byers 1999). Sensitive periods of development are common in many mammals and some bird species (Byers 1998b). It seems to be during such periods that the potential to modify developmental systems through experience becomes apparent. Byers (1998b) states that it is reasonable to suppose that play, coinciding with periods during which the development of the brain and body might be altered, may be a performance-dependent development.

1.5.5 Play and cognition

The neural basis for the development of skills through play still remains comparatively unexplored. Indeed, fairly little is actually known about the developing brain during the early and late phases of the juvenile period, a time during which social and cognitive learning escalates, and play is at its most prominent (Casey et al. 2000). Iwaniuk et al. (2001) found that at an interspecies level in primates, there was no correlation between play and total brain size. Lewis (2000) found that in primates, social, but not other forms of play behaviour, correlate significantly and positively with neocortex size across taxa. It might be expected that the neocortex is important to the onset of play behaviour, as the development of the neocortex begins and is strongest early in the postnatal phase (Dąmbska & Kuchna 1996). It is in this early postnatal period that play is especially prevalent. Dunbar (1992, 1995a), and Dunbar & Bever (1998) have demonstrated a relationship between neocortex size and group size in primates and carnivores, arguing that the larger the social group, the greater the cognitive load in maintaining social relationships. Whilst comparative studies of cognition have focused exclusively on the neocortex, it has recently been established that the neocortex has tended to evolve together with the cerebellum (Barton & Harvey 2000; Whiting 2002, but see Clark et al. 2001 and Barton 2002), suggesting that the cerebellum ought to be given more attention. It is likely that different parts of the brain are involved in different aspects of play behaviour, but the extent of this is currently unclear. With increasing evidence that motor development and cognitive development are much more tightly interrelated than was previously thought, (Willingham 1999; Diamond 2000; Joseph 2000), this thesis will further delineate the parts of the brain on which to focus, and the extent to which we can link cognitive abilities to play.

1.5.6 Social Skills and social intelligence

The social play of animals is likely to have an influence upon other social skills pertaining to the individual within the social group, allowing individuals to learn and maintain social relationships (Lee 1983; Mendoza-Granados & Sommer 1995). For example, Joffe (1997) suggests that primates are selected for an extended juvenile period, and that this is presumably related to their need to learn. One mechanism of learning adult social skills is through play behaviour, and the extended juvenile period in primates thus suggests that there is increased play behaviour during this period in order to maximise learning potential. It may be the case that play behaviour in juveniles is a factor in the formation of dominance hierarchies and social ranking in some species (Bramblett 1976). Indeed, there might also be a clear preference to play with individuals of a similar dominance rank, or indeed with infants of mothers who are high-ranking (Cheney 1978; Berman 1983; Colvin 1983; Lee 1983; Koyama 1985). As an infant slowly matures, it spends increasingly more time away from its mother, forming peer bonds with similarly-aged and -ranked individuals with whom to engage in playful interactions (Berman 1983; Govindarajulu et al. 1993). Initially, there will be no injury as a direct result of play, but as the animals grow in maturity and strength, there will be increasing incidences of injury. It is argued that the individuals who are playful but injured less frequently may acquire a higher social rank than the possibly weaker individuals who sustain more injuries, or who retire from playful interactions with their peers (Bramblett 1976: 36; deWaal 1996). So, play *may* function directly in establishing rank relationships. However, it has been argued that allo-grooming is a better indicator of social bonds than social play behaviour, especially as it is less energy consumptive (Colvin 1983; Poole 1985). Also, dominance hierarchies may be decided through direct threat and submissive behaviours, thus play-fighting for instance might not be used in this pursuit due to the relaxed nature of play and occurrences of self- handicapping (Poole 1985; Pereira & Preisser 1998). Furthermore, there is evidence to suggest that social play does not underpin group socialisation due to the fact that some solitary animals demonstrate rather complex social play episodes with siblings or nest mates (e.g. *Ursus americanus*, Henry & Herrero 1974; *Mustela putorius*, Poole 1978; *Pongo pygmaeus*, Rijksen 1978; Zucker 1978). Similarly, some social species (*Mus musculus*) are not observed to play (Poole & Fish 1975; Poole 1985). So, play may aid only some aspects of socialisation, forming bonds and obtaining information regarding strength and dominance (e.g. Bekoff 1978; Bramblett 1978), although this might not be the case universally in mammals. The question of play as socialisation further indicates the functional enigma of play behaviour.

Generally, juveniles are unable to reproduce, thus usually unable to contribute genes to the next generation. It may be the case that developing skills and relationships through play to aid survival into adulthood will increase their lifetime fitness (Janson

& Van Schaik 1993: 57). Adult skills, or the pathways leading to them, need to be acquired at some point prior to attaining adulthood, and thus it seems probable that play may aid, at least in part, the development and learning of such skills (Fagen 1993). Play and learning are important to developmental patterns, and may be especially useful in practising mating and mothering behaviour patterns. Play-mothering in juvenile females may allow for the practise of behaviour patterns and skills utilised in motherhood. Thus the experience of a mothering rôle, through a relaxed context such as play, might prove beneficial (Lancaster 1971). A lack of such practice has shown an increased likelihood of females becoming aggressive mothers (Lancaster 1971). Thus play as social practice, might be adaptive. However, it is also argued that play does not seem to represent a developmental stage of the equivalent adult behaviour (Poole 1985) not least because adults in some species demonstrate play (e.g. Hall 1998). In coyotes (*Canis latrans*) and hyaenas (*Crocuta crocuta*), play emerges after the development of aggressive behaviour that determines dominance (Drea et al. 1996).

1.6 Causation

Understanding the proximate causation of play – its contexts, eliciting stimuli, and physiology – remains crucial (Fagen 1981). Studies specifically concerning the causation of play are less common in the literature than those pertaining to the functions of play, for example. Indeed, in spite of ethological studies and computer modelling (Fagen 1981), one argument against play as a separate motivational behavioural category has been its apparent lack of physiological or neurophysiological evidence (e.g. Welker 1971). Recent laboratory research however, has gone some way in elucidating our "play knowledge" with respect to the neurobiology of play behaviour (e.g. Panksepp et al. 1987; Siviy & Panksepp 1987; Panksepp et al. 1994; Vandershuren et al. 1995, 1997; Hol et al. 1999; Pletnikov et al. 1999; Van den Berg et al. 1999), as well as understanding the hormonal influences on the ontogeny of play as a sexually-differentiated behaviour (e.g. Collaer & Hines 1995; and see Chapter 7).

1.6.1 Neurobiological elicitation

Play usually derives from the physiology and neurochemistry of healthy individuals, and (as is discussed in section 1.7 and elsewhere) the amount of play is therefore reduced by emotional and physical stress, anxiety, fear, hunger, and illness (Panksepp 1998). By extension, play is enhanced, and its duration and persistence increased, in relaxed contexts. Although we are some way off an understanding as to the full play-neurochemical system, much of our understanding of "play-circuitry" comes from the laboratory. Play has been artificially stimulated through administering opioids such as low doses of morphine, to animals in laboratory situations (e.g. Vanderschuren et al. 1995). Low dosage is essential, as higher doses of opiates reduce all social behaviour and may result in catatonic immobility (Panksepp 1998: 294). Similarly, some neuropeptides such as oxytocin have been shown to reduce playful expression in laboratory rats (Panksepp 1998: 294). Guard et al. (2002) found that morphine significantly increased social play and play motivated responses ("play-twittering") in common marmosets (*Callithrix jacchus*), but that non-social play behaviours were unaffected. They therefore use these results to argue that social play is a distinct category of social behaviour. Chapter 7 will address the neurology and neurobiology of play in more detail.

1.6.2 Play signals

How does a player or an observer distinguish between play and other categories of behaviour? Agonistic signals occur during play-fighting in some species which can make the distinction between play and other behaviours that much harder to accurately define. It seems that it is not so much the actual behavioural patterns that are used, but the way in which they are performed that is important (Pellis & Pellis 1998), and this is where distinct play signals may come into operation. As it would be especially risky for an animal to misinterpret the intention of any behaviour pattern, play signals have evolved to distinguish serious from non-serious behaviour patterns, allowing an appropriate and constant response to another individual (Bekoff & Allen 1998). Play cues are often seen in their more functional contexts in other forms of behaviour. The play face typifies such a play-signal: the relaxed open-mouth display that appears in playing primates, carnivores and rodents (Fagen 1981). Fagen (1981: 48) states that as the primate play-face typically occurs in conjunction with other behavioural gestures or postures that are structurally similar to that of other taxa, it may form a *"phylogenetic link between primate play signals, and the play signals of rodents and ungulates"*. It is certainly a signal that can occur in all play contexts (i.e. solitary, object, and social play). In chimpanzees, a play face is often accompanied with a vocalisation that approximates to, but is distinct from, human laughter (Marler & Tenaza 1977), and baboons often emit a play-chuckle (Deborah Custance, *pers. comm.*). In rats, Panksepp & Burgdorf (2000) even report chirps as possible laughter in response to being tickled, and many carnivores also emit play vocalisations to signal motivation to play (Bekoff 1974) (see also section 1.4.4). Other examples of play-eliciting behaviours include a play-soliciting behaviour that is more usually witnessed between adults as a prelude to sexual mounting in seals (*Phoca vitulina concolor*, Wilson & Kleiman 1974); head-tossing in ungulates, which is also seen in fight-flight behaviour (Müller-Schwarze & Müller-Schwarze 1968); and head-shakes during playful body odour investigation in giant pandas (*Ailuropoda melanoleuca*) which are seen in scent-marking behaviour (Wilson & Kleiman 1974).

Play signals are not known to occur in all species of animal that are known to play, yet they are very common in primates, canids, and rodents (Bekoff 1977; Rose 1977b) and may differ between species (Fagen 1981). Such signals are certainly more readily recognised by observers when the signals are visual, but auditory cues exist, as do olfactory ones, which might be especially important to those species that rely most heavily on olfaction in daily life (e.g. carnivores, rodents) (Wilson 1973; Fagen 1981). Touch however, is the dominant sense within the play of any given animal: tickling, pinning, and other forms of rough-and-tumble play are reliant on tactile stimulation above any other visual, auditory or olfactory response within play (Panksepp 1998). Laboratory trials of anaesthetising rats may reduce the amount of rough-and-tumble pinning, but it does not reduce the motivation to engage in play. Panksepp (1998) therefore claims this as good evidence for an innate desire to play, rather than it being reliant on sensory stimuli alone.

Play signals may have their behavioural basis in other functional categories of behaviour, such as fighting or mating, yet they are usually exaggerated actions, and thus unique to play behaviour (Fagen 1981; Watson & Croft 1993). Play-signals are not necessary for play to occur (Watson 1998), yet their inclusion might aid in initiating and maintaining a play bout (Fagen 1981). Some locomotor-rotational movements also act as play signals in some species, and resemble some acts seen in functional contexts such as predator defence (Fagen 1981). This might be especially true of some canid species, whereby the play bow usually occurs just before an action that could be misinterpreted as aggression (such as a bite) (Bekoff 1977). In this context, play-signals seem to convey the message "This is [still] play" (Symons 1978; Fagen 1981; Bekoff & Allen 1998).

1.7 Environmental correlates of play

The exhibition of play behaviour in animals is sensitive to ecological and environmental variables (Lee 1983), and there are numerous variables that suppress play in mammals, particularly under adverse conditions (Baldwin & Baldwin 1974; Fagen 1981; Burghardt 1984). Moreover, play is so susceptible to external stresses that it is amongst the first behavioural categories to disintegrate when such circumstances arise (e.g. Burghardt 2001). These will be discussed in more detail in Chapter 6.

1.7.1 Food

Hunger is usually considered to be a dominant motivational system (Martin 1984a; Hall & Bradshaw 1998). Play however, is often considered to be a weaker "subordinate behaviour tendency" (Arnold & Trillmich 1985). Thus it is expected that there will be a reduction in play activity upon long-term reduction in food availability (Dasman & Tauber 1956, Loy 1970, Zimmermann et al. 1975). Even short-term deprivation of food can decrease play rather rapidly, (see Baldwin & Baldwin 1976; Müller-Schwarze et al. 1982). Similarly, play may be an indicator of habitat quality (Sommer & Mendoza-Granados 1995; Blackshaw et al. 1997; Jensen et al. 1998). In a rich habitat, a band of Hanuman langurs (*Presbytis entellus*) were shown to play 6-7 times more than a band living in a poor-habitat area. The frequency of play-fighting and locomotor play was negatively correlated with the amount of leaves (low-energy food) in the diet (Sommer & Mendoza-Granados 1995). This supports the theory that play is diminished under sub-optimal environmental conditions (Fagen 1981; Burghardt 1984).

1.7.2 Confinement

When the possibility to exercise is reduced through close confinement of an individual, play is also reduced. It is therefore predicted that an individual should play vigorously upon release. Smith & Hagan (1980) found that when children were confined indoors, they exhibited high levels of physical activity (expressed through play) when released outside. Similar effects have also been seen in other animals (Müller-Schwarze 1968; Chepko 1971; Jensen 2001; Christensen et al. 2002). Interestingly however, an opposite effect is witnessed in zoo animals, in that captive-housed animals tend to exhibit a greater amount of play behaviour; this may be due to the need for sensory stimulation, regression to an immature state in adults, or more simply that captivity constrains variables such as predator pressure and food availability, freeing up more play time (Fagen 1981: 301). The fact remains that in most modern zoos, care has been taken to ensure that space is provided in enriched captive environments (Erwin & Deni 1979; Maple 1979; Markowitz 1979), and it is specifically *close* confinement that prevents physical exercise and the exhibition of play. Additionally it might be argued that *"some aspects of social behavior may remain relatively unaffected by captivity"* and that captive play closely resembles play in the wild (King et al. 1980).

1.7.3 Temperature and weather

Play in animals tends to occur with greatest frequency during daylight hours, particularly in the morning (e.g. *Alouatta palliata*, Altmann 1959; *Cercopithecus ascanius*, Galat-Luong 1975) and evening (e.g. *Papio anubis*, Rose 1977a; *Macaca arctoides*, Bernstein 1980; *Lutra canadensis*, Beckel 1991), avoiding the periods of the day when both the temperature and subsistence activities are at their peak (e.g. *Ovis canadensis*, Berger 1980). There exist few data on the play of nocturnal species, or indeed the play of diurnal or cathemeral species at night. This may be in part due to the difficulty in observing animals at night, but the scarcity of the occurrence of nocturnal play may be due to the costs and benefits of performing play at this time, and also the costs and benefits of performing other behaviours at specific times (Fagen 1981). Nocturnal species are often also largely solitary, and rely on use of their physical stealth under the cover of darkness to find food. The performance of play at such times might demonstrate greater costs in terms of risk of predation to nocturnal species, than to those that are diurnal and typically social.

Inclement weather has also been found to reduce the playing time of individuals, and in this way acts rather like confinement (Fagen 1981; Burghardt 1984; Bernstein & Baker 1988). Immoderate weather, such as extreme temperatures, heavy rains, and high winds reduce play behaviour in animals (Bernstein 1980), and so an improvement in bad weather should lead to the immediate increase of play again. The last opportunity to play before heavy rains or confinement often reveals a final exertion of energy through play behaviour (Fagen 1981). Restricting play during hot weather, for example, might occur to avoid overheating; play behaviour has also been shown to reach its highest peaks during cool weather, which poses the question that perhaps there is an added cost of play: thermal stress (Fagen 1981); conversely, it could be argued that a benefit to play is in preventing hypothermia.

As temperature affects play, play usually occurs during the cooler parts of the day, such as early in the morning, or at sunset (Bernstein 1972; Dugmore 1986). Seasonal temperatures also pose an effect, thus play may be reduced during hot, dry seasons, or wet seasons (Richard 1974). Kavanagh (1978) found that adult douc langurs (*Pygathrix nemaeus*) rarely played, yet when play did occur, it was on a sunny day.

1.8 Other Forms of Play

1.8.1 Interspecific play

Interspecific social interactions are rare occurrences, but interspecific play behaviour is rarer still (e.g. Watson 1998). This is because many interspecific acts are by their nature incompatible (Fox 1976), as the play behaviour of different species is often motivationally distinct (Rooney et al. 2000). The most common form of interspecific play is between humans and other animals, usually in a captive or domestic setting (Watson 1998; Rooney et al. 2000). Interspecific play amongst wild animals is known to occur however, and rare occurrences have been reported for example between red-necked wallabies (*Macropus rufogriseus*) and Australian magpies (*Gymnorhina tibicen*) (Watson 1998), although interspecific play typically appears to be more common in some primate species (Rose 1977b; Fagen 1981). Between black and white colobus monkeys (*Colobus guereza*) and vervet monkeys (*Cercopithecus aethiops*), interspecific play behaviour accounted for 40% of all interspecific interactions (Rose 1977b). Baboons (*Papio* spp.) are known to be especially playful with other species, such as jackals (Saayman 1970), but also are also party to predatory behaviour with the same species as they both play with, and are hunted by, chimpanzees; they also play with, yet hunt, vervet monkeys (van Lawick Goodall 1968; Altmann & Altmann 1970). Even in situations where play completely diminishes, hunting aspects of interactions with these species continues. It is perhaps for this reason that much of the interspecific play behaviour observed includes play patterns involving no bodily contact between players; if contact is made, it is generally fleeting (Rose 1977b).

Play between different species involves various different behaviour patterns, often unseen in other areas of nature. Indeed, the occurrence of interspecific play further fuels arguments against play as group socialisation (Poole 1985). In order for play to be maintained between two different species, there has to be present some kind of interspecific communication (Fagen 1981). Therefore, interspecific play would be facilitated where species share common play-specific motor patterns, and similar temporal organisation. Even then, interspecific play interactions are usually short in duration (Rose 1977b). If play is to be successfully maintained, the players must be able to judge with increased accuracy the appropriate responses and actions to the behaviour of the other species (Fagen 1981). There should be some self-handicapping and compromise where species differ in size, and play-bout preferences have to be overcome if play is to exist for any reasonable amount of time (Fagen 1981; Pereira & Preisser 1998). It is expected therefore, that interspecific play bouts should occur only between animals of a similar size and age-range (Rose 1977b). Rose (1977b) also states that interspecific play is most likely to occur between species where the foraging and resting patterns of sympatric species are similar over time. This would obviously allow for the possibility of interactions to occur in the first instance. If the patterns are relatively stable then this allows some element of prediction as to the appropriate nature of engaging in interspecific play at any given time.

1.8.2 Play in humans

Although this thesis does not deal with the play of humans, it is important to mention some of the continuities and discontinuities between the play of animals and the play of humans. It seems difficult to deny that a behaviour so ubiquitous in human children as play has important functions: play must surely help children develop their minds and bodies, enhance learning, and be a source of art and creativity (Smith & Simon 1984). The fact that much play in both people and animals can be dangerous and risky, a costly diversion from more "productive" activities, destructive, and even cruel, is too often ignored. In humans, most kinds of play involve rough-and-tumble behaviour patterns, socio-dramatic, imitation and make-believe, rôle-playing (Singer 1995), problem-solving, object-play (with toys) (Goldstein 1995; Kline 1995) and, later in life, games and arguably sports (Chick & Barnett 1995). Virtually every kind of human play can be seen to have roots in the behaviour of other species, and thus a full understanding of human play requires a widespread evolutionary analysis (Byers 1998a; Burghardt 2001).

Rough-and-tumble play, or chasing and play-fighting, is one form of play that is typical of pre-school children, but in many cases endures throughout childhood and into early adolescence (Smith & Boulton 1990), as is the case for play-fighting in other animals (Aldis 1975). This type of play is relatively universal across human societies (Whiting & Whiting 1975) and seems to be relaxed-aggressive behaviour, as is also the case in non-human animals (Fagen 1981). Rough-and-tumble play is argued to have its roots in a gentler version shared between adults and infants (Aldis 1975), and as the child progresses in age, noticeable sex-differences emerge with boys performing rough-and-tumble play significantly more frequently and more roughly than girls (Humphreys & Smith 1984). Arguably, this is due to both hormonal influences (e.g. Hines 1982) as well as parental reinforcement of gender rôles (Thompson 1975). Similar gender patterns in aggressive play can be seen with the use of some toys and games (Goldstein 1995).

Yet, the play of humans forces us to deal with many more psychological, cognitive and symbolic issues than the play of non-human animals. Human play, in children and adults, may represent an area for the creation and appropriation of culture (Chick & Barnett 1995). Knight (1999) discusses the possibility of the symbolic culture of human ritual being a form of "pretend-play" whereby the "players" agree to suspend their usual beliefs. Indeed, symbolic ritual may aid the social cohesion of the group, just as play behaviour aids in the social interactions of non-human animals. In animal play however, we do not witness the extent of conscious social agreement to suspend reality for the projection of imaginary scenarios that we see in the play of humans. We can detect imagination in the context of human interactions; we cannot do so within the context of non-human animals. This is of course where human play greatly differs from that of other animals, even if the basics are present. Freud's (1975) suggestion that belief in God [or gods] in human society is no more than a fantastical creation of a father-companion gives us pause. Consider the occurrence of imaginary playmates in human children. The psychological phenomenon of imaginary friends typically occurs in children who have experienced stress, either through negative circumstances, or other life-changing occurrences (Partington & Grant 1984; Dawson et al. 1999). The characters these children create seem acutely real to them, and the children relate to them accordingly. Play in most animals may be severely reduced during times of stress (Freeman & Alcock 1973; Wolff 1981; Burghardt 1984; Sommer & Mendoza-Granados 1995; Jensen et al. 1998). Indeed, Dawson et al. (1999) found that infants of severely depressed mothers were significantly less playful and affectionate than the infants of "normal" mothers, and that the depressed mothers were less in tune with the developing behavioural requirements of their infants.

Dawson and her colleagues (1999) found that this negatively influences the emotional well-being of the infant, in turn affecting the "normal" development of brain and of behaviour. Similarly, Mol Lous et al. (2000) found in a study of 3-6 year olds, that depressed children engage in significantly less play behaviours than non-play behaviours in comparison to non-depressed children. Thus for example, if imaginary friends are, at least in part, stress-created, this suggests that fantasy "play" at least, may have a different function. Perhaps imaginary friends do occur during a child's play-time *because* of the relaxed nature of play behaviour; it does not necessarily mean that their creation is actually play *per se.* Children under stress may indeed exhibit more fantastical imagery during play, and in this sense, this type of "play" may be similar to that of adult ritualistic symbolism. Therefore, fantasies of this sort are not so much play, but suggest something more psychological. It is interesting to note, however, that the typical age range of children creating imaginary playmates for themselves is between 3 and 6 years old (Partington & Grant 1984), which seems to tie in with the age-specific play range and neural development of most mammals, including humans (Diamond & Goldman-Rakic 1989; Dawson et al. 2000). Sutton-Smith (1979) states that play behaviour in children may bridge the gap between reality and fantasy in some children. If this is so, then this fantasy play might indeed enhance behavioural flexibility as it provides a forum in which the child can exercise skills such as language, thoughts, and so on, testing the boundaries of meaning for social relationships and inanimate objects, facilitating "*divergent thinking abilities*" (Smith & Simon 1984). Imagination therefore, is not necessarily play, but may occur within the *context* of play in humans. In order to deal fully with human play behaviour, it becomes necessary to look at the entire context of human society, especially in terms of beliefs, fantasy, and ritual, as well as other psychological issues. This is clearly beyond the scope of this PhD, and I do not focus upon human play in detail in the context of this thesis. However, given the consensus that great apes exhibit socio-cognitive abilities beyond that of other non-hominoid primates (e.g. theory of mind, see Byrne & Whiten 1988), it would be interesting if future work were to test for differences in those play behaviours that are shared with humans.

1.9 Major phylogenetic patterns

Two decades ago, Fagen (1981), Burghardt (1984), and others called for more comparative studies of play to be undertaken to further our understanding of the origins of play. Previous play studies have tended to focus only upon specific elements of the behaviour with regard to relatively few species. Whilst these elements remain crucial to play research, no major comparative study has been conducted into the evolution and function of play. This pursuit requires a comprehensive collection of data on the play behaviour of more species, and in more diverse orders than is currently in existence. Moreover, in order to conduct comparative studies with any degree of confidence, reasonably resolved phylogenies are required (e.g. primates: Purvis 1995; rodents: Watts & Baverstock 1995; carnivores: Bininda-Emonds et al. 1999). Those few comparative studies of play behaviour that do exist include a plea for further data, in increased detail, and on more species (e.g. Byers 1999).

Although this thesis deals only with comparative data on primates and carnivores due to the relative lack of data on other orders, it is important to contextualise this with reference to other comparative studies, and also with reference to what is known about play in other taxa. One of the principal difficulties in comparative analyses is that lack of suitable quantitative data (see Chapter 2).

Robert Fagen's (1981) review of animal play provides an excellent basis by which to begin to understand the patterns and distribution of play in birds and mammals, and it is this book that collates all the fragmentary evidence for play in a number of species, regardless of the quality and usability of the data, the basis of which is included in the following sections on play in various orders.

1.9.1 Monotremata

Monotremes (the egg-laying mammals) may yield interesting insights into the evolution of play, given their phenotypic and phylogenetic divergence from other mammalian lineages (Fagen 1981). Very scanty evidence exists for any such play in either the duck-billed platypus (*Ornithorhynchus anatinus*), or the two species of echidna (*Tachyglossus aculeatus* and *Zaglossus bruijni*) (Fagen 1981), and that which does is concentrated on obsolete observations (e.g. Bennett 1834; Owen 1848) usually in captivity, and primarily focused on mother-infant observations (Fagen 1981). With increasing evidence as to the behaviour and evolution of these fascinating animals (e.g. Pettigrew et al. 1998; Kirsch & Mayer 1998; Hughes & Hall 1998) it should soon be possible to proceed with comparative analyses of monotreme play.

1.9.2 Marsupiala

Marsupials offer a great diversity in many areas of socio-ecology, life-history, and behaviour (Watson 1998), and due to their low metabolic rate and variability in brain size, are a good place to start when testing for functions of play (Byers 1999). The Artiodactyla are the closest living placental equivalent to the Marsupialia in that some representatives of the two groups have convergently evolved similar digestive systems and behaviours as a result of similar selection pressures for diet and lifestyle, in spite being phyletically distinct for 130 million years (Watson 1998). Marsupials have been the focus of comparative study (Byers 1999; Iwaniuk et al. 2001), and it has been shown that some species within the order play, and some do not, or have not been observed to, play. Thus again offering a suitable place to commence research into the evolution of play behaviour (Watson 1998; Byers 1999). Based on a three-point scale, demarking play as either absent, rudimentary, or common, Byers' (1999) study showed that play exists in the Dasyuridae (e.g. marsupial mice, marsupial cats, and Tasmanian devils), *Myrmecobiius* (numbat), Vombatidae (wombats), and Macropodoidea (wallabies, quokka, and kangaroos), but that it is absent in all other species (e.g. Petauridae [possums]). Reasons for this patterning are somewhat unclear given that social structure, activity timing, habitat, and diet are variable across these families. Most (but not all) species in these families are nocturnal and solitary, but may come together for feeding and mating, and have overlapping home ranges (Fisher & Owens 2000; Long 2001; Oakwood 2002). Play in macropods and potoroids takes the form of high speed hopping, and sparring; in larger species of dasyurids as play that mimics prey-capture; in vombatids as energetic and frequent bouts of social and locomotor play; and as running and chasing in numbats (Byers 1999); play is virtually absent from the behavioural repertoires of marsupial adults (Watson 1998). Interesting to note is the difference between the rudimentary play of koalas

(*Phascolarctos cinereus*) and the common play of wombats (*Vombatus ursinus*), as the two species are considered to be closely related (Kirsch 1977); however, koalas have small smooth brains, whereas wombats exhibit large and well-folded brains (Haight & Nelson 1987). This further fuels Byers' hypothesis that marsupial play functions to modify postnatal brain development, as play is correlated with relative brain mass and not with relative body mass or metabolic rate in marsupials (Byers 1999).

1.9.3 Insectivora

Few reports exist concerning insectivore play patterns other than a handful of information regarding hedgehogs (*Erinaceus europaeus*) and some species of shrew (Fagen 1981). It appears that juvenile hedgehogs may engage in play-fighting and other forms of locomotor play (Dimelow 1963), similar to that of elephant shrews (Fagen 1981). Fagen (1981) reports that in a study by Mohr (1936 a, b) specifically seeking play in solenodons (*Solenodon paradoxus*), no play was observed, although some affiliative social interactions occurred. Similarly, no play behaviour has been reported in tenrecs (Eisenberg & Gould 1970).

1.9.4 Chiroptera

Extremely little is known about the play of bats, due in part to the difficulty in observing wild populations. Some good data exist for play in the megachiropterans (social and diurnal Old World fruit bats), and typically describe chasing and wrestling forms of play (*Pteropus rodricensis*, Carroll 1979; McCammond & Chock 1998). Fagen (1981) reports that the social play of bats can be highly complex. Vampire bats (*Desmodus rotundus*) engage in play not dissimilar from that of the flying foxes (Schmidt & Manske 1973) and an early report by Dubkin (1952) details episodes of play-biting by brown bats (*Myotis lucifugus*). Bats offer an interesting focus for comparative studies given the diversity in socio-ecology, sociality life-history, and phylogeny; they would make an excellent taxonomic group for the study of play with an increase in ethological studies.

1.9.5 Primates

This chapter, and subsequent chapters in this thesis, deal with primate play in considerable detail, and thus I will not repeat those facts here. Primates are an interesting taxonomic group for comparative study as there is such a diversity of species with differing socio-ecological and life-historical patterns. Studies on play in captive and wild primates discuss patterns that describe social, locomotor, and object play (see Table 1.1. for more details), including kicking, pulling (Voland 1977), biting, rolling (Owens 1975a), grappling, tugging (Baldwin & Baldwin 1978), grasping, and tickling (Enomoto 1990), and come under various "sub-headings" which might include: chasing, wrestling (Chalmers 1980; Hayaki 1983), and furthermore, play-fighting, rough-and-tumble play (Smith 1995; Welker et al. 1990), sexual play (Latta et al. 1967), play-mothering (Lancaster 1971), and interspecific play (Rose 1977b). Interestingly, with the exception of chimpanzees, there are few or no wild studies that report object play (Fagen 1981). Unsurprisingly, primates have formed the basis of some of the few comparative studies of play behaviour currently in existence. In defining the character states of adult-adult play-fighting, a behaviour associated with courtship in some species of primate, Pellis & Iwaniuk (1999a) incorporated a four-point scale of intensity (0 = play rare, 1 = play occurs but without wrestling elements, 2 = play as courtship reported, 3 = play as courtship common). Using independent contrasts analyses (Felsenstein 1985; Purvis & Rambaut 1995), they show that play-fighting as courtship correlates with a lower incidence of male-female association, and mating system (Pellis & Iwaniuk 1999a). They speculate that the primitive condition of adult play-fighting is a scenario in which bouts of play-fighting punctuate sessions of male-female allo-grooming and that this eventually leads to copulation, thus play-fighting in this case functions as an optional strategy in counteracting unfamiliarity between potential pair mates, and presumably as a means of assessing mate-quality. Pellis & Iwaniuk (1999a) thus argue that with the evolution of increased male-female sociality, play-fighting as a courtship strategy decreased in value; or that with the reduction in male-female association, the value of this behaviour increases. Thus the prevalence of adult play-fighting is likely to be strongly associated with socio-ecology. Pellis & Iwaniuk (1999a) further corroborated these results in a further comparative study (Pellis & Iwaniuk 2000b) in which they state that adult-adult play is a "*byproduct of the occurrence of play in sexual contexts*", and that the function of adult play-fighting is for social assessment, with an added courtship mechanism in some species. They further suggest that adult play-fighting may have evolved in a social context in species that typically have minimal social contacts between males and females.

1.9.6 Edentata

Evidence for play behaviour in armadillos, sloths and anteaters derives primarily from old captive literature reports but include anecdotal suggestions for rudimentary social, locomotor, and object play in two-toed sloths (*Chloeopus didactylus*) and giant anteaters (*Myrmecophaga tridactyla*) (Crane 1966 and Honigmann 1935, respectively). Further empirical and phylogenetic study is required to differentiate the distribution of play in the Edentata given their low metabolic rates (Burghardt 1984) coupled with traits typical of playful species such as longevity and parental care (Fagen 1981).

1.9.7 Philodota

That play might be the last behaviour in a species' repertoire to be studied with any intensity is illustrated by the paucity of any ethological data for pangolins. However, social play is reported in the usually solitary African pangolin (*Manis tricuspis*) in the form of juvenile play-fighting between litter-mates (Pagès 1975).

1.9.8 Lagomorpha

Rabbits are not the subjects of a great many studies that incorporate play behaviour, however locomotor play has been recorded in the literature on European rabbits (*Oryctolagus cuniculus*), and playful behaviour patterns appear to persist well into adulthood in this species (Lockley 1974). Mountain hares (*Lepus timidus*) also engage in locomotor-rotational play in this way (Flux 1970).

1.9.9 Rodentia

Rodentia is an order comprising squirrels, beavers, the cricetids (hamsters, gerbils, voles and lemmings), rats, mice, dormice, porcupines, and caviomorphs (guinea pigs, acouchis, pacas, and other South American rats and mice), and play has been described in most of these at the family level at least, although the patterns of these behaviours differ markedly between taxonomic families (Fagen 1981). Rodents appear to perform as many of the categories of play as are seen in other mammals, and as a diverse taxonomic group they therefore represent a good point of reference for comparative studies of behaviour (Fagen 1981). Indeed, an evolutionary comparative study of play-fighting in muroid rodents demonstrates that the complexity of social play in rodents is not necessarily correlated with phylogenetic relationships, or even patterns of sociality (Pellis & Iwaniuk 1999b). Pellis & Iwaniuk (1999b) claim that changes in the complexity of social play evolved independently from the assumed ancestral form, which is arguably likely to have been that of a modest level of complexity in play-fighting. They conclude that this pattern may demonstrate adaptive radiation.

1.9.10 Cetacea

Cetaceans, with their complete independence from land, are the mammals to have lived longest in marine environments, believed to have diverged from primitive artiodactyls approximately 60 million years ago during the Paleocene epoch; other theories suggest a more recent evolutionary history, placing the divergence at 27-30 million years ago during the Oligocene (Lowenstein 1985). For an order that comprise highly social species and those that are commonly considered as playful as are the cetaceans, surprisingly little quantitative play data exists, which is due not least to the problems in attempting to observe these animals (Fagen 1981) due to weather conditions and water visibility (DeLong 1999). Reports of play by bottle-nosed dolphins (*Tursiops truncatus*), both at sea, and in captivity are relatively more common than reports of play in other cetaceans (Fagen 1981; Galhardo et al. 1996), and generally comprise the key categories of play observed in other playful mammalian groups (DeLong 1999): social (e.g. chasing), locomotor (e.g. spinning, surf-riding, lob-tailing), and object play (e.g. nosing, drop-catch, balancing) (Fagen 1981; Galhardo et al. 1996); captive bottle-nosed dolphins have even been observed playing distinct games ("King of the Mountain", Theia DeLong, *pers. comm.*). In killer whales (*Orcinus orca*), social play appears to take the form of intentional stranding, or beaching, which is a behaviour commonly seen in hunting (Guinet

1991). No play has been recorded in baleen whales (Fagen 1981), although our knowledge of play behaviour in the majority of cetaceans is limited by the problems encountered in observing them in the wild. In spite of this however, it casually appears to be the propensity for play that makes cetaceans popular in aquaria and other captive environments.

1.9.11 Carnivora

Carnivores offer a good basis for comparative study as the order offers much in terms of diversity of behaviour, life-histories, diet, distribution, and species richness. The order is currently believed to be monophyletic (Bininda-Emonds et al. 1999; Purvis et al. 2001), and there are 129 genera comprising 271 extant species of carnivores over two major clades: the Feliformia (cats, hyaenas, civets and mongooses), and the Caniformia (dogs, bears, weasels, skunks, and racoons) (Purvis et al. 2001). Additionally, extinction rates among carnivores have been far higher than that of any other order, with approximately 352 genera having gone extinct (McKenna & Bell 1997). Carnivores are species that subsist principally on a meat-based diet, although most species supplement their diet with other foods (Bekoff et al. 1984). Some carnivores however, are not meat eaters but subsist as insectivores (e.g. white-tailed mongoose, *Ichneumia albicauda*; bat-eared fox, *Otocyon megalotis*), or folivores and frugivores (e.g. black bear, *Ursus americanus*; red panda, *Ailurus fulgens*; giant panda, *Ailuropoda melanoleuca*) (Bekoff et al. 1984). This order is classified on the basis of "*les trets carnassiers*": sectorial dentition adapted for tearing flesh (as opposed to grinding); a flexible vertebral column; a long tail; a large relative brain size; anal and forehead scent glands; quadrupedal locomotion ranging from plantigrade (soles of feet) to digitigrade (on toes), and fur-covered bodies (Bekoff et al. 1984). Studies examining the taxonomic distribution of carnivore play are rare (Bekoff 1989b), however play behaviour within the order Carnivora shows some parallels with the play of primates in that differences in physiology are less marked than in other orders of mammal, allowing some level of "*interspecific similarity*" (Fagen 1981). However, there are differences in social structure between families of carnivore species, such as pack-living wolves (*Canis lupus*), and habitually solitary bears (Ursidae) (Fagen 1981; Bekoff et al. 1984). Play begins early postnatally in carnivores, and can continue through to adult stages in many species. Social bonds within and between young and adult group members, and group social organisation, may be affected by variation in social play experience during the juvenile period (*Canis latrans*, Ortega 1988), especially in terms of eventual dispersal (Bekoff 1989b). Highly social canids exhibit much chasing, predatory play, muzzle-wrestling, and biting, and incorporates use of the open-mouthed play-face, usually associated with primates, and these patterns are seen also in bears, canids, procyonids (e.g. racoons, coatis), mustelids (e.g. weasels, ferrets, polecats, otters), hyaenas. Bears engage in mother-infant play as their prominent play category, but have also been seen to play with objects, both in the wild, and in captivity (*Ailuropoda melanoleuca*, Wilson & Kleiman 1974; *Thalarctos maritimus*, San Diego Zoo, *pers. obs.*). Play-fighting is observed in most bear species, and in polar bears has even been witnessed in adult males (Latour 1981). Play that involves pouncing, batting, and other forms of play, sometimes with objects, are typical of felids and viverrids (e.g. mongooses, civets).

1.9.12 Pinnipedia

Limited quantitative analyses of pinniped play data are analysed alongside carnivore play data in this thesis, although I differentiate them from carnivores in this section for clarity. Pinnipeds are believed to have diverged from terrestrial carnivores approximately 30 million years ago during the late Oligocene and early Miocene epochs. There has been much debate as to whether modern pinnipeds are biphyletic in origin, having evolved two superfamilies independently (Repenning 1976), or monophyletic, having evolved through common descent (Demere & Berta 2001). The biphyletic hypothesis states that phocid (true) seals descended from otter-like carnivores during the Miocene, and that walruses and eared seals descended from bear- or dog-like carnivores during the Oligocene (Repenning 1976). Recent molecular evidence, however, suggests that a monophyletic descent is most likely (Wyss 1988).

Pinnipeds (sea-lions, seals, and walruses) differ markedly between species and families in terms of social organisation, breeding, and dietary behaviours (Fagen 1981). This order is certainly generally considered to be playful, but like sea otters (*Enhydra lutris*) and cetaceans, for example, are often difficult to observe. Walruses

(Odobenidae) are typically believed to be less playful than seals or sea-lions, but it is suspected that their play is virtually all sub-aquatic and only a few episodes of play-fighting have been recorded (Miller 1975). The play of sea-lions and fur seals (Otariidae) and true seals (Phocidae) appears more common, and comprise play-fights, lunging, shaking, torpedoing, object play with kelp, spinning, porpoising, chasing, bouncing, and mother-infant patterns, either in dyads or in peer groups (Farentinos 1971; Gentry 1974; Wilson 1974; Harcourt 1991).

1.9.13 Proboscidea

Elephants are highly social and long-lived mammals with a large relative brain size, and play in African elephants (*Loxodonta africana*) is relatively well documented (e.g. Sikes 1971; Laws et al. 1975) and these elephants exhibit the social, locomotor, and object play patterns seen in other taxonomic groups that show similar life-history traits, such as primates and cetaceans (Fagen 1981). The onset of play occurs early and may persist into adulthood, exhibiting self-handicapping between mismatched players (Douglas-Hamilton & Douglas Hamilton 1975). Play in Asian elephants (*Elephas maximus*) appears to show similar patterns, but fewer reports exist in the literature (McKay 1973; Fagen 1981).

1.9.14 Sirenia

Almost nothing is known of play in manatees (*Trichechus manatus*) and dugongs (*Dugong dugon*), and few behavioural studies appear to exist on these enigmatic aquatic creatures, especially in the wild (e.g. Fagen 1981). Hartman (1979) reports twisting, rolling, social nibbling and nuzzling, categories he assigns to play behaviour.

1.9.15 Perissodactyla

The odd-toed ungulates (horses, asses, zebras, rhinoceroses, and tapirs) are a taxonomic group that appear to play quite keenly (Fagen 1981). Play is almost always in the form of solitary locomotor play in young foals and calves, and develops slowly into social play episodes, usually in the form of play-fighting (*Equus caballus*, Fagen & George 1977; Crowell-Davis et al. 1987; *Diceros bicornis*, Dittrich 1967; *Ceratotherium simum*, Owen-Smith 1975; Fagen 1981; Byers 1984).

1.9.16 Artiodactyla

The play of the even-toed ungulates (pigs, hippopotamuses, giraffes, deer, antelope, sheep, and goats) is typically characterised by leaping, kicking, running, and twisting: solitary locomotor movements; however, social play patterns such as butting and wrestling are also common to their repertoires, and pigs and hippopotamuses engage in much mother-infant play (Wilson & Kleiman 1974; Fagen 1981; Byers 1984). The amount of time devoted to play in this taxonomic group appears to differ markedly; for example, cervids (e.g. deer) and bovids (e.g. sheep) are relatively playful, whereas giraffes (*Giraffa camelopardalis*) are consistently reported as unplayful in contrast (Langman 1977), but do exhibit solitary locomotor play and play-fighting both in the wild (Pratt & Anderson 1979) and in captivity (Fagen 1981).

1.9.17 Aves

It should also be noted that play behaviour is present in some species of birds, although accounts of this are often rather scarce. Studies of play in birds however, should be of great behavioural and evolutionary interest given that birds are not ancestral to mammals, thus it can be asserted that aside from play in common reptilian ancestors (Burghardt 1988, 1998, 2001), play arose independently in both birds and mammals (Fagen 1981). Avian play behaviour often takes the form of object play in drop-catch games in gulls (e.g. herring gulls, *Larus argentatus*, Gamble & Cristol 2002), object manipulation in parrots and parakeets, and playing with dead prey and inedible objects in birds of prey (Fagen 1981). Corvids and larger species of parrot have a large relative brain size (Ortega & Bekoff 1977), and are renowned for their especially playful behaviour both with objects and in social play behaviors (Heinrich & Smolker 1998). Other forms of avian play include "playful" swooping, jumping, "hustling", and "play-bathing" (see Fagen 1981; Heinrich & Smolker 1998). This thesis will not deal with the play of birds directly, but birds may indeed offer an excellent outgroup comparison for mammalian play behaviour in future studies.

1.9.18 Overview of general phylogenetic patterns

Generally, play appears to be present in some form, however simplistic or disputed, in all extant mammalian orders. One of the difficulties in making generalisations however, especially with regard to play behaviour, is that many species have not been observed to play. This may be due to several reasons:

1. The species does not play.
2. The species plays very rarely, at low frequencies, or at specific developmental periods only.
3. The species is difficult to observe, (due to dense habitat, nocturnal activity timing, threatened conservation status, etc.), and thus
4. Little is known about their behaviour, and/or
5. Few reports exist as to their behaviour, life-history, socio-ecology, etc., and thus
6. Observing play is not deemed to be the most important ethological consideration.

Play is often the last behaviour to be observed or recorded in a species due to historical and continuing debate as to its appearance and function (e.g. Bekoff & Byers 1985, 1998). Thus all play is not equal to all mammalian orders, and patterns can be observed in the phylogeny of play. Figure 1.1 details a phylogenetic reconstruction of play distribution across mammalian orders. The reconstruction is based upon what is known from existing reports of play in mammalian orders; thus orders containing species about which much is known, may be better represented by stronger evidence for play, or higher play frequencies (e.g. primates) than relatively less well known orders (e.g. sirenians). The reconstruction indicates that play is present, or deemed *likely* to be present, in all extant orders; those orders that are more disputed are the Macroscelidea (elephant shrews), Dermoptera (flying lemurs), Sirenia (dugongs and manatees), Hydracoidea (hyraxes and dassies), and Monotremata (platypuses and echidnas). These orders represent those species about which our knowledge is scantier, due to the species' distribution or life-style. It is possible that these species do not play, but it is equally likely that play is not reported, especially given that in most cases, the most recent common ancestor to that order is likely to have engaged in play, even at low levels.

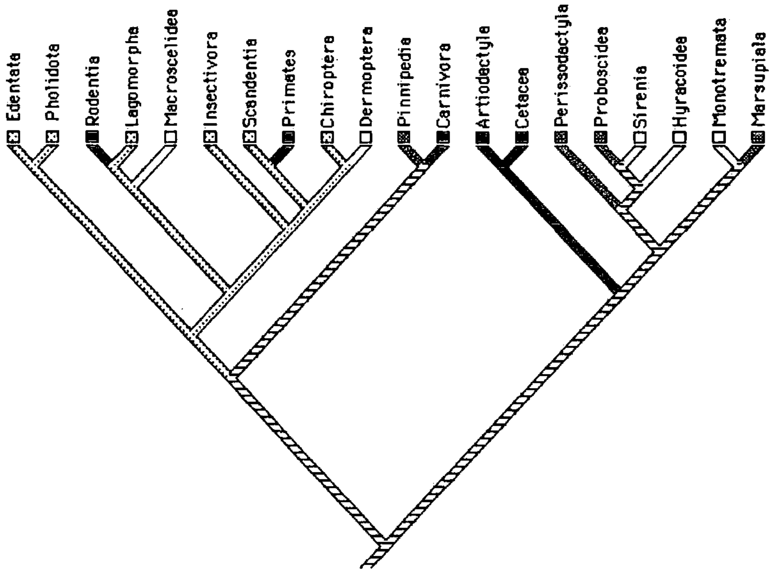


Fig. 1.1 Hypothesised phylogenetic reconstruction of play frequency in mammalian orders

☐ 0
▨ 1
▩ 2
■ 3
⊟ equivocal

Legend:
0 = play not reported, or reports obsolete
1 = few reports known, but play reported even if simple in form
2 = play reported in some families, but amount may be

Play is well-known in Rodentia, Primates, Carnivora, Artiodactyla, and Cetacea; it is unlikely to be a coincidence that these orders also comprise many species that are large-bodied or highly social, thus rendering them ideal subjects of extensive behavioural observations. Chapter 3 will deal with the phylogenetic patterning of play across the orders Primates and Carnivora, in more detail.

1.10 Summary

This thesis focuses upon evolutionary patterns in primate and carnivore play behaviour, paying particular attention to the development and function of the brain and its components, aspects of socio-ecology and life-history, and inter-specific and intra- specific play behaviour. Chapter 2 will describe the general methodology of the study, and discusses how the comparative method can be used to elucidate the phylogenetic relationships between play behaviour and other variables. Chapter 3 will look in more detail at the phylogenetic patterns of play behaviour in primates and carnivores using data from the literature. Chapter 4 looks more closely at intra-specific play, or how members of different groups of the same species in different regions or habitats engage in play behaviour. Chapter 5 deals with the life-historical variables of play behaviour, such as gestation period and lifespan. Chapter 6 focuses upon the socio-ecological variables of play behaviour, such as group size and diet. Chapter 7 will specifically analyse and discuss evolutionary relationships between play behaviour and the brain. Finally, Chapter 8 offers some conclusions to the questions arising from chapters 3-7, and speculates on possible applications for future research.

By analysing how different variables contribute to and affect the play behaviour of primates and carnivores, it is possible to assess and further speculate upon the phylogenetic relationships at work within play behaviour, and the place of play in evolution.

Chapter 2:

Methods

2.1 Introduction

This thesis has been designed to investigate the evolutionary correlates of play behaviour in primates and carnivores using a phylogenetic comparative approach. Thus, the data incorporated here come not from observational or experimental work carried out specifically for the purposes of this thesis, but have been collated from the existing primate and carnivore behavioural literature. Surveying the literature on animal behaviour can prove useful to comparative studies, but it is also fraught with difficulties. Accounts may pertain to hundreds of species across several orders, but the detail of such reports may differ markedly. This is a problem noted by other researchers of comparative behaviour (e.g. Fagen 1981). In this thesis, I use only data that detail specific quantitative measures, primarily time-budgets, and that are available through local academic libraries. Thus, the scale of this comparative study whilst not all-inclusive, is certainly representative of the existing literature and available quantitative data.

In essence, there are two principal methodologies incorporated in this thesis, that of a) comparative analyses, which focus upon relationships across taxa, and b) intra-specific analyses (Chapter 4), which focus upon relationships within species. The methodological feature that binds the various areas of this thesis is the incorporation of the comparative method.

2.2 The Comparative Method

2.2.1 What is it?

Current research evaluating evolutionary patterns increasingly incorporates use of the comparative method; this is basically a statistical methodology used in addressing questions about adaptation and evolution (Harvey & Pagel 1991; Martins 2000). The comparative method differs from the experimental method in that it is not possible to conduct experiments addressing cause and effect in variation over evolutionary time (MacLarnon 1999); but the comparative method provides a model that allows the use of data concerning extant species, to hypothesise their most likely evolutionary relationships (Harvey & Pagel 1991; Purvis & Webster 1999). The comparative method is therefore the comparison of trait variation within and between different taxa (Ridley 1996; Nunn & Barton 2001). It usually involves correlating two phenotypic variables across taxa (e.g. body size and brain size), or comparing one phenotype with an environmental variable (e.g. body size and habitat range) (Felsenstein 1985). The use of a phylogeny (hypothesised tree of evolutionary relatedness) bases the output of comparative analyses within an evolutionary framework, and theoretically ensures the statistical independence of data (Martins & Hansen 1996).

2.2.2 Why use it?

Although in theory, the comparative method can be used as a statistical means for studying anything from noodle quality (Nemeth et al. 1994) to language variation (Holden 2002), in practice, it is most usually employed in analysis of trait variation and evolution in species of plants or animals (e.g. Martins 1996). The use of phylogenetic information has become increasingly important in comparative studies, and the techniques for reconstructing evolution can be very powerful in this pursuit. It is important to use phylogenetic information for comparative studies to control for statistical dependence (Martins & Hansen 1996), that is, to remove the effect of relatedness between species descended from a common ancestor. Closely related species are likely to be similar, as they share a recent evolutionary history (Purvis &

Webster 1999; Nunn & Barton 2001); this is referred to as "phylogenetic inertia" (Harvey & Pagel 1991). The comparative method allows us to analyse the variation between species *independently* of their phylogenetic relatedness, offering an effective method by which to investigate evolutionary events (Nunn & Barton 2001). It is vital to any study that independent data are used: this means using data that are not "tainted" by other confounding variables, and that are free from phylogenetic inertia (Nunn & Barton 2001). In order to evaluate the evolution of any given trait, it is necessary to elucidate the independent differences between taxa, rather than claiming similarities exist purely through recent common ancestry. The use of phylogeny within analyses allows us to identify independent data points more clearly (Harvey & Pagel 1991).

Comparative methods are used when the hypothesis predicts that some species should have a different form of an adaptation from those observed in another species (Ridley 1996). There are different reasons for carrying out analyses using comparative data, for example: in order to assess whether two traits have evolved through correlated evolution; to estimate the degree of phylogenetic inertia; the ancestral states of a character; or to estimate the rate of phenotypic evolution (Martins & Hansen 1997). Comparative methods offer statistical techniques by which to carry out these kinds of analyses.

Phylogenetic information is extremely powerful in the reconstruction of correlated evolution (Nunn & Barton 2001), that is, the adaptive co-evolution of two traits (Harvey & Pagel 1991). Incorporation of phylogeny also reduces the effects of unmeasured confounding variables (Nunn & Barton 2001), which can occur through traits shared purely by common descent. Similarly for example, it is possible to compare related groups of species living in different circumstances. However, as evolution is modification through descent, the ways in which related species are similar might have as much to do with the ways in which their environments are alike as well as any other common cause of modification (Bell 1989). A classic example of this might be that of brain size in primates. Relatively large brain size across primate taxa may be due to a shared recent common ancestry, because these taxa have independently evolved large brains due to another variable, such as body size (Bell 1989). To overcome this problem of phylogenetic inertia, evolutionary scientists have developed statistical techniques that enable us to use the data measured in extant species to infer aspects of character evolution (Martins & Hansen 1996). These comparative methods allow examination of the adaptive significance of a trait that is subject to natural selection (see Harvey & Pagel 1991).

2.2.3 Phylogenies

A phylogeny is required in order to reconstruct evolutionary change (Ryan 1996); but what is a phylogeny, and why is using one so important in comparative studies? A phylogeny is akin to a family tree, showing paths of evolutionary relatedness between taxa. The branches leading from one taxon to another represent evolutionary time, with longer branch lengths typically indicating longer periods of evolutionary change. Thus a phylogenetic tree features a common ancestor and all of its descendents. Usually, the common ancestor is unknown and thus hypothetically derived. Phylogenies can be based on several traits, and new ones are published frequently. They are typically derived from morphological characteristics or molecular data to reconstruct relatedness between taxa (Martins & Hansen 1996), and the characteristics on which phylogenies are based tend to be discrete (Robson-Brown 1999). By conducting statistical analyses on data that control for phylogeny, results are more likely to be representative of independent evolutionary change (Harvey & Pagel 1991).

2.2.4 Independent contrasts

Although there are many types of comparative method, the technique used most commonly in the analyses of multi-species data (especially if the variables are continuous), and throughout this thesis, is that of independent contrasts (Nunn & Barton 2001). Independent contrasts is a model based on a Brownian motion (or random walk) evolutionary paradigm, which assumes that each evolutionary change on a given branch is independent of any change that may have gone before (Felsenstein 1985; but see also Harvey & Rambaut 2000 and section 2.2.7). Thus, a contrast details the difference in traits between species (or at higher levels), indicating instances of independent evolutionary change that has arisen since those species last shared a common ancestor (Purvis & Webster 1999). If differences in the dependent variable (Y) are correlated with differences in the independent variable (X), it suggests that those traits have co-evolved; thus one of the key uses in the method of independent contrasts is to test hypotheses concerning correlated evolutionary change (Harvey & Pagel 1991; Purvis & Webster 1999; Nunn & Barton 2001). This is the primary use of the comparative method throughout the following chapters in this thesis. The key word is "independent"; as a species is part of a phylogeny, it renders the results statistically weak if species are used as data points (Felsenstein 1985). Instead, the contrasts, or differences, between species act in this way within normal statistical analyses, whilst taking account of phylogeny. Incorporating phylogenetic information in this way ensures the independence and statistical validity of the results. Figure 2.1 depicts a simple clade; the arrows indicate the contrasts between two species (at the end of the branches), and between sister clades. Notice that in spite of four extant species (A-D), there are only three data points that will be used in the statistical analysis (i.e. three independent contrasts).

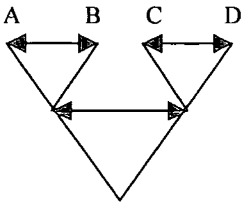


Fig. 2.1 Illustration of independent contrasts

2.2.5 Continuous and discrete data

Within this thesis, most variables are continuous. That is, the traits have a measurement such as time (e.g. gestation period), space (e.g. home range size), mass (e.g. body size), or number (e.g. group size). Some variables however, are discrete, or categorical. These traits typically describe a dichotomous character state as, for example, present or absent. Independent contrasts typically take continuous traits as their variables, as the focus is on the relative differences between character states, rather than whether they are present or absent; and this is the general focus of the method of independent contrasts. Discussion in this chapter, unless stated otherwise, typically refers to the analysis of continuous variables. It is important to note however, that categorical data can also be analysed by the independent contrasts approach.

Ostensibly within comparative methods, we use discrete data to count instances of evolutionary change from one character state to another along the branches of a phylogeny. We might correlate, for example, species colouration as either aposematic or cryptic (dichotomous variable), with group size (continuous variable). An evolutionary transition is deemed as having occurred when there is a change in state in either or both of these characters along a branch (Harvey & Pagel 1991). In this thesis, discrete variables are only measured against continuous ones; comparisons of categorical variables however, can be made (Read & Nee 1995) using different statistical methodologies, such as the concentrated changes test (Maddison & Maddison 1992). This test assumes that the ancestral character states are reconstructed; one variable is taken as independent, and the other as dependent, assuming no correlation between the two traits. The test shows which character states are gained and lost throughout the tree; thus whether changes in the dependent character are concentrated in parts of the tree that have a particular character state for the independent variable (Maddison & Maddison 1992). One failing of this method is that it assumes all branch lengths are equal; modifications to this method attempt to rectify this (Pagel 1994). The development of computer packages has made the analyses of comparative data far quicker.

2.2.6 Computer packages

Associated with the comparative method are the tools designed to implement it. As the comparative method relies on statistical modelling and algorithms, application of the techniques are best achieved through the use of various computer software designed to ensure the analyses are user-friendly. The output files from these programmes can usually be transferred for use in familiar statistical packages. One of the most popular programmes for independent contrasts, and the main programme used in the analyses throughout this thesis, is that of CAIC (Comparative Analysis of Independent Contrasts) (Purvis & Rambaut 1995). CAIC is designed for use on Apple Macintosh computers and enables the analysis of multi-species data that includes at least one continuous variable (Purvis & Rambaut 1995). Testing for correlated evolution between discrete variables however, is better employed through the use of packages such as MacClade (Maddison & Maddison 1992, and see below).

CAIC reads the data inputted by the user from a text file; when inputting the data, it is important to bear in mind some evolutionary and statistical assumptions. Firstly, CAIC is based on Felsenstein's (1985) method of phylogenetically independent contrasts, which makes the assumption that evolutionary change follows a Brownian model of random change. For this reason, data should be log-transformed, as regardless of species, change should be proportional (Felsenstein 1985; Purvis & Rambaut 1995; Freckleton 2000). An example commonly used to explain the reasons for this, is that an increase of a kilogram is likelier to occur in a large-bodied species, such as a whale, than it is in a small-bodied species, such as a mouse (Purvis & Rambaut 1995). Log-transformation standardises the data, which makes them more suitable for regression analyses (Freckleton 2000). Similarly, to meet the assumptions of conventional linear statistics the contrasts are standardised relative to the time of evolutionary divergence (branch lengths). Regression models assume that residuals have the same mean and variation at all points along the regression line. Use of branch lengths (estimates of evolutionary time between clades) and standardised contrasts ensures this assumption is met (Purvis & Rambaut 1995; Purvis & Webster 1999). In conducting statistical analyses of independent contrasts, it has been demonstrated that a constraint needs to be placed on the fit by forcing the regression through the origin; that is, the regression line has no intercept (Garland et al. 1992). More recently, this practice has been advised with caution, given that regression through the origin does not always offer the line of best fit (Neter et al. 1996). Others suggest further permutation tests to reduce asymmetric statistical error (e.g. see Legendre & Desdevises, in press). For the purposes of this thesis, and to conform to the standard practice in carrying out independent contrasts, all regressions are set through the origin.

CAIC offers two statistical algorithms for measuring evolutionary change: CRUNCH and BRUNCH (Purvis & Rambaut 1995). Both methods are based on Felsenstein's (1985) original model of independent contrasts using a Brownian model of evolution (although BRUNCH does not *require* change to be a random walk model), but can be used without the phylogeny being completely resolved. CRUNCH is used for calculating contrasts between taxa when the variables are continuous; BRUNCH is usually used for comparing an independent discrete variable (X) and a dependent continuous variable (Y) (Purvis & Rambaut 1995), as is the case in this thesis. Additionally, BRUNCH can be selected to measure continuous variables if they cannot be measured under a Brownian motion assumption (Purvis & Webster 1999).

The other computer package used within this thesis is MacClade (Maddison & Maddison 1992), which also runs on Apple Macintosh computers. MacClade does not rely on an already-present phylogeny and branch length file in the way that CAIC does. Data are inputted into a data file, which produces a default phylogeny; the user can then manipulate the branches of this clade. I follow the same phylogenies that I used in CAIC (i.e. Purvis 1995 and Bininda-Emonds et al. 1999) in reconstructing the clade. MacClade is especially powerful in tracking and displaying evolutionary change over a phylogenetic tree. We would expect any taxa to share and exhibit some similarities with related taxa that have existed previously. Phenotypes of more recently-diverged taxa will be more similar to one another than older ancestral relatives. We can use the level of phylogenetic correlation to infer evolutionary change (Martins & Hansen 1996) and to track likely behavioural changes over time by "projecting back" onto a phylogeny (Ryan 1996).

With the increasing development of molecular tools for drawing accurate phylogenies of living organisms (e.g. Baum 1992; Bininda-Emonds et al. 1999), the evolutionary relationships between groups of mammals have become much clearer. We are able to use this information to look at evolutionary patterns of adaptation (Harvey & Pagel 1991). Characters may have evolved over long periods of time, so it may be necessary to look at the origins of a trait in an evolutionary context to evaluate this adaptation (Bell 1989). Some workers however, have questioned the extent to which an adaptation can actually be inferred through analysis of comparative data (Frumhoff & Reeve 1994; Leroi et al. 1994; Martins 2000).

2.2.7 Criticisms of the comparative method

One of the criticisms levelled against use of the comparative method is that errors in the dataset lead to invalid evolutionary conclusions (see e.g. Benton 1999). It is true that care must be taken to reduce sampling error, particularly with independent contrasts given that the model assumes that any differences between species will be due to evolutionary change, and not data error (Purvis & Webster 1999). However, regardless of whether a study is phylogenetic or non-phylogenetic, data error is a factor that affects any statistical research (Martins & Hansen 1997). Similarly, some authors claim that we cannot draw useful conclusions from using phylogenetic comparative methods due to the errors in reconstructing ancestral character states (Schluter et al. 1997, and see Martins 2000). However, such errors seldom significantly affect the conclusions drawn from comparative analysis (Benton 1999). Indeed, *not* using phylogenetic information is far more likely than sampling error, or unresolved phylogenies, to increase the probability of Type I errors (likelihood of rejecting a null hypothesis) (Nunn & Barton 2001). Failure to incorporate phylogenetic analysis is problematic, as one must assume that all relationships between species are equal; in that case the study may incorrectly assume that all species are descended from a single common ancestor (termed a *"star phylogeny"*, e.g. Nunn & Barton 2001; see Figure 2.2). Thus, for the purposes of accuracy, it is better to use some phylogenetic information, in order to focus upon independent differences between species, than to use none at all (Felsenstein 1985; Nunn & Barton 2001).

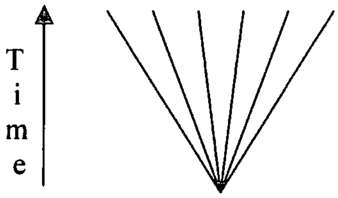


Fig. 2.2 Illustration of a "star"-phylogeny where all taxa radiate from a single point

Although having become decidedly popular in recent years, independent contrasts has again become the topic of some debate (e.g. Harvey & Rambaut 2000). The argument stems from discussion over whether independent contrasts truly offer anything over and above the results of cross-species (i.e. non-phylogenetic) analyses and the hypotheses they generate. One of the major perceived problems of phylogenetic comparative methods is their reliance on phylogeny. If a phylogeny has not been fully resolved, what can the results using such a phylogeny really impart? This is a problem that affects any scientific pursuit: data can always be bettered. A common cry from researchers suggests "You can only work with what you've got!"; this does not mean the results are of no use. Garland et al. (1992) demonstrate that independent contrasts is a robust method for analysing multi-species data, even if the branch lengths are inaccurate. Indeed, a study by Lewis (2000) on social play frequency and neocortex ratio in captive primates, which incorporated independent contrasts, but which did not use branch length information, shows the same pattern of variation across taxa as when branch lengths are used (this will be demonstrated in Chapter 7).

Harvey & Rambaut (2000) claim that a niche model might be better applied in standardising contrasts, as closely-related species share similar environs due to adaptive radiation. They advise caution in applying independent contrasts blindly, as niche adaptation may not follow a Brownian model of evolutionary change. They suggest that other non-Brownian models (e.g. Price 1997) might better explain character evolution during adaptive radiation; in this case, Felsenstein's (1985) model of independent contrasts would not perform as well as non-Brownian cross-species analyses (Harvey & Rambaut 2000). Their model assumes that as niche spaces are invaded by a new species, and that over time, that same species adapts to the niche and speciates, then traits are correlated in niche space. This means that over time there will be effectively more traits than niches, and thus as niche space becomes available, phenotypically-similar species will compete for space. Whilst Harvey & Rambaut's (2000) model certainly explains how environmental neighbours will be similarly adapted, it is not a model of correlated evolutionary change, rather a correlation of traits within niche space (see e.g. Nunn & Barton 2001).

Another criticism of comparative methods is that they focus too heavily on evolutionary change over the effects of stabilising selection; this is because change can be measured as independent far more easily than can periods of evolutionary stasis (Nunn & Barton 2001). The selection for species to remain unchanged for long periods of time might be just as crucial to our understanding of adaptation as periods of rapid evolutionary change (Martins 2000). In any case, phylogeny must be used in answering these questions, and Hansen (1997) has developed a new phylogenetic comparative method, which aims to redress this by looking at species in terms of traits evolving in response to environmental factors during periods of evolutionary stasis.

These, and other such phylogenetic methods, can only serve to improve and widen our knowledge concerning evolutionary relationships and associated change.

Despite some early protests, there currently exists a general consensus as to the importance of using phylogenetic comparative methods in addressing evolutionary questions (Ryan 1996). There remains however, some debate as to which of the current comparative methods are most appropriate; perhaps the choice of phylogenetic comparative methods is very much "horses for courses". The use of comparative methods in recent years has undoubtedly revolutionised the field of evolutionary biology and studies reliant on multi-species data. Further applications of these methods can only serve to further enhance our understanding of evolutionary processes.

2.3 Data

The first, and arguably most crucial stage of this thesis was to collate a database on play behaviour and other relevant variables in the taxonomic groups chosen (the orders Primates and Carnivora). Comparative or interspecific analyses increasingly rely on already published work for their data. This is partly as academia has produced a vast body of knowledge on specific species, and partly due to practical constraints of time and finance that preclude comparative researchers from collecting all necessary data first hand (Martins & Hansen 1996). Independent contrasts are especially sensitive to sampling error, and the error variance will be a greater proportion of the total variance when comparing closely related taxa, as any differences between taxa are assumed by the model to be due to evolutionary change (especially when the taxa being compared are closely related) (Purvis & Webster 1999). I recognise that some margin of error is almost inevitable when collating multi-species data, but care has been taken to ensure use of as high quality information as possible in the collation of this database. It is hoped that one significant contribution of this thesis to the current field of play behaviour and evolution, will be the database, on which this work is centred (see Appendix for full tabulation).

2.3.1 Species

There are 57 species of primate and 19 species of carnivore variously incorporated into the analyses in this thesis. Table 2.1 details these species. References are given in the Appendix.

Table 2.1 Species incorporated within this study

Order	Family	Species	Common name
Primates			
	Loridae	*Nycticebus coucang*	Slow loris
	Lemuridae	*Lemur catta*	Ring-tailed lemur
	Callitrichidae	*Callithrix geoffroyi*	Geoffroy's tufted-eared marmoset
		Callithrix jacchus	Common marmoset
		Saguinus fuscicollis	Saddle-back tamarin
		Saguinus midas	Red-handed tamarin
		Saguinus oedipus	Cotton-top tamarin
	Cebidae	*Callicebus moloch*	Dusky titi monkey
		Cebus albifrons	White-fronted capuchin
		Cebus apella	Tufted, or brown capuchin
		Cebus capucinus	White-throated capuchin
		Cebus olivaceus	Weeper, or wedge-capped capuchin
		Saimiri sciureus	Squirrel monkey
		Pithecia monachus	Monk saki
		Pithecia pithecia	White-faced saki
		Cacajao calvus	Bald uacari
		Alouatta caraya	Black-and-gold howler
		Alouatta palliata	Mantled howler
		Ateles geoffroyi	Black-handed spider monkey
	Cercopithecidae	*Macaca arctoides*	Stump-tailed macaque
		Macaca fascicularis	Long-tailed, or crab-eating macaque
		Macaca fuscata	Japanese macaque, or snow monkey
		Macaca nemestrina	Pig-tailed macaque
		Macaca nigra	Celebes, or crested black macaque
		Macaca radiata	Bonnet macaque
		Macaca mulatta	Rhesus macaque
		Macaca silenus	Lion-tailed macaque
		Macaca sinica	Toque macaque
		Macaca sylvanus	Barbary macaque
		Macaca thibetana	Tibetan macaque
		Papio anubis	Olive baboon
		Papio cynocephalus	Yellow baboon
		Papio hamadryas	Hamadryas baboon
		Papio ursinus	Chacma baboon
		Mandrillus sphinx	Mandrill
		Theropithecus gelada	Gelada baboon
		Cercocebus torquatus	Sooty mangabey
		Lophocebus albigena	Grey-cheeked mangabey
		Allenopithecus nigroviridis	Allen's swamp monkey
		Erythrocebus patas	Patas monkey
		Cercopithecus aethiops	Vervet monkey
		Cercopithecus diana	Diana monkey
		Cercopithecus hamlyni	Hamlyn's monkey

Order	Family	Species	Common name
		Cercopithecus mitis	Blue monkey
		Cercopithecus neglectus	De Brazza's monkey
		Colobus guereza	Eastern black-and-white colobus
		Procolobus badius	Western red colobus
		Semnopithecus entellus	Hanuman langur
		Trachypithecus johnii	Nilgiri langur
		Trachypithecus pileatus	Capped leaf monkey
		Pygathrix nemaeus	Red-shanked douc langur
	Hylobatidae	*Hylobates lar*	White-handed gibbon
		Hylobates syndactylus	Siamang gibbon
	Pongidae	*Pongo pygmaeus*	Orangutan
	Hominidae	*Gorilla gorilla*	Gorilla
		Pan paniscus	Bonobo, or pygmy chimpanzee
		Pan troglodytes	Chimpanzee
Carnivora			
	Herpestidae	*Helogale undulata*	Mongoose
	Felidae	*Panthera leo*	Lion
		Felis silvestris	European wild [feral] cat
		Acinonyx jubatus	Cheetah
	Hyaenidae	*Crocuta crocuta*	Spotted hyaena
	Canidae	*Canis latrans*	Coyote
		Cerdocyon thous	Crab-eating fox, or common zorro
		Speothos venaticus	Bush dog
	Ursidae	*Ursus americanus*	American black bear
		Ursus arctos	Brown, or grizzly bear
		Thalarctos maritimus	Polar bear
		Selenarctos thibetanus	Asiatic black bear
	Ailuridae	*Ailuropoda melanoleuca*	Giant panda
	Mustelidae	*Lutra canadensis*	River otter
		Mustela putorius	European ferret or polecat
		Mustela vison	American mink
Pinnipedia			
	Otariidae	*Arctocephalus australis*	South American fur seal
	Phocidae	*Haliochoerus grypus*	Grey seal
		Phoca vitulina	Harbour, or common seal

2.3.2 Database

This database was collated by "trawling" the existing mammalian journals, book chapters, personal libraries, relevant theses, and occasionally unpublished data, for instances of measured play behaviour in primates and carnivores; that is, articles that specifically give a time budget or frequency measure of play and its types relating to species of primate and carnivore. There are inherent problems in using time budgets for which only "social activity" is measured, without delineating which social activities are included (see Dunbar 1988: 90-91); and thus only literature which specifically deals with play and its elements has been included here. Time budgets are at present the best practicable way to measure investment in significant behaviours across groups or species (Post & Baulu 1978), and these have been used as detailed by the authors in cases where they appear in the literature. Elsewhere, where sufficient and appropriate information is available, raw data given in the literature, such as tables, graphs and histograms, were measured and transformed through simple calculations to give a mean time budget percentage for social play for each study species, based on the length of the study.

As an example, King et al.'s (1980) study on chimpanzee social behaviour was allocated a time budget mean of 5.3% for social play. Based on 170 hours of observation, King et al. (1980) reported the number of minutes per hour spent in social play for each of seven conspecifics. The mean of these individual scores is calculated as 5.3%. Where two or more suitable replicates for any one species were found in the literature, a time budget percentage of social play was taken for each study. A mean was calculated from these percentages for each species, and used in the phylogenetic analysis. For example, studies on gorillas by Fossey (1979), Fischer & Nadler (1978), and Freeman & Alcock (1973) state time budget means for social play as 22.2%, 6.4%, and 15.7% respectively. These individual totals are summed (44.3) and divided by the number of studies for gorillas, to give a species average: 44.3 / 3 = 14.8. This number is then log-transformed for analysis to meet the assumptions of the test (see Martins & Hansen 1997; Nunn & Barton 2001): log (14.8) = 1.17.

2.3.3 Data quality

Any comparative study is affected by the quality of data on which the analyses lie. This is largely because the studies from which the data are taken, have not necessarily been originally observed with multi-species comparative analysis in mind, and thus data quality is often variable (Harvey & Clutton-Brock 1985). It may therefore be necessary to weight data based on quality, or to standardise data accordingly (Martins & Hansen 1996). With a behavioural trait such as play, where studies containing suitable data are scarce, the problem of data collection is further confounded. In this thesis, I have used field studies where possible, but these are supplemented with data from captive studies. In many cases, species values were derived from both field and captive studies. The following list details certain considerations when collating data from the available literature:

1. Established phylogenies and existing databases are used where possible (e.g. Purvis 1995; Watson 1998; Barton 1999).
2. All data are "quality-checked" in terms of its established contribution to academic literature (e.g. high = peer-reviewed paper, to low = undergraduate thesis). Also in terms of the length of the study and the techniques used within it.
3. Does the publication refer to a field or captive study?
4. What is the context of the play data? (e.g. introduction of novel object)
5. Does phylogenetic data exist for most of the species in question?
6. Does play data exist for most of the species in question?

2.3.4 Data categories

There are many categories of data incorporated within the database for analysis. These categories are explained below in Table 2.2.

Table 2.2 Data categories

Category	Explanation
Basic information:	
Species	Taxonomic (Latin) and common name of species
Source	Published literature reference information
Study length	Length of study in observation hours and in months spent in the field
Captive/Wild	Dichotomous variable: 0 = captive, 1 = wild
Demographic information:	Age (mo), age-category (infant, juvenile, sub-adult, adult), and sex composition (number of males and females) of each group
Play categories:	
Total play	Percentage of time budget engaged in playful activity
Solitary locomotor-rotational play	Percentage of time budget engaged in solitary play (see Table 1.1)
Object play	Percentage of time budget engaged in object play
Social play	Percentage of time budget engaged in social play
No. of play behaviours	The number of different types of play behaviours within the species play-repertoire
Play bout length	Average duration of play bout in seconds.
Dyadic play	Dichotomous variable: does play between 2 partners occur? 0 = no, 1 = yes
Polyadic play	Dichotomous variable: does play between 3 or more partners occur? 0 = no, 1 = yes
Adult play	Dichotomous variable: do adults engage in any type of play? 0 = no, 1 = yes
Adult-adult play	Dichotomous variable: do adults engage in play with other adults? 0 = no, 1 = yes

Category	Explanation
Adult male play	Dichotomous variable: do adult males engage in any type of play? 0 = no, 1 = yes
Sex play	Dichotomous variable: do adults engage in sexually-oriented play sequences, such as mounting? 0 = no, 1 = yes
Interspecific play	Dichotomous variable: does the species engage in any type of play with other species? 0 = no, 1 = yes
Vocalisation	Dichotomous variable: does the species emit play-specific vocalisations? 0 = no, 1 = yes
SSD	Dichotomous variable: Significant sex difference? Play is more frequent in one sex (usually males) 0 = no, 1 = yes
SSP	Dichotomous variable: Significant sex preference? Players preferentially engage in play with members of their own sex. 0 = no, 1 = yes
SAD	Dichotomous variable: Significant age difference? Play is performed more frequently by one age category (usually juveniles 0 = no, 1 = yes
SAP	Dichotomous variable: Significant age preference? Players preferentially seek play-partners of their own age category 0 = no, 1 = yes
Sibling	Dichotomous variable: Players preferentially seek to engage in play with their siblings 0 = no, 1 = yes
Relatedness	Dichotomous variable: Players preferentially seek to engage in play with their kin 0 = no, 1 = yes
Dominance	Dichotomous variable: Play may be used to strengthen dominance relationships 0 = no, 1 = yes
Play-mothering	Dichotomous variable: Play appears to resemble mothering behaviour in female juveniles 0 = no, 1 = yes
Place	Dichotomous variable: Play occurs more frequently in trees (1) or ground (0).
Life-history variables:	
Gestation	Length of gestation period (days)
Neonatal weight	Average weight of newborn (g)
Litter size	Average number of neonates per litter
Age at weaning	Age in days or years at which an individual is weaned
Juvenile period	Length of the juvenile period (years); period between weaning and sexual maturity
Age at independence	Age in days at which individual is no longer dependent on parental investment
Age at sexual maturity	Age in months at which an individual is capable of reproduction and therefore adult
Age at 1st conception	Average age in days at which an individual first conceives
Age at 1st reproduction	Average age in months at which first offspring is born
Lactation period	Duration in months for which a female produces maternal milk
IBI	Inter-birth interval. Average time in years between births in an individual female
Lifespan	Maximum longevity in years
Socio-ecological variables:	
Body size	Average weight of a species member (g)
Mean group size	Average number of individuals forming a stable group
Actual group size	Actual number of individuals in each study group
Feeding group size	Number of individuals congregating for the purposes of feeding
Foraging group size	Number of individuals participating in co-operative foraging
Clique size	Number of primary social partners of an individual
Network size	Broader number of individuals who are socially linked to an individual

Category	Explanation
Population size	Maximum group size (individuals of the same species sharing a common home range area)
Home range size	Area in km within which a group primarily lives
Day range length	Distance (km) travelled by a group on a daily basis
% Leaves	Percentage of diet from leaves
% Fruit	Percentage of diet from fruit
% Prey	Percentage of diet from animal matter
BMR	Basal metabolic rate
Growth	Rate at which an individual reaches adult weight
Sex ratio	Proportion of males and females within a group
Activity timing	Dichotomous variable: 0 = diurnal, 1 = nocturnal/arrhythmic/ crepuscular
Usual stratification	Dichotomous variable: 0 = arboreal, 1 = semi-terrestrial/terrestrial
Frugivory	Dichotomous variable: 0 = non-frugivorous, 1 = frugivorous (over 50% diet from fruit)
Folivory	Dichotomous variable: 0 = folivorous (over 50% diet from leaves), 1 = non-folivorous
Zonation	Dichotomous variable: 0 = terrestrial/terrestrial and occasionally arboreal, 1 = aquatic
Diet	Dichotomous variable: 0 = carnivorous (flesh-eater)/omnivorous, 1 = insectivorous/piscivorous/frugivorous and folivorous
Vegetation (primary habitat)	Dichotomous variable: 0 = open grassland/forest/woodland, 1 = aquatic
Prey size	Dichotomous variable: 0 = small, 1 = medium-large.
Space per individual	Refers to captive-housed species; enclosure area (m) divided by the actual number of individuals housed within that space
Brain components:	
Adult brain weight	Average species brain weight (g)

Other brain component data from Stephan et al. 1981 (pons from Matano et al. 1985); brain components are measured in volume (mm^3).

One of the key problems with using data from the existing literature is that "species-data category matches" are not always available; that is, it is not always possible to find information for one or more data category (e.g. social play) *and* information on another independent variable (e.g. brain size) for all species. This is a problem inherent in multi-species datasets. Throughout the following chapters in this thesis, instances of $n = < 4$ are indicated in the appropriate tables.

2.3.5 Considerations for play

Play is a behavioural category that appears to be affected by many variables, such as age, sex, diet, habitat, etc., as have been discussed throughout Chapter 1. Throughout this thesis, these factors will be addressed in relevant chapters, and attempts made to delineate which are the most important with regard to the exhibition of playful behaviour. There are two variables that are commonly considered to affect play: whether or not the individuals are wild or captive-housed; and developmental age.

The question of captivity will be dealt with in Chapter 6, but it is worth noting here that the database deals with reports from both captive and wild studies. Certainly, captive studies are likely to show higher frequencies of play than do wild studies, as less time is devoted to finding food, avoiding predators, etc. Captive studies may demonstrate the *potential* or *possible* play capacities of a species, given these parameters; for this reason, I believe them to be important. Similarly, captive studies offer the observer a window by which to view species-typical play behaviours, which might not otherwise be observable in the wild (e.g. King et al. 1980). Some analyses in this thesis separate captive and wild studies. Elsewhere, captive *and* wild studies represent play averages for most species contained within this database, thus demonstrating a fair representation of species playfulness. Importantly, the captive studies incorporated here derive from animals housed under similar husbandry conditions; thus across species, variation should not be significantly biased.

Developmental age is typically a measure of an infant's development in terms of body size or motor skill, expressed in terms of standard age, and thus is deemed a factor affecting the exhibition of play. Throughout this thesis, two parameters have been used to deal with this issue: age at which social play first occurs; and weaning age. All of the species within the database have been shown to exhibit social play, albeit in varying amounts. The emergence of social play also corresponds with the time at which myelination occurs in the CNS (see also Chapter 6 & 7) (Gibson 1991). Similarly, weaning age is usually a good indicator of the period of most play frequency, and is a parameter that is known and reported in many species (more so than onset of social play). For this reason, many analyses control for developmental age, using these two factors.

2.3.6 Phylogenetic & statistical analyses

Once the data have been sorted, and hypotheses generated, the next stage is that of phylogenetic analysis. This thesis principally aims to test for correlated evolution between play variables and socio-ecological, life-history, and brain component variables. These hypotheses are detailed specifically in each of the following chapters. The data are converted from StatView (version 4.0) data files into text files, which can be read by the CAIC programme (Purvis & Rambaut 1995). Already present within the CAIC programme are the branch length files, and phylogeny files (primates from Purvis 1995; carnivores from Bininda-Emonds et al. 1999), which read in the degree of evolutionary relatedness (phylogeny) and time between character states (branch lengths) for each species in the dataset. The programme calculates the independent contrasts and transfers the results to an output file, which can be imported into spreadsheets and statistical applications such as StatView. The CAIC programme file identifies any major outliers in the data, if the contrasts are greater than 2.0 standard deviations (SD). In very few instances in the following chapters, these outliers have been removed from the regression analyses. In this case, it is noted in the accompanying text.

The primary statistical test used on the independent contrasts output from CAIC is standard linear regression analysis. This both calculates and illustrates the relationship between the variables (Sokal & Rohlf 1995). In this way it offers an insight as to the possible adaptive co-evolution between traits (Harvey & Pagel 1991). In some cases, partial correlation analyses have been carried out to remove the effect of one variable from the analysis, such as correcting for the effect of body size from group size. The specific methods, and details of residual regression are detailed in each chapter. Graphs are usually presented only for significant results, although the primary independent variable used in residual analysis may be used for all play types as a point of illustration (e.g. Chapter 5 details regression of body size and each type of play, regardless of significance, as body size is a key confounding variable).

MacClade was used for analyses of character change in discrete traits; an example of this has been seen in Chapter 1 (Figure 1.1); other use of this will be seen in Chapter 3. Character states of play rates (low, medium or high frequency) were assigned to primate and carnivore taxa and transitions in these states were traced onto a tree using the "track changes" option which "paints" the character states onto a default tree (Maddison & Maddison 1992). I manipulated the branches to match those of the standard phylogenies employed in this thesis (i.e. Purvis 1995 and Bininda-Emonds et al. 1999).

In addition to comparative (inter-specific) analyses, intra-specific (within-species) analyses were also conducted to look for differences within different populations of the same species. These analyses are detailed in Chapter 4.

2.4 Summary

Data on play, socio-ecology, life-history, and brain components were collated for primates and carnivores. Data were log-transformed to meet the assumptions of the analyses. Using the method of phylogenetic independent contrasts, these data were analysed using existing computer packages and standard statistical applications to test for correlated evolution across multi-species data. The use of phylogeny is important, as due to shared recent ancestry, species themselves are not statistically independent; the differences between them however, are. For this reason, independent contrasts are employed, as species cannot be used as data points. Regression and residual analyses were conducted to measure the relationship between these variables, and significant results presented in graphs. Regression was set through the origin. Intraspecific analyses were carried out to look for differences in different groups of the same species. Specific details are presented in each chapter.

Chapter 3:

Phylogenetic Patterns of Play

3.1 Introduction

The evolutionary origin and function of a trait can often be better understood through analysis of its phylogenetic distribution (Byers 1999). The results chapters in this thesis (chapters 3-7) deal with evolutionary correlations of play in primates and carnivores. This chapter aims to provide a background for subsequent chapters through focus on the phylogenetic patterning of play behaviour. Chapter 1 outlined some of the major phylogenetic patterns of play in mammalian taxa (section 1.9). This chapter however, is concerned with addressing the patterning and distribution of play across the two focal orders of this thesis: primates and carnivores. It is hoped that by focusing on the ancestral conditions for play in these taxa, the conditions associated with playful behaviour in other orders will be better elucidated.

3.1.1 Searching for the origins of play

Historically, it was believed that only "higher" mammals engaged in play; it was thought that this was due to them being better equipped to find food, mates, shelter, and protection, and thus a glut of surplus energy meant that spare time could be devoted to "fun" (i.e. play) (Spencer 1872; and see Chapter 3 in Burghardt, in press). This has led to one argument for play being "behavioural fat" (as was discussed in Chapter 1). Play however, is rather unlikely to be a mere byproduct of excess energy, given its developmental timing, trajectory, and somatic effects during periods of developmental plasticity (Byers & Walker 1995; Fairbanks 2000; Burghardt, in press). Similarly, as recent studies suggest, play is not simply the domain of the perceived mammalian intelligentsia (e.g. primates), being reported in reptiles and cephalopods, for example (Burghardt et al. 1996; Kramer & Burghardt 1998; Mather & Anderson 1999; Burghardt, in press).

As was discussed in Chapter 1, one theory as to the origin of play was its rôle in motor training (Byers 1984). Byers has argued that in order to delineate what aspects of motor function may be connected to play, the focus needs to be on training responses that are age-limited; that is, those physiological responses to "exercise" that occur during the same time frame that play is performed (Byers & Walker 1995; Byers 1999). He therefore argues that if the prime benefit of playing is to perfect physiology, then play should be limited by metabolic rate (Byers 1999). However, Byers (1999) refutes this hypothesis, finding no correlation between metabolic rate or body size and play in marsupials, concluding that the true function of play is to modify brain development. Chapter 7 will deal with these issues in more depth.

Pellis & Iwaniuk (1999a) looked at the possible origins of adult-adult play in primates. Adult play, if it occurs at all, is generally directed towards juveniles. In some species however, adult-adult play sequences occur, and these often take the form of male-female play-fighting. Such sequences often precede copulation (e.g. grizzly bears, *Ursus arctos*, Herrero & Hamer 1977; giant pandas, *Ailuropoda melanoleuca*, Kleiman 1983). It is widely believed that adult-adult play of this nature serves as a means of social and sexual assessment. This is especially believed due to the fact that adult-adult play is more prominent in solitary species than in more gregarious species. Pellis & Iwaniuk (1999a) strongly argue the case that adult-adult play serves to overcome unfamiliarity between males and females of solitary-living species in overlapping territories. Such species typically demonstrate mother-offspring groups with solitary males (e.g. nocturnal strepsirhines: see Chapter 6). Male-female interactions may therefore be agonistic for the vast majority of time, coming together only for mating. Pellis & Iwaniuk (1999a) state that adult-adult play may have evolved as a means to dispel aggression, assess potential mates, and be a prelude to copulation. They show that when male-female association frequency is low, instances of adult-adult play increase. Therefore, for adult-adult play at least, play may have evolved as part of the sexual behavioural repertoire.

3.1.2 Phylogenetic reconstructions

Throughout this thesis, the dominant comparative technique employed is that of independent contrasts, as is discussed in Chapter 2. This chapter however, focuses on phylogenetic reconstructions of particular play behaviours. A major area of questioning in play research concerns the origins of play (Burghardt 1998a). What did the earliest forms of play look like, when did it emerge, and which species were doing it? I do not attempt to answer these questions for all animal taxa; however, by using what is known about the play of extant species of primate and carnivore, it may be possible to glean a further understanding of the likely evolutionary processes that led to what we currently identify as play, and why it is so important and complex in many extant taxa (e.g. Burghardt 1998a). As play is widely considered to be such a tricky category of behaviour, phylogenetic analysis is required if we are to gain any real insight as to its origins and functions (Byers 1999; Burghardt, in press). Indeed, modern evolutionary thinking is obsolete without use of the comparative method (Losos 1999). We want to be able to see whether play has arisen independently in taxa, and to be able to track those changes throughout the branches of a phylogenetic tree.

Reconstructing possible phylogenetic relationships is a useful means of identifying behavioural divergence. This can mean tracking likely patterns in the divergence of behaviour, as well as possible ways in which behaviour has influenced other adaptations (Ryan 1996). The use of programmes such as MacClade in reconstructing character states is useful, since the algorithms are currently believed to be robust, and also offer the most parsimonious relationships across the tree (Maddison & Maddison 1992; Martins 2000). These trees infer patterns of consensus between character states (i.e. different forms of the characters), as well as the degree of change relative to time (indicated by the branch lengths). As the common ancestor of any given taxon is not usually known, MacClade reconstructs the hypothetical (i.e. statistically most likely) ancestor (Maddison & Maddison 1992).

The phylogenetic reconstructions presented in this chapter represent the most parsimonious (i.e. statistically conservative) evolutionary relationships. Insofar as the trees are concerned, this means explaining each phylogenetic tree in terms of the most homologies. In simple terms, a homology is similarity due to common descent. A homologous character evolves once, and is assumed to share the same character state as the most recent common ancestor; thus between two species, a character is homologous when it is inherited from those species' last common ancestor (Futuyma 1986). This is sometimes considered to be a somewhat old-fashioned term to many evolutionary biologists (e.g. Ridley 1996), but is used here to mean "similarity through common ancestry". This is in contrast to homoplasy, whereby similarities between character states evolve separately by convergence. If a character is a homoplasy, it may be present in two species but *not* present in their common ancestor. This means that although two species may appear phenotypically similar, such as the marsupial Tasmanian wolf (*Thylacinus cynocephalus*), and the eutherian European wolf (*Canis lupus*), their evolutionary histories are very different. These species actually share no common ancestry, and have evolved similar characteristics in response to comparable environmental constraints, rather than descent (e.g. Ridley 1996). The most parsimonious phylogenetic tree will depict fewer changes, and therefore the least homoplasy. Homology shows phylogenetic relatedness; homoplasy does not. Thus, the reconstructed trees enable us to see which character state currently found in extant taxa is ancestral.

3.2 Methods

Use of the comparative method is vital to any study investigating evolutionary patterns in behaviour. Similarly it is necessary to compare behaviours that derive from the same repertoire, rather than those that simply appear to be phenotypically similar (Burghardt, in press). Some discrepancies in the play literature render analysis potentially tricky. Which variables can and should be used to measure variance in the distribution of play? I have chosen to use time spent playing as a measure of the relative importance of the execution of play behaviour across taxa.

3.2.1 Behavioural measures

Later chapters will deal with the exhibition of play expressed as a mean time budget across species. This chapter also deals with time budgets, but in a broader manner. I wanted to see whether investment in different types of play behaviour follows the same patterns across taxa. I also wanted to test whether species that appear to invest relatively more time in play, also exhibit different behavioural repertoires through the course of their play.

3.2.1a "Continuous" variables

Although given a maximum of four character states, thus for the purposes of this chapter appearing discrete, there are four key "continuous" variables used here: total play, solitary locomotor-rotational play, object play, and social play. These variables appear as continuous throughout subsequent chapters in this thesis, but were formulated into discrete variables for the purposes of analysis in this chapter, by breaking them down into frequency measurements. The frequency measures are based on categorising species time budget measures of each play category (as used throughout this thesis) into percentage brackets (see Table 3.1).

Table 3.1 Explanation of play category character states for "continuous" variables

Character state	**Explanation**	**Frequency measure (time spent in play %)**
0	No play reported in that category	0%
1	Low frequency of play in that category	0.1-5%
2	Medium frequency of play in that category	5.1-10%
3	High frequency of play in that category	10.1% +

These frequency measures are based on the widely-reported evidence for the play of most species to be between 1-10% of the daily time budget (Fagen 1981; Burghardt 1984; Bekoff & Byers 1992). Therefore, a play time budget either side of this range could be distinguished as high or low, with a midpoint as a reasonable estimate of a medium frequency play time budget.

3.2.1b Discrete variables

The other variables in these analyses concern primate play only; these variables deal primarily with whether or not a particular behavioural category for play is present or absent in extant primates (see Table 3.2). The character states (0, 1) represent absent (0) or present (1) in each case.

Table 3.2 Explanation of play category character states for discrete variables

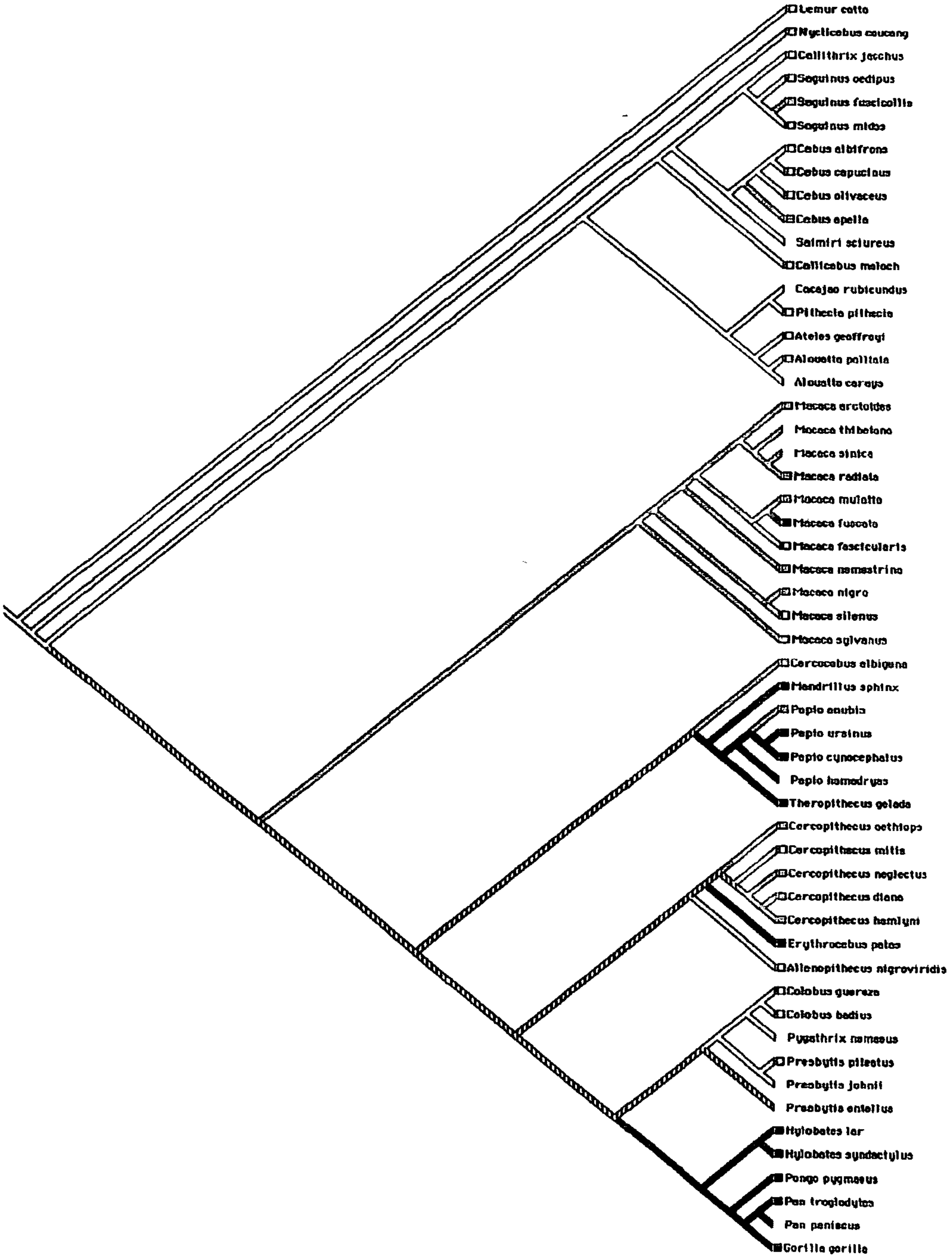
Variable	**Explanation**
Dyadic play	Engages in play with two partners
Polyadic play	Engages in play with more than one other partner
Adult play	Adults of either sex are reported to play
Adult-adult play	Adults engage in play with other adults
Adult male play	Adult males engage in any play behaviour
Sex play	Adults engage in sexually-oriented play sequences, such as mounting
Interspecific play	Species observed to engage in play with other species
Vocalisation	Species emits play-specific vocalisations

3.2.2 MacClade

The phylogenetic trees were generated using the MacClade (version 3.01) software package (Maddison & Maddison 1992). This is a useful programme for reconstructing character sates and mapping their changes across a phylogeny (Ryan 1996), allowing the user to "explore" ancestral character states (Maddison & Maddison 1992). Branches were manipulated to fit Purvis' (1995) primate phylogeny, and Bininda-Emonds et al.'s (1999) carnivore phylogeny. One of the fundamental assumptions within the MacClade programme is that a character can only have one state at any given point on the branch; thus "*ancestral species are presumed to be monomorphic* [and] *polymorphism is* [only] *allowed in the terminal taxa*" (Maddison & Maddison 1992: 31); this simplifies the evolutionary assumptions within the programme, rendering them more parsimonious. Indeed, MacClade traces the most parsimonious changes in character state over the tree, and thus where a character state is dubious it is shaded "equivocal". This appears in the legends in the tree figures presented in this chapter. The trees in this chapter have been produced using the "unordered" algorithm within MacClade. This algorithm calculates the most likely character states at the nodes based on the state of the two terminal taxa immediately above it. These states are determined in a top-down fashion, thus the extant taxa are used as a starting point for "projecting back" through the tree the most likely character state. In this way, the root of the tree represents the most parsimonious character state relative to the entire tree (Maddison & Maddison 1992). As phylogenies group species according to recent common ancestry (e.g. Ridley 1996), I deemed this to be the most independent algorithm, and thus the most appropriate in the study of a behavioural category such as play.

3.3 Results

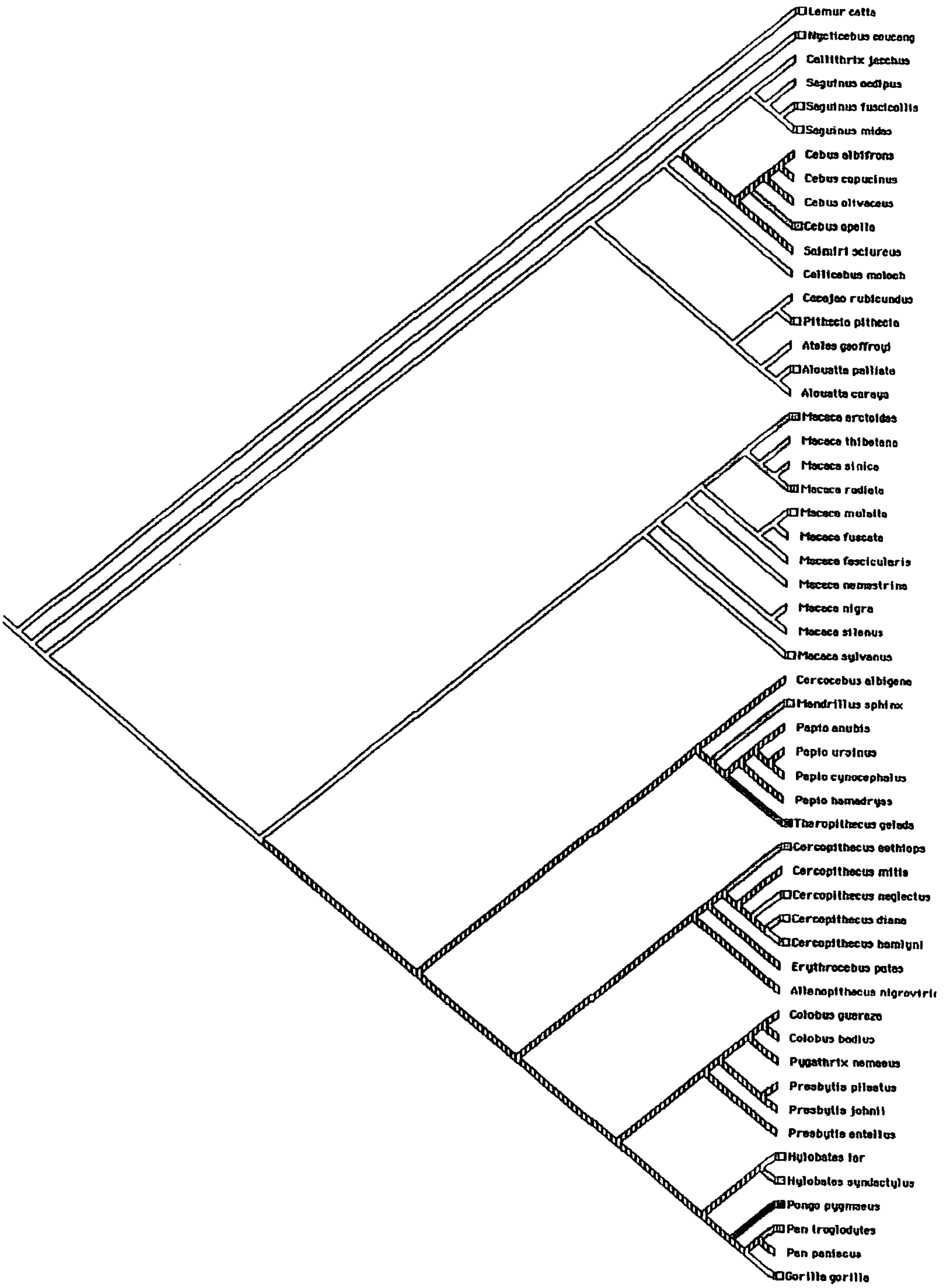
The phylogenetic reconstructions are detailed below in Figures 3.1-3.4 for primate, and 3.5-3.8 for carnivore "continuous" play categories (i.e. total, solitary, object, and social play), and 3.9-3.16 for primate discrete play categories.



☐ 1
▨ 2
■ 3
☰ equivocal

Legend:
1 = low frequency of total play
2 = medium frequency of total play
3 = high frequency of total play

Fig. 3.1 Phylogenetic reconstruction of total play distribution in primates



☐ 1
▨ 2
■ 3
▤ equivocal

Legend:
1 = low frequency of solitary play
2 = medium frequency of solitary play
3 = high frequency of solitary play

Fig. 3.2 Phylogenetic reconstruction of solitary locomotor-rotational play distribution in primates

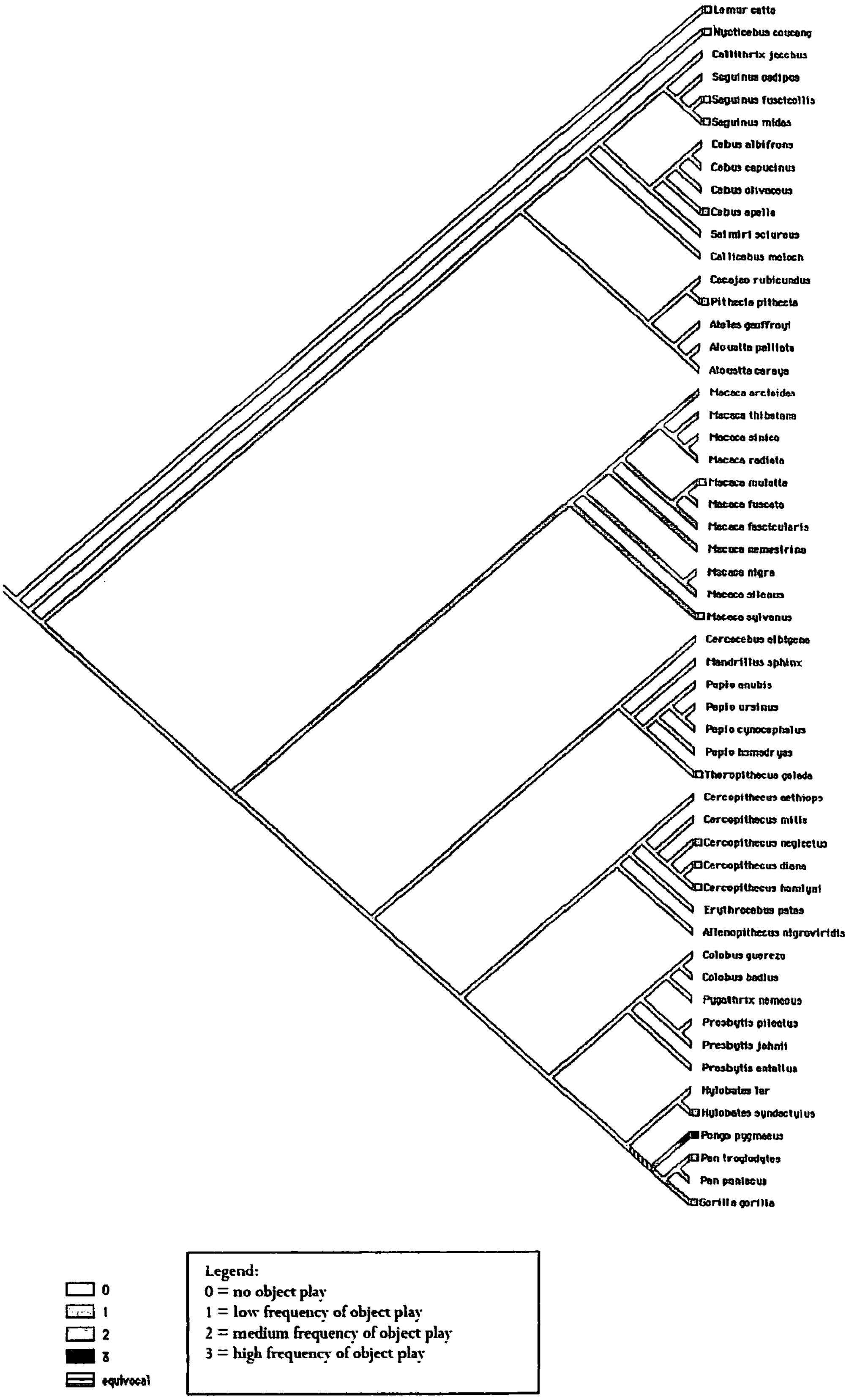
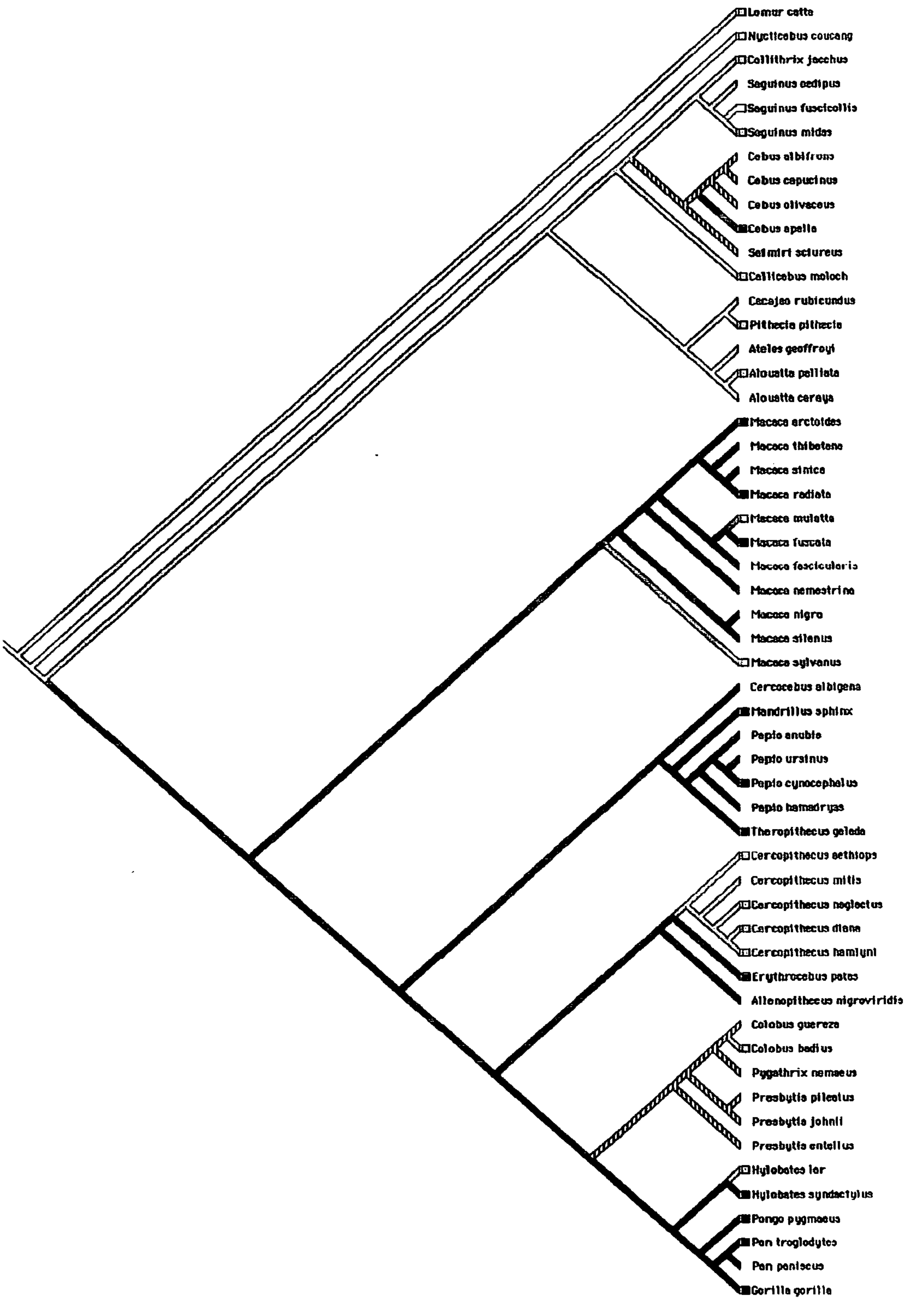


Fig. 3.3 Phylogenetic reconstruction of object play distribution in primates



☐ 0
▨ 1
▤ 2
■ 3
☰ equivocal

Legend:
0 = no social play
1 = low frequency of social play
2 = medium frequency of social play
3 = high frequency of social play

Fig. 3.4 Phylogenetic reconstruction of social play distribution in primates

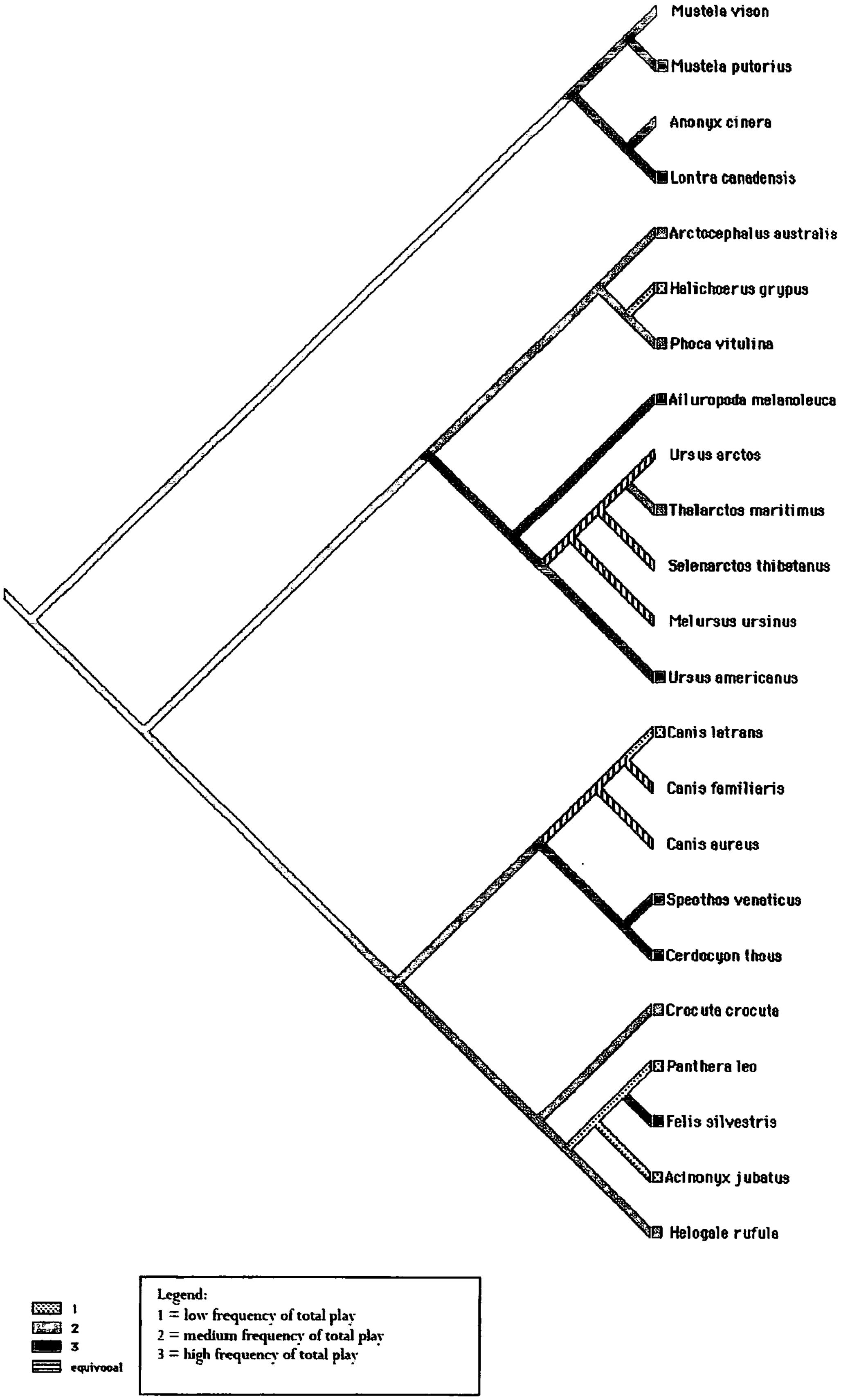


Fig. 3.5 Phylogenetic reconstruction of total play distribution in carnivores

Fig. 3.6 Phylogenetic reconstruction of solitary locomotor-rotational play distribution in carnivores

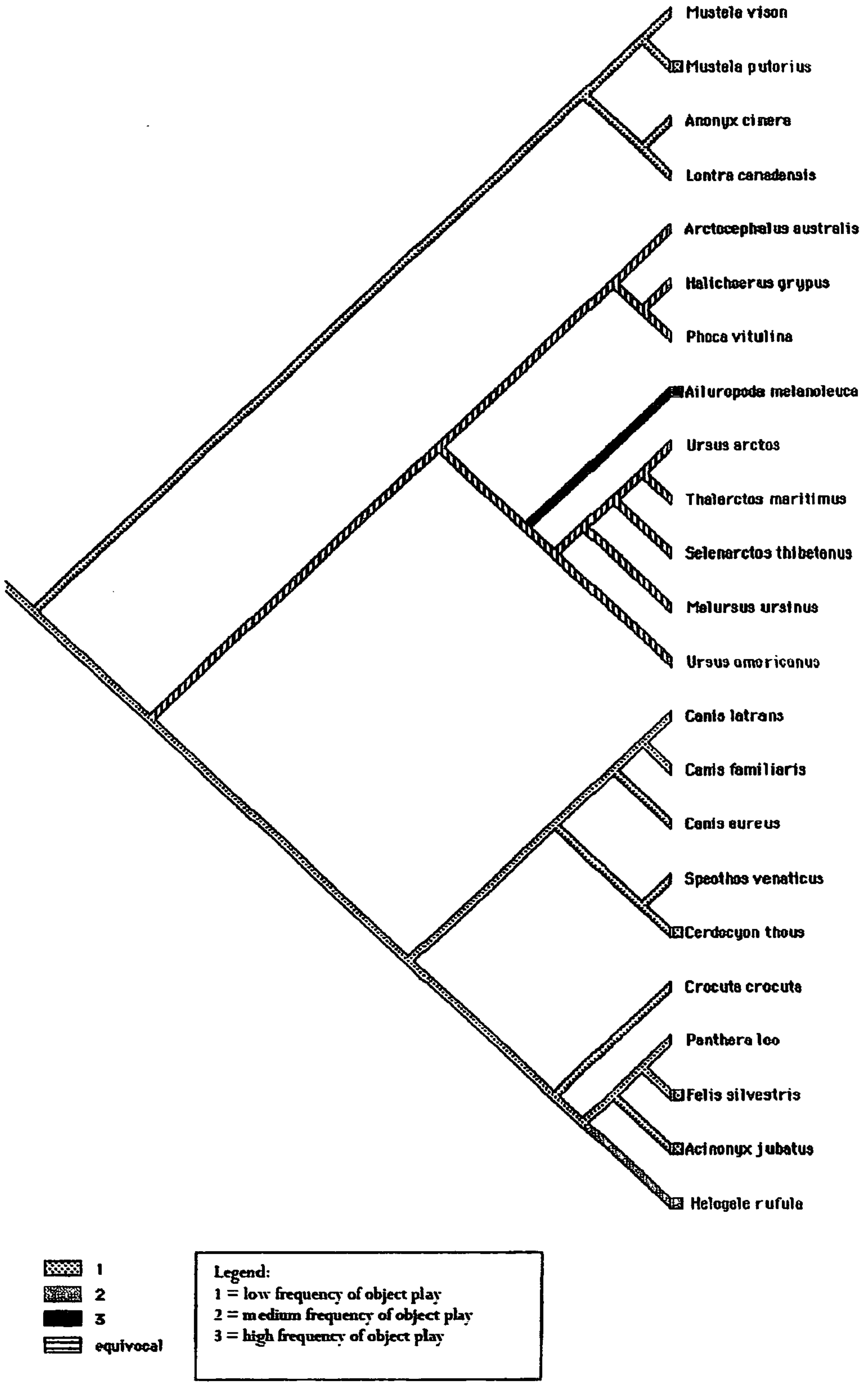


Fig. 3.7 Phylogenetic reconstruction of object play distribution in carnivores

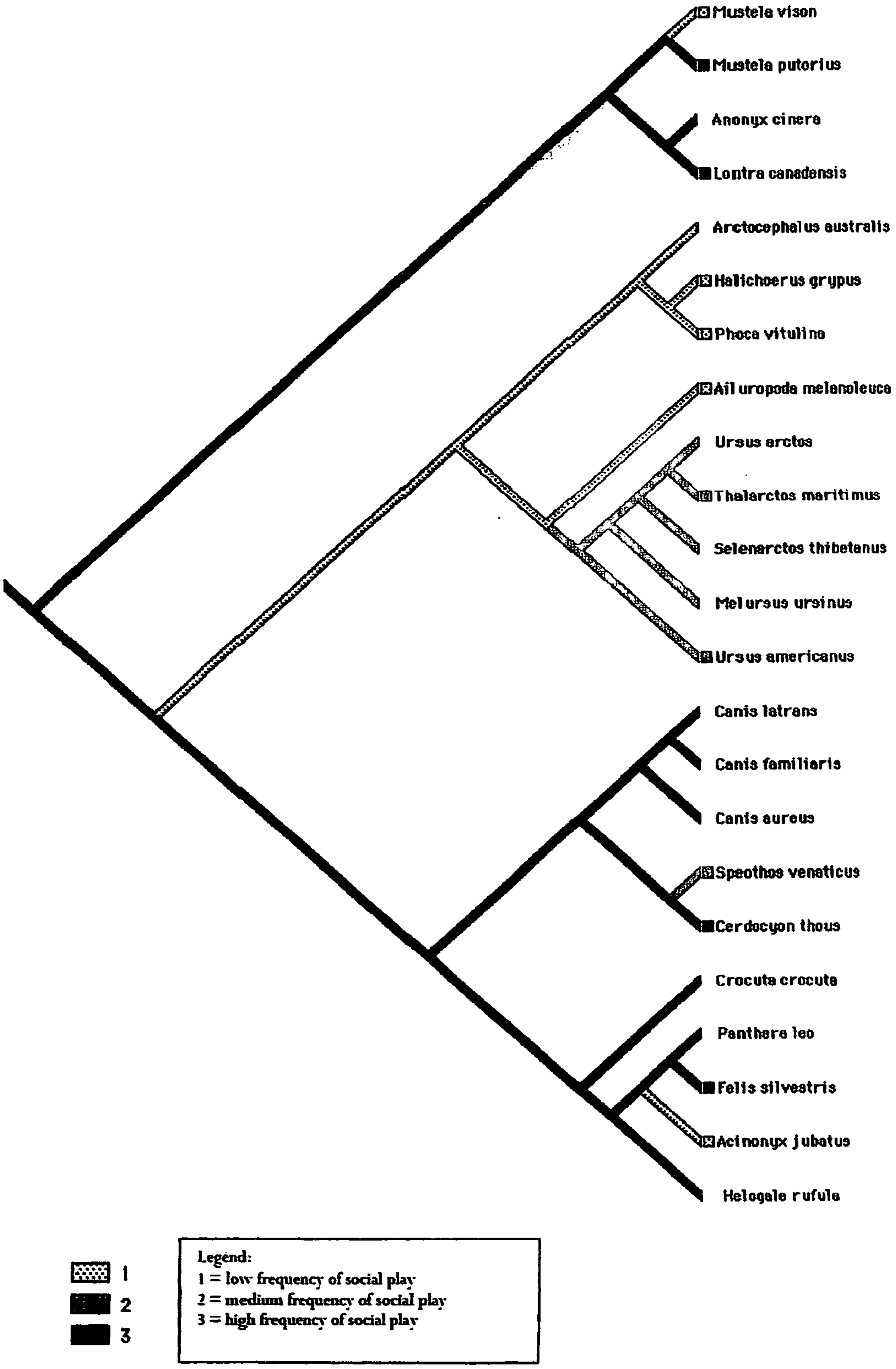


Fig. 3.8 Phylogenetic reconstruction of social play distribution in carnivores

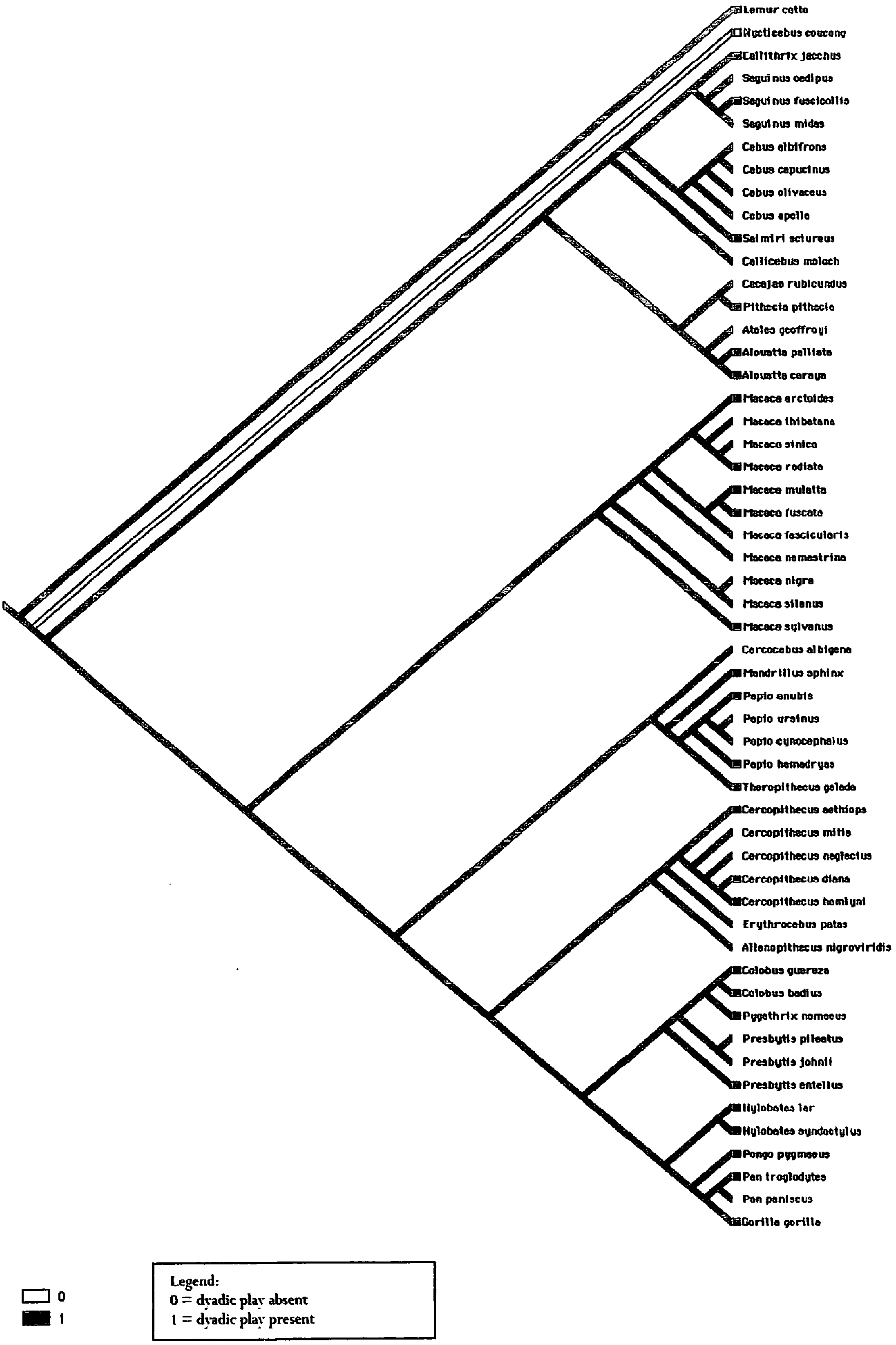


Fig. 3.9 Phylogenetic reconstruction of dyadic play distribution in primates

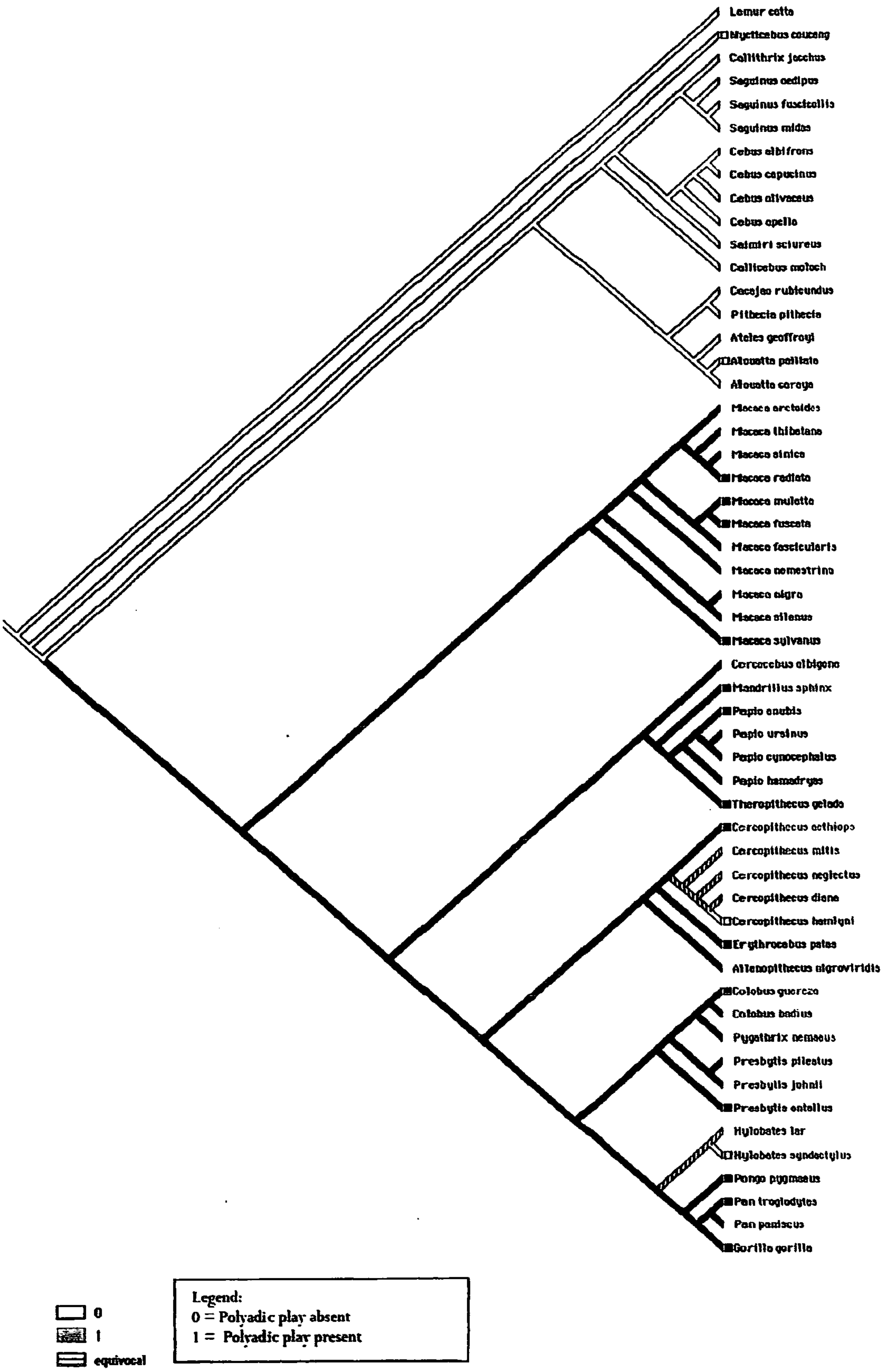
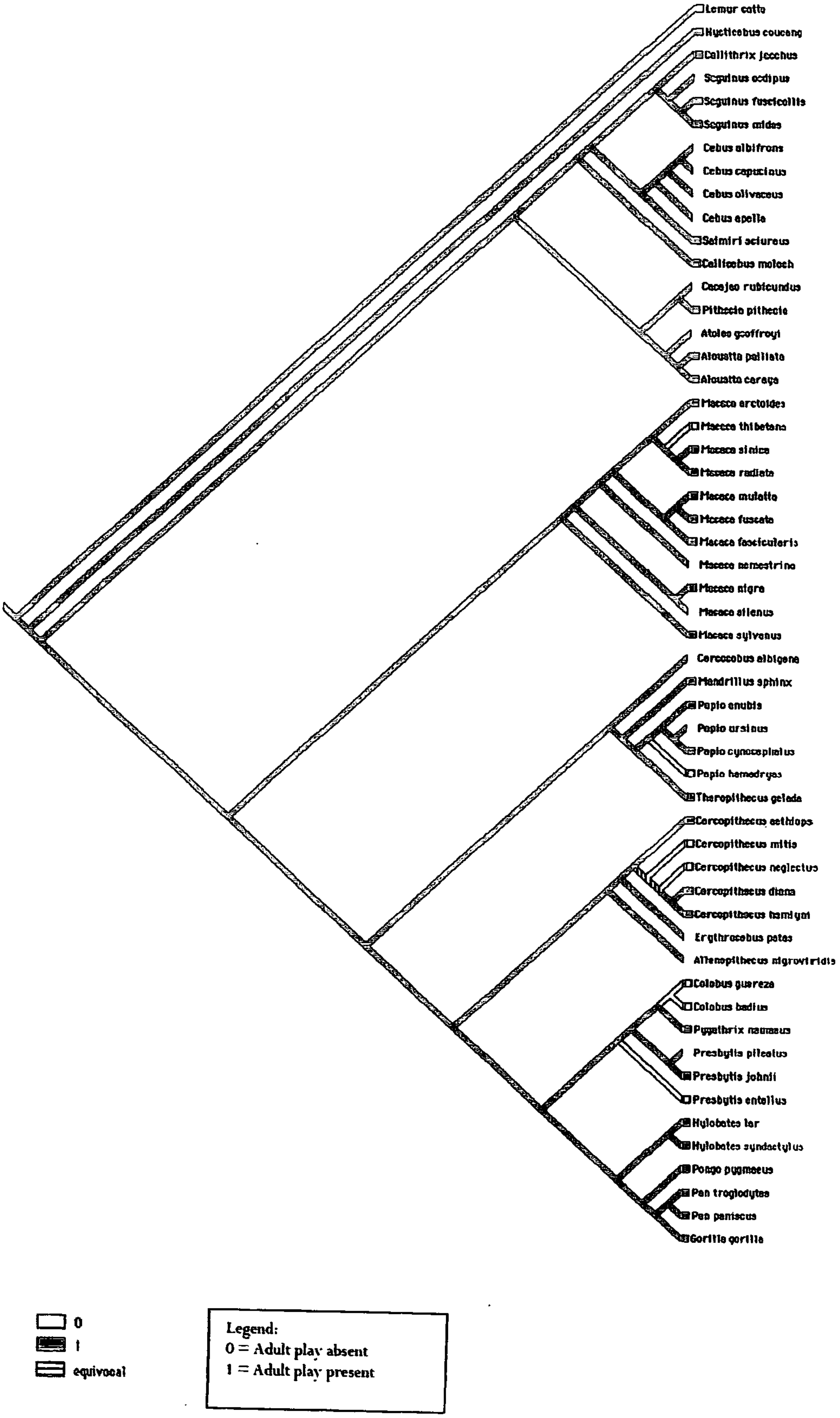


Fig. 3.10 Phylogenetic reconstruction of polyadic play distribution in primates



Legend:
0 = Adult play absent
1 = Adult play present

Fig. 3.11 Phylogenetic reconstruction of adult play distribution in primates

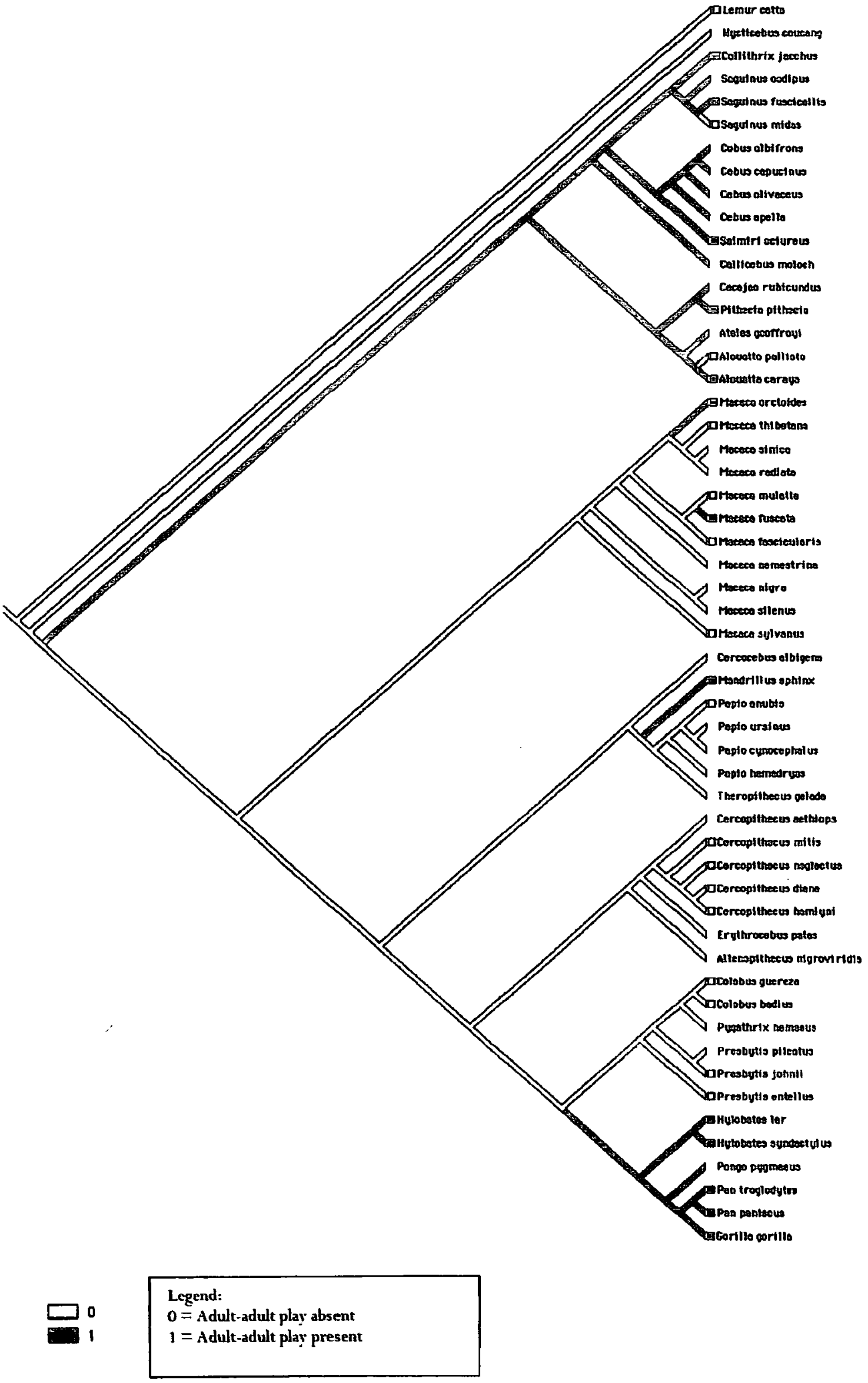


Fig. 3.12 Phylogenetic reconstruction of adult-adult play distribution in primates

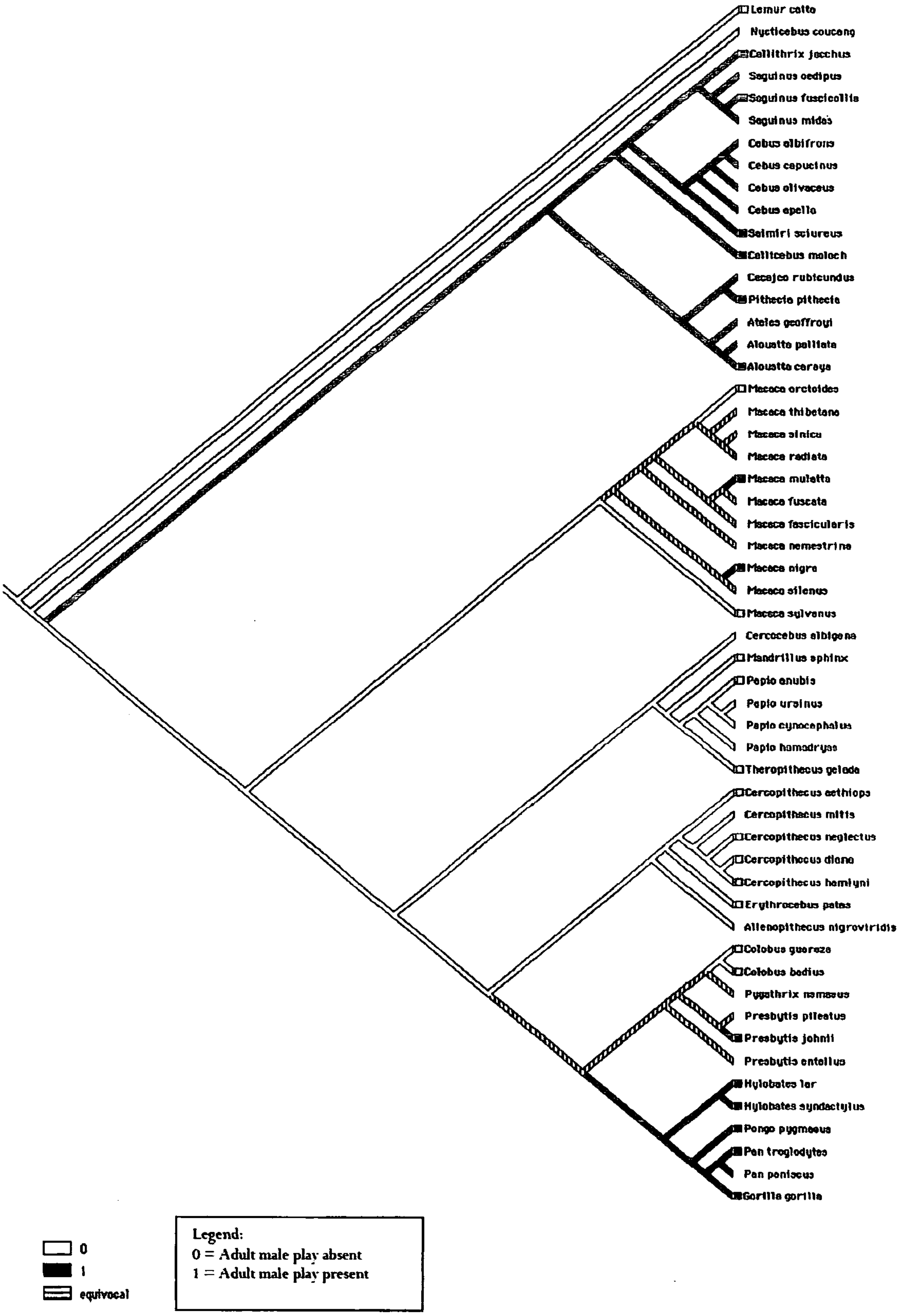


Fig. 3.13 Phylogenetic reconstruction of adult male play distribution in primates

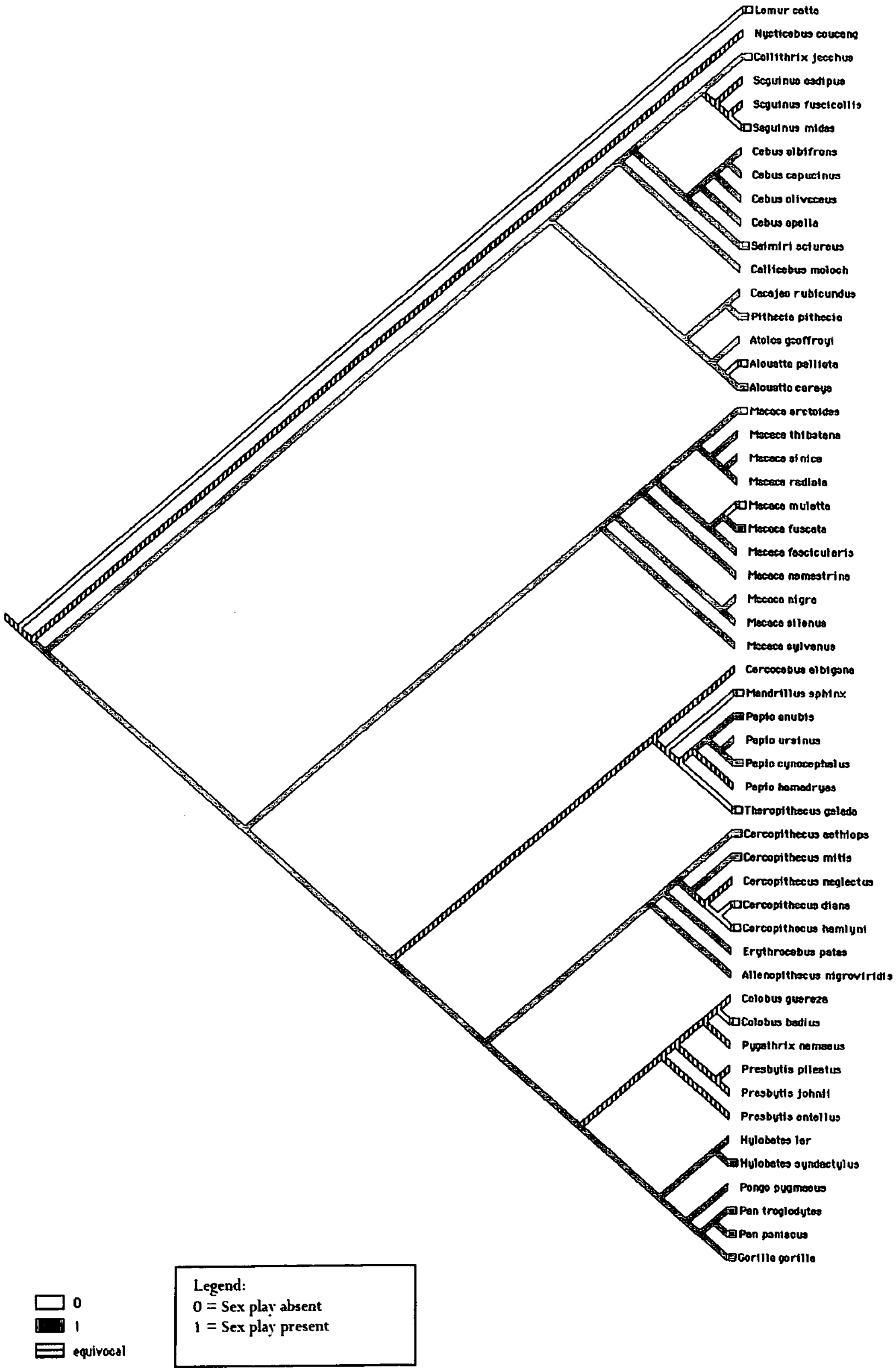


Fig. 3.14 Phylogenetic reconstruction of sex play distribution in adult primates

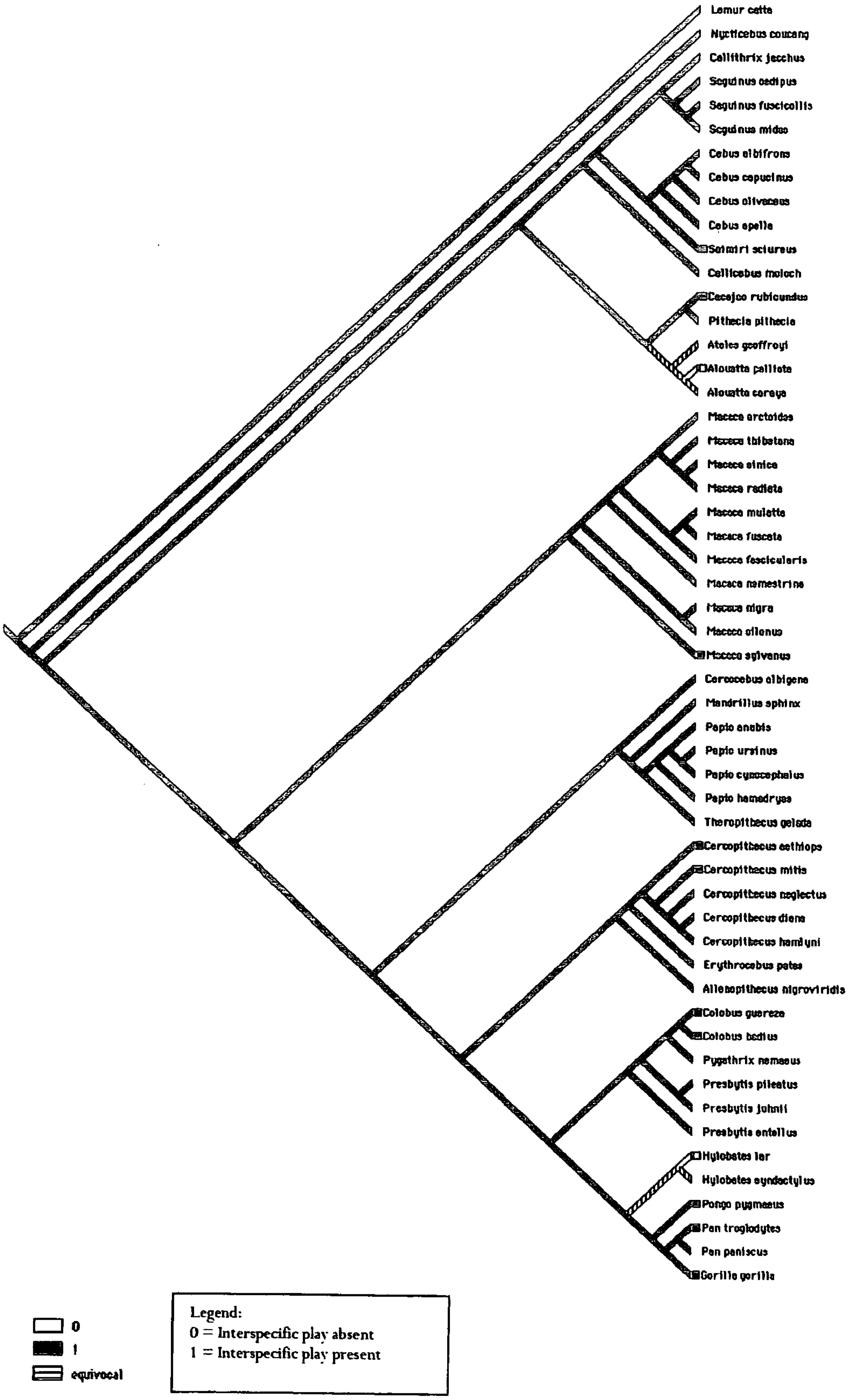
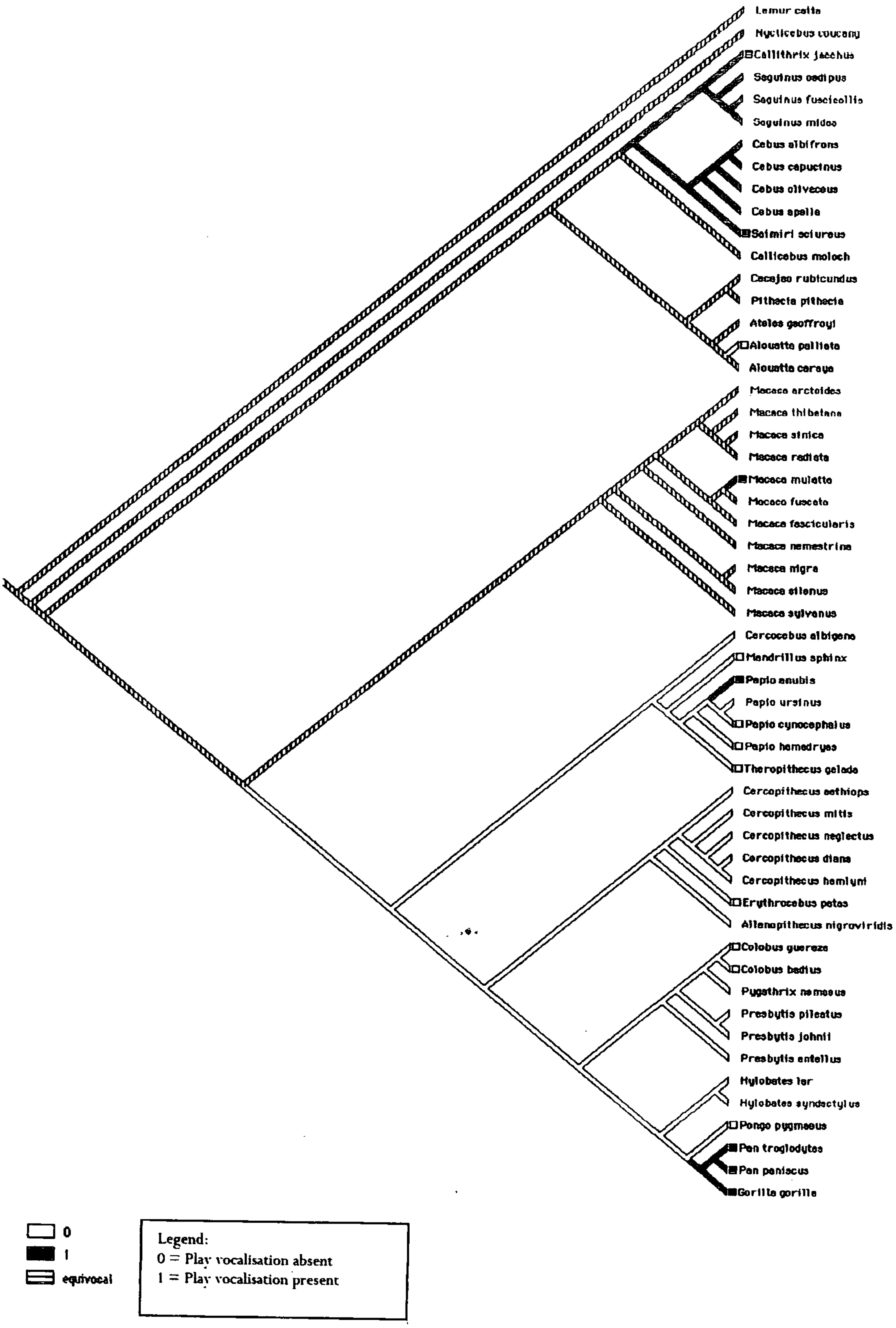


Fig. 3.15 Phylogenetic reconstruction of interspecific play distribution in primates



Legend:
0 = Play vocalisation absent
1 = Play vocalisation present

Fig. 3.16 Phylogenetic reconstruction of play vocalisation distribution in primates

3.4 Discussion

3.4.1 Primates: "continuous" variables.

The character evolution diagrams offer a useful means for tracing the most parsimonious patterning of play types across each order. Total play in primates appears to have originated in very low amounts (0-5%) at the common ancestor of extant primates (see Figure 3.1). The branches leading to extant strepsirhines and platyrrhines have retained this low-level frequency of play in all major nodes; this pattern is consistent across solitary, object, and social play also (see Figures 3.2-3.4). There are two independent adaptations towards a medium-level (5-10%) exhibition of play at the nodes leading towards *Saguinus fuscicollis* and *Cebus apella* (which is a very manipulative species), suggesting that the propensity for increases in play arose at the node for extant callitrichinae and cebinae; this pattern is retained for social play. For solitary locomotor play, the medium level frequency occurs in *Cebus apella*, but not in *Saguinus*. Object play is common to the platyrrhines at a low-level only, throughout the clade. Object play is unlikely to have been present in the common ancestor of lemurs and lorises according to the clade (Figure 3.3).

Play is likely to have been present in the common ancestor of the cercopithecoidea and apes, although at which level is unclear. Total play appears to have arisen at a medium frequency in the branch leading towards extant macaques, although the level of play that persists from this node branching towards the baboons, guenons, colobines and apes is more doubtful. The reconstruction for solitary play suggests that the common ancestor of platyrrhines and catarrhines engaged in this type of play at very low rates, and this persists deep into the tree. Object play too, seems to have arisen and retained a low frequency at the ancestral node, and diverged at the strepsirhine-haplorhine node, persisting in haplorhines but not in strepsirhines. Object play again diverges at the node branching towards macaques at a medium level, and persisting at a low level throughout the tree, until diverging to a high frequency only at the common ancestor of the great apes. Social play however appears to have a slightly different evolutionary history. Social play appears to have been present at very low levels in the primate common ancestor. This level persisted in the lemurs, but diverged at the lorisid branch, where social play appears to have been selected against; presumably due to the solitary nature of these nocturnal primates. At the platyrrhine-catarrhine node, play diverged into low levels in platyrrhines, and high levels throughout the catarrhines, suggesting that social play is the most common and the most persistent form of play in catarrhine primate evolution. Social play however, evolved at medium levels in the branch leading to the macaque species that is considered to represent the most likely primitive *Macaca* condition, *Macaca sylvanus* (e.g. Purvis 1995), and again is independently reduced to a medium level in the branch leading to modern *Macaca mulatta.* Social play persists at high levels throughout the Papio clade, and arguably throughout the species that represent the most primitive guenon condition, *Erythrocebus patas*, and *Allenopithecus nigroviridis* (e.g. Purvis 1995). At the node leading to extant cercopithecines however, the level of social play diverges again to a low rate. The ancestral condition of social and solitary play is unclear in the colobines, although both total play and social play persist at high rates in the common ancestor of the extant apes.

These phylogenetic trees suggest that low levels of all play categories were present in the common ancestor of primates, and that higher levels of playfulness have been selected for largely in the catarrhine clade. High levels of social play are also almost exclusive to the catarrhines, the one exception being in *Cebus apella*; capuchins are known to be especially playful (Visalberghi & Guidi 1998); they are also a common laboratory and zoo species. Macaques, baboons, and apes are consistently shown to be the most playful taxa, and amongst catarrhines, the colobines are the least playful. This may be due to energetic constraints of folivory. Indeed, the patterns of play category frequency in colobines is similar to that of the platyrrhine clade, which also contains many species whose primary diet is based of leaves (e.g. atelines and *Alouatta* spp.). Chapter 6 will investigate socio-ecological variables in the expression of play.

The patterning of character states on the primate trees for the four key categories of play suggest that social play is the evolutionarily oldest form of play, persisting deep into the tree and at high frequencies. This suggests that social play has its roots before the divergence of primate ancestors from other mammalian stock. Primates are considered to be a gregarious order, and most species are group-living. Social play may have evolved as social-assessment behaviour to cope with the demands of living in social groups. Social play may be an effective way to size up potential mates, alliances, and agonistic conflict (Byers 1984; Pellis & Iwaniuk 1999a). Indeed, social play in its earliest form is likely to have evolved in response to mating strategy; it might be expected to see more play-fighting between males in polygynous species where males defend both territory and access to mates (Byers 1984).

3.4.2 Primates: discrete variables

The patterns shown in the evolution of play categories are also supported by phylogenetic analysis of discrete traits. Unsurprisingly, dyadic play (play between two individuals) is common to all branches, except that of the solitary-foraging lorises. The prevalence of dyadic play throughout the clade is likely to be reflective of the general sociality of primate species. The patterning for polyadic play (play between three or more individuals) supports the evolution of social play in the catarrhine clade, the primary exception being that of *Hylobates*; gibbons tend to live in small family groups containing approximately two offspring (Chivers 1984), thus offering little opportunity to engage in polyadic play in comparison with species in larger groups. The other exception is that of *Cercopithecus hamlyni*, which, from casual observation, may be said to be a "quiet" species that appear to show a preference for dyadic allo-grooming rather than for playing in large groups (*pers. obs.*).

The primate clade tends to suggest that adult play (in this case including play with offspring) occurred in the common ancestor, and in most branches leading to extant species. This may simply reflect the tendency of parents to engage in play with their offspring. Play between two adults is far less common however, and has evolved throughout the platyrrhines and the apes, and appearing in few cercopiths, seemingly emerging independently. Play by adult males follows almost the exact same trend. It seems possible that the propensity for adult play has evolved with breeding structure and sexual dimorphism, especially within platyrrhines; species with relatively reduced dimorphism, such as *Callithrix* and *Saimiri* exhibit adult play. This is not necessarily true of the ape clade however. Thus, these results do not support the conclusions of Pellis & Iwaniuk (1999a) who argue that adult-adult play should be prominent in solitary species such as nocturnal strepsirhines as a means for mate assessment when male-female association is low. However, the agreement between my results and the results of Pellis & Iwaniuk (1999a) might be clearer with the inclusion of more strepsirhine species (but see below). Sexual play appears relatively common across extant taxa, and may have originated early in primate evolution, possibly as a means to practice adult sexual behaviour or to develop and maintain social bonds, or assess potential biological fitness. This parameter does not distinguish between juvenile "pseudo-sexual" play and adult courtship play, but remains a measure of sexual behavioural repertoire within play. In this way, Pellis & Iwaniuk's (1999a) argument for adult-adult play as courtship is better supported. However, it is unclear from the results presented here whether this pertains to nocturnal strepsirhines or not, given that the result is equivocal for *Nycticebus coucang*. Again, the inclusion of more solitary strepsirhine species within the reconstruction may help further elucidate this discrepancy.

The potential for inter-specific play also is likely to have arisen early in primate evolution, arguably to dispel or reduce competition for resources among neighbouring troops of different species, or to assess or display the potential fitness of or to potential prey species. Alternatively, it may be a non-adaptive side-effect of the propensity to play, given that it appears almost uniformly throughout the tree.

Vocalisation during play is typically rare, although has been reported predominantly among platyrrhines in the form of "play peeps" (*Saimiri*, Biben & Symmes 1986; *Saguinus oedipus*, Goedeking & Immelmann 1986). Indeed, the phylogenetic tree (Figure 3.16) supports this view indicating the emergence of play calls at the node for callitrichids and cebines; this is however, a relatively recent occurrence in terms of evolution. Play-chuckles and laughter are reported in the African apes and some baboons, and may have arisen independently in these clades. The reasons for this are unclear. Play vocalisations may have arisen as contact-calls, signalling to nearby adults that any apparent fight between juveniles is playful, or to demonstrate a continued desire to play (Burghardt, in press). Play in most primates and carnivores, is silent, presumably to avoid the risk of attracting the attention of predators whilst distracted by play (Burghardt, in press).

3.4.3 Carnivores: "continuous" variables

The phylogenetic reconstructions for carnivores also offer an interesting insight to the divergence and evolution of play behaviour (refer to Figures 3.5-3.8). Total play (i.e. all types) at the high frequency level appears to be the key ancestral condition for carnivores, persisting in mustelids and lutrines and permeating through ursids, canids, and felids. The otariids and phocids are demarked by a change in this condition to a reduced frequency of play and the medium-level (and low in *Haliochoerus*). The trend is unclear for some of the ursids, with *Ailuropoda* (giant pandas) and *Ursus americanus* having evolved from exceptionally playful ancestral stock, whilst other ursid species appear to have lost this trait. Arguably this occurred with the increasing onset of behavioural solitude, however, all bears are predominantly solitary. Interestingly, the phylogenetic trees show that *Canis* is less playful than reports from the literature appear, but the common ancestor of the Canidae is likely to have been very playful (high play frequency), which is demonstrated by the extant *Speothos* and *Cerdocyon*. At the node where canids and felids diverge, so too does the character for high play frequency, with medium levels branching off into the herpestids and hyaenids, and low frequencies within the felids. One exception is in the domestic cat with high levels of playfulness, although this may be due to domestication and the selection for neotenous traits (Hemmer 1990), which may include exceptionally high levels of playfulness, as well as the likelihood of constant (human) playmates.

Solitary play appears far more widespread and constant in its evolutionary distribution, persisting at low frequencies throughout the order. Exceptions are in *Phoca vitulina* and *Thalarctos maritimus* where solitary play occurs at high frequencies. Two explanations for this relationship are to combat the cold and to develop aquatic skills for hunting. Object play too, is very widespread among the Carnivora, but tends to persist at low levels throughout the clade. One exception is in the giant panda (*Ailuropoda melanoleuca*), which displays high frequencies of object play, presumably due to its highly solitary behaviour and extractive foraging in processing bamboo stalks for food (e.g. Sandell 1989). Social play persists at high levels throughout the clades of species with relatively large social group sizes, such as the mustelids and lutrines, and the canids and felids. Low levels have evolved in the branches leading to the pinniped and ursid clades and diverge to medium levels in the true bears. This adds further weight to the argument that social play evolved as a means for coping with living in social groups, and arguably for the social assessment of conspecifics.

3.5 Summary

Discrete play variables have been mapped onto a phylogenetic tree using the MacClade computer programme (Maddison & Maddison 1992). Primates and carnivores are dealt with separately. These trees depict changes in the character states of different play categories over time, and thus this type of analysis may help to elucidate the origins of play in each taxonomic order. The prevalence of play behaviour in extant species can be used to infer that play is a behaviour very likely to have been present at the origin of both primates and carnivores, and that solitary locomotor-rotational, object, and social play are likely to have been featured in the play of the common ancestor to all primates and carnivore clades. In primates, this is further supported by the exhibition of dyadic play in all major clades; polyadic play is however restricted to Old World monkey and ape clades. Adult play is common to all major primate clades, and is believed to be exhibited as parent-infant play interactions. Other forms of adult play do not appear to demonstrate an extensive evolutionary history, although sex play (e.g. mounting as opposed to play-fighting) is present in the common ancestor of haplorhines and may be indicative of courtship behaviour. Interspecific play occurs in all major clades and may act as a means for assessing other species in the environment. Play vocalisations show a relatively recent ancestry, being present in the common ancestor of callitrichids and *Cebus*, and having evolved independently in the African apes.

The following chapters (4-7) will focus upon these evolutionary relationships in more detail, with regard to intra-specific relationships, life-history, socio-ecology, and neurobiology.

Chapter 4:

Intra-specific Play

4.1 Introduction

Further chapters will deal with evolutionary relationships between play and life-history, socio-ecology, and brain structures, focusing on between-species analyses of primates and carnivores. Play is a behaviour that is subject to much variability (Bekoff & Byers 1998), and as such it is important to understand the variance of play within species, and the factors that may influence this variance. Thus we need to establish whether differences in species means are likely to represent true species differences or simply error variance. One way to do this is to assess the amount of variance within species versus the amount of variance between species. In addition, it may be possible to correlate play and socio-ecological variables at the intraspecific level providing tests of hypotheses about influences and constraints. In terms of age-related intra-specific trends, developmental trajectories in play behaviour are of relevance to hypotheses concerning the functions of play, particularly in the context of behavioural development. Finally, study duration may influence numbers of play types recorded, and an analysis of this methodological influence is important in aiding interpretation of data.

A defining character of any given species is that it differs from every other in one or more ways. Some of the key factors involve social groupings, habitat, and feeding ecology (e.g. Oates 1987). These aspects will be dealt with comparatively elsewhere in this thesis (see especially Chapter 6). Due to lack of available data on the specifics of feeding ecology at an individual population level, for which there is also available play data, it is not possible to deal with play and intra-specific feeding ecology statistically in this chapter. This chapter does however focus on the intraspecific variance in the play behaviour of the following species: chimpanzees (*Pan* *troglodytes*), red colobus monkeys (*Colobus badius*), olive baboons (*Papio anubis*), and Japanese macaques (*Macaca fuscata*). Developmental trajectory data for play over the juvenile period are presented for a greater number of species: mantled howler monkeys (*Alouatta palliata*), vervet monkeys (*Cercopithecus aethiops*), gorillas, stump-tailed macaques (*Macaca arctoides*), Japanese macaques, rhesus macaques, chimpanzees, olive baboons, yellow baboons (*Papio cynocephalus*), hamadryas baboons (*Papio hamadryas*), and saddleback tamarins (*Saguinus fuscicollis).* Unfortunately, there are insufficient replicates of carnivore species data to permit statistical analyses of intraspecific variables, and thus this chapter deals only with primates.

4.2 Methods

One enduring problem in analysing intra-specific (as opposed to inter-specific) play is a general lack of suitable data. It is true that there are problems in the existing mammalian play literature with a disappointing lack of quantitative data. Although qualitative data are undoubtedly useful to the general play literature, it requires the support of quantitative data to effectively bridge gaps in our "play knowledge". In too many cases, play, and its subsequent categories, are not distinctly recognised, sufficiently detailed or described, or fully incorporated into the literature (Burghardt 2001). Much of the ethological literature that specifies behavioural content does not detail the amounts of time devoted to it, either in time budget or frequency data, or indeed length of study. Thus here, to avoid such entanglements, time budgets of play have been incorporated, as is the case for other chapters in this thesis.

The data presented in this chapter derive directly from each field study on a particular group of a given species: hence intra-specific analyses of species replicates. This includes group composition in terms of age and sex of the conspecifics described in each study, research effort in terms of how long a particular study lasted, and environmental particulars, such as space per individual. The "space per individual" category is calculated by taking the enclosure space measurements as detailed in each paper from the literature, and dividing it by the number of individuals in each group, as detailed below.

E.g. $\frac{(38 \times 38)}{83} = 17.40$ m per individual

(Ehardt & Bernstein 1987)

All data in this chapter were analysed using standard statistics in the StatView (version 4.0) statistical programme. The data on developmental trajectories are taken from the literature and plotted using bivariate analyses in the StatView programme. Regression graphs are given for significant results only, unless otherwise stated.

4.3 Hypotheses

The following hypotheses are presented for play in primates with regard to intra-specific variation. The null hypothesis, H_0, states that there will be no association between play behaviour and the variable in question. Below, alternative hypotheses, H_a, are proffered.

1. The relationship between study length and the play behaviours observed (and reported) will be asymptotic.

As a study progresses in length it is likely that the number of different behaviours recorded will also increase. However, after a sufficient duration, all likely behaviours will have been observed, and thus if the study persists beyond such a time, no new behaviours will be recorded. Thus this relationship is likely to be an asymptotic one. Using these data also enables the ensuing analyses to be controlled for research effort.

2. Groups with more infants and juveniles present will be those that exhibit higher play frequencies.

As play in adults is far less common than play in juveniles (Hall 1998), it is predicted that groups with the greatest proportion of conspecifics of playing age (i.e. infants and juveniles) will be those observed to engage in the most play.

3. Play should differ between males and females

Play, like sex and aggression, is a sex-differentiated form of behaviour (Hines 1982), thus we should expect to see differences between the amounts of play exhibited by males and females. This is an observation that pervades the existing literature for several species (e.g. Biben 1986; Eaton et al. 1986; Brown 1988). One reason for sex-differences in play derives from the fact that males tend to reach sexual maturity later than females, and thus in effect have a longer period during which to prepare for adult skills. It is also likely that these sex-differences in play occur partly due to hormonal influences (Hines 1982; Hines & Shipley 1984), which in turn dictate sex-specific behaviour (Collaer & Hines 1995). Thus, male and female behaviour show distinct differences in adulthood; therefore play may assist these changes in being sex-differential itself. Play in species that rely heavily on intraspecific fighting in adulthood, might therefore be based on male-male rough-and-tumble play during the juvenile period. Thus it is predicted that polygynous species will show relatively higher levels of rough-and-tumble play behaviour in males during the juvenile period as a means of preparation for adult life. This might also explain the tendencies of some species for female allo-mothering play (Lancaster 1971). It is expected that species in larger groups will express a preference for partners of a similar age and sex, and that older individuals will play far less than infants or juveniles (Fagen 1981). Similarly, play complexity, or range of play behaviours should be greater in species that exhibit a greater degree of polygyny (Byers 1984).

4. Groups with more juvenile males present will be those that exhibit higher play frequencies.

Infant and juvenile males are frequently reported to be most playful demographic (e.g. Meaney et al. 1985; Biben 1986; Eaton et al. 1986; Brown 1988; Fedigan 1993;

Collaer & Hines 1995; Pruetz & Bloomsmith 1995), and thus it is predicted that the more juvenile males in a group, the more play will be observed.

5. Groups housed in relatively large enclosures will be the most playful.

As play is susceptible to environmental effects, and especially to the effects of confinement (Fagen 1981), it is predicted that species groups housed in enclosures that offer the most space per individual will exhibit greater amounts of play than groups housed with less space.

4.4 Data

Table 4.1 details the species incorporated into the intra-specific analyses, research effort in observation hours and in length of study in months (as specified in each source), the number of different play behaviours observed in each study pertaining to that species, the time-budget percentages for total, solitary locomotor, object, and social play behaviour as detailed in each source (or derived from each source [see Chapter 2]), actual group size (the number of individuals within each study group, as opposed to species mean group size used in other chapters), and source information.

Analysis of variance (ANOVA) of each species and total play, number of play behaviours, and actual group size, show that species differ significantly in play, but not in length of study, thus differences are not confounded by methodology. This accounts for within species variability, and thus it can be concluded that species differences shown in the comparative analyses of subsequent chapters in this thesis are meaningful.

Table 4.1. Intra-specific data for play and research effort in primates

Species	Source	No. of observation hours	Length of study (mo)	No. of play behaviours	Total play %	Solitary play %	Object play %	Social play %	Actual group size	Space per individual (m)
Colobus badius	Struhsaker 1975	-	-	-	2.6	-	-	-	-	-
	Struhsaker 1975	-	-	-	2.7	-	-	-	-	-
	Struhsaker 1975	-	-	-	4.2	-	-	-	-	-
	Marsh 1978	-	-	-	2.6	-	-	-	-	-
	Marsh 1981	-	14.0	-	3.4	-	-	-	-	-
	Clutton-Brock 1974	-	2.0	5	3.3	-	-	-	64	-
	Clutton-Brock 1974	-	14.0	5	4.0	-	-	-	82	-
	Clutton-Brock 1974	-	2.0	5	1.0	-	-	-	58	-
Macaca fuscata	Rostal & Eaton 1983	-	-	-	10.2	-	-	-	316	51.00
	Hayaki 1983	-	-	-	-	-	-	-	100	-
	Eaton et al. 1986	-	10.0	10	23.5	-	-	23.5	304	106.0
	Glick et al. 1986a	-	16.0	-	-	-	-	-	274	58.80
	Glick et al. 1986b	-	16.0	2	21.28	-	-	21.28	314	51.30
Pan troglodytes	Bloomsmith et al. 1994	792.0	60.0	-	18.96	12.34	-	6.63	-	23.05
	Bloomsmith 1989	225.0	7.0	-	11.08	-	-	11.08	-	-
	Horvat & Kraemer 1981	1443.5	36.0	-	32.61	-	-	-	23	-
	Kraemer 1979	18.5	-	24	4.1	0.51	0.22	3.59	6	-
	Lewis 2000	-	2.5	-	18.94	22.1	11.2	21.5	12	-
	Pruetz & Bloomsmith 1995	311.0	10.0	-	3.73	-	-	-	29	28.47

Species	Source	No. of observation hours	Length of study (mo)	No. of play behaviours	Total play %	Solitary play %	Object play %	Social play %	Actual group size	Space per individual (m)
Papio anubis	Merrick 1977	-	11.0	17	6.94	-	-	-	7	-
	Mendoza-Granados & Sommer 1995	44.0	4.0	14	19.0	4.99	6.14	14.2	25	400.00
	King et al. 1980	40.0	15.0	7	13.19	7.88	-	5.31	7	-
	Kraemer et al. 1982	-	-	-	7.68	-	-	7.68	-	-
	Tomasello et al. 1989	-	-	-	-	-	-	-	7	35.75
	Tomasello et al. 1990	-	-	-	-	-	-	-	15	48.00
	Owens 1975a	-	16.0	12	5.93	-	-	-	65	-
	Owens 1975b	-	16.0	12	-	-	-	-	65	-
	Rose 1977a	140.0	1.0	21	3.10	-	-	-	65	-
	Chalmers 1980	231.0	6.0	30	7.5	-	-	-	71	-

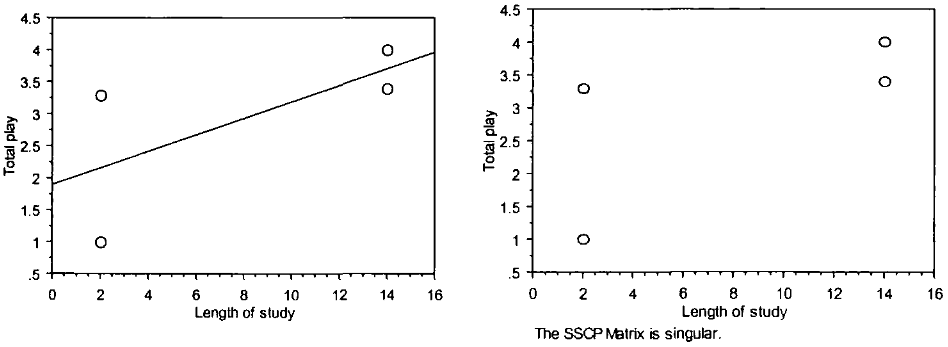
Table 4.2 ANOVA table for within-species differences in total play, actual group size, length of study and number of different play behaviours.

	DF	Sum of squares	Mean	F-value	P-value	Lambda	Power
Total play							
Species	3	552.11	184.04	14.3	0.002	42.90	0.99
Residual	7	90.09	12.87				
Actual group size							
Species	3	12143.55	40476.18	511.46	<0.0001	1534.37	1.0
Residual	7	554.0	79.14				
Length of study							
Species	3	86.97	28.99	0.84	0.52	2.51	0.15
Residual	7	242.67	34.67				
Number of behaviours							
Species	3	461.88	153.96	4.37	0.05	13.11	0.62
Residual	7	246.67	35.24				

4.5 Results

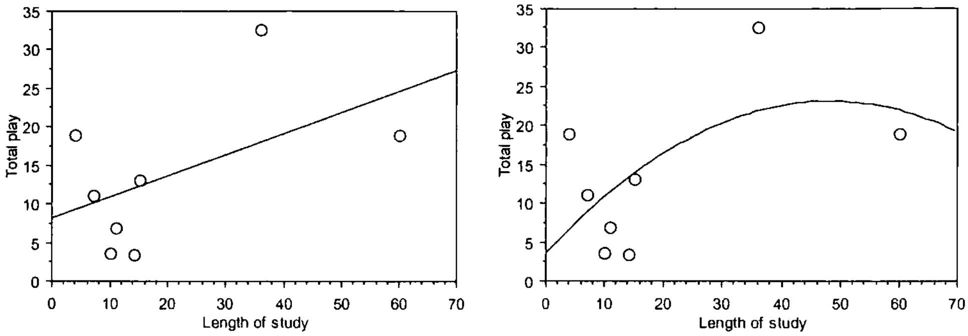
4.5.1 Fitting the data

Figures 4.1-4.8 show scatter plots of play time budgets on length of study in the species dealt with in this chapter. Graphs on the left detail linear scatter plots, whereas graphs on the right detail the relationship fitted to a second-order polynomial regression, as the relationship is unlikely to be linear. The graphs show that a linear fit is poor, and that based on r^2, a second-order polynomial provides a better fit to the data.



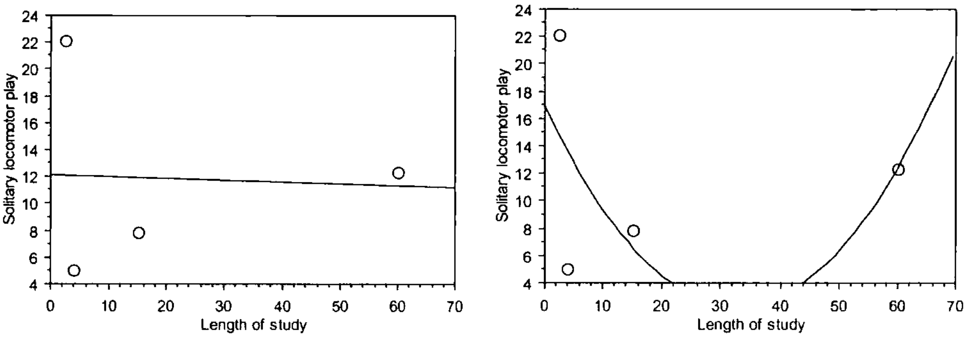
Figs. 4.1 & 4.2 Linear regression and 2^{nd} order polynomial regression plots of total play on length of study in months in *Colobus badius*

(Linear: F (1,3) = 1.70, p = 0.32, co-efficient = 0.13, r^2 = 0.46; 2^{nd} order polynomial: The SCCP matrix is singular).



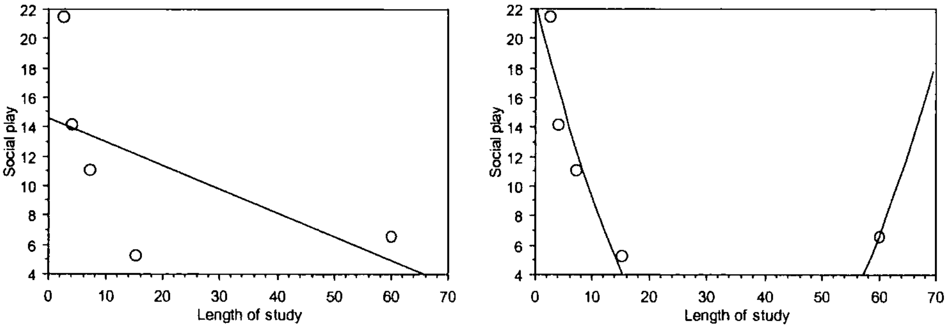
Figs. 4.3 & 4.4. Linear regression and 2nd order polynomial regression plots of total play on length of study in months in *Pan troglodytes*

(Linear: F (1, 7) = 1.51, p = 0.27, co-efficient = 0.20, r2 = 0.20. 2nd order polynomial: F (2, 6) = 0.75, p = 0.25, co-efficient = 0.81, r2 = 0.33)



Figs. 4.5 & 4.6 Linear regression and 2nd order polynomial regression plots of solitary locomotor play on length of study in months in *Pan troglodytes*

(Linear: F (1, 3) = 0.005, p = 0.95, co-efficient = -0.01, r2 = 0.002. 2nd order polynomial: F (2, 1) = 0.15, p = 0.87, co-efficient = 0.89, r2 = 0.23).



Figs. 4.7 & 4.8 Linear regression and 2nd order polynomial regression plots of social play on length of study in months in *Pan troglodytes*

(Linear: F (1, 3) = 1.65, p = 2.90, co-efficient = -0.16, r2 = 0.35. 2nd order polynomial: F (2, 2) = 8.65, p = 0.10, co-efficient = -1.51, r2 = 0.90).

4.5.2 Length of study and play category

The following analyses use polynomial regression to test for a relationship between the length of a field study and the number of behaviours seen within the play repertoire of that species. I have used a second-order polynomial regression, as the hypotheses predict that the relationship will be asymptotic. As a study progresses in length, it is expected that more behaviours will be seen, until such a time as all likely behaviours are observed.

4.5.2.i Number of play behaviours

4.5.2.ia *Colobus badius*

Using second-order polynomial regression, there is a positive and significant relationship between the length of a field study (mo) and the number of different individual play behaviours seen within the play repertoire of red colobus monkeys (F (2, 4) = 6.88, p = 0.04, co-efficient = 3.91, $r^2 = 0.73$) (Figure 4.9). Compare this with a linear regression analysis, which reveals a positive correlation, but a non-significant one (F (1, 5) = 2.34, p = 0.18, co-efficient = 3.56, $r^2 = 0.28$), demonstrating that second-order polynomial regression offers a better fit than linear regression.

4.5.2.ib *Macaca fuscata*

Using second-order polynomial regression, there is a positive, but non-significant relationship between the length of a field study (mo) and the number of different individual play behaviours seen within the play repertoire in Japanese macaques (F (2, 2) = 2.55, p = 0.41, co-efficient = 32.91, $r^2 = 0.84$). Linear regression analysis also reveals a positive but non-significant correlation (F (1, 2) = 0.04, p = 0.86, co-efficient = 4.16, $r^2 = 0.02$).

4.5.2.ic *Pan troglodytes*

Using second-order polynomial regression, there is a slightly negative, but non-significant relationship between the length of a field study (mo) and the number of different individual play behaviours seen within the play repertoire in chimpanzees (F (2, 2) = 0.43, p = 0.69, co-efficient = 21.49, r^2 = 0.30). Linear regression analysis also reveals a negative but non-significant correlation (F (1, 3) = 1.18, p = 0.36, co-efficient = 20.07, r^2 = 0.28).

7.5.2.id *Papio anubis*

Using second-order polynomial regression, there is a slightly negative, but non-significant relationship between the length of a field study (mo) and the number of different individual play behaviours seen within the play repertoire in olive baboons (F (2, 2) = 0.30, p = 0.77, co-efficient = 21.82, r^2 = 0.23). Linear regression analysis also reveals a negative but not significant correlation (F (1, 3) = 0.89, p = 0.41, co-efficient = 21.65, r^2 = 0.23).

4.5.2.ii Play categories (play time budgets)

4.5.2.iia *Colobus badius*

Table 4.3 shows regression analyses for research effort in months against each play category in red colobus monkeys. There were too few entries for solitary play and object play to permit statistical intra-specific analyses. Linear regression analyses show that total play and social play are positively, but not significantly, correlated with research effort in months. Second-order polynomial regression analyses show that total play is positively but not significantly correlated with research effort in months, with an increase in total play reported after 5 months. Social play is significantly correlated with research effort in months, with a decline in social play reported by 13 months (Figure 4.10).

Table 4.3 Regression analyses of research effort in months and play categories in red colobus monkeys

Analysis	Play category	DF	F-value	p-value	co-efficient	r^2
Regression	Total	1, 6	0.28	0.61	0.02	0.05
2nd order polynomial	Total	2, 5	1.30	0.35	-0.02	0.34
	Social	**2,**	**5.88**	**0.04**	**0.57**	**0.70**

4.5.2.iib *Macaca fuscata*

Table 4.4 shows regression analyses for research effort in months against each play category in Japanese macaques. There were too few entries for all types of play except total play to permit statistical intra-specific analyses. Linear regression analyses show that total play is positively, but not significantly, correlated with research effort in months. Second-order polynomial regression analyses show a positive correlation with total play percentage seen declining after 12 months of study (Figure 4.11).

Table 4.4 Regression analyses of research effort in months and play types in Japanese macaques

Analysis	Play type	DF	F-value	p-value	co-efficient	r^2
Regression	Total	1, 2	0.96	0.50	0.99	0.49
2nd order polynomial	Total	2, 0	-	-	9.24	1.0

4.5.2.iic *Pan troglodytes*

Table 4.5 shows regression analyses for research effort in months against each play category in chimpanzees. Linear regression analyses show that total play is positively, but not significantly, correlated with research effort in months. Linear regression analyses reveal that solitary locomotor play and social play are negatively, but not significantly correlated with research effort in months. Second-order polynomial regression analyses show that total play is positively but not significantly correlated with research effort in months. Solitary locomotor play and social play is negatively, but not significantly, correlated with research effort in months. There were too few observations of object play to permit statistical analyses of intra-specific variables.

Table 4.5 Regression analyses of research effort in months and play types in chimpanzees

Analysis	Play type	DF	F-value	p-value	co-efficient	r^2
Regression	Total	1, 6	1.51	0.27	0.20	0.20
	Solitary	1, 2	0.005	0.95	-0.01	0.002
	Social	1, 3	1.65	0.28	-0.16	0.36
2nd order polynomial	Total	2, 5	0.75	0.52	0.53	0.23
	Solitary	2, 1	0.15	0.87	0.89	0.23
	Social	2, 2	8.65	0.10	-1.51	0.89

4.5.2.iid *Papio anubis*

Table 4.6 shows regression analyses for research effort in months against play types in olive baboons. There were too few entries for all types of play except total play to permit statistical intra-specific analyses. Linear regression analyses show that total play is positively, but not significantly, correlated with research effort in months. Second-order polynomial regression analyses show that total play is positively and significantly correlated with research effort in months (Figure 4.12).

Table 4.6 Regression analyses of research effort in months and play types in olive baboons

Analysis	Play type	DF	F-value	p-value	co-efficient	r^2
Regression	Total	1, 2	0.30	0.68	0.14	0.23
2nd order polynomial	Total	**2, 0**	-	-	**1.36**	**1.0**

4.5.3 Group size

The following analyses show intra-specific variation in all play types with actual group size (actual number of animals in the study group as detailed in the literature for each study), controlling for the effect of research effort in months.

4.5.3a *Colobus badius*

Table 4.7 shows partial correlation analyses for actual group size against each play category in red colobus monkeys, controlling for the effect of research effort in months. There were too few entries for solitary locomotor and object play to permit statistical intra-specific analyses. Partial correlation analyses show that total play is positively, but not significantly, correlated with actual group size. Social play is positively and significantly correlated with actual group size even after controlling for the effect of research effort (Figure 4.13). These findings correspond with the inter-specific independent contrasts analyses detailed in Chapter 6.

Table 4.7. Partial correlation analyses of play category, research effort (mo) and actual group size in red colobus monkeys

Play category	**DF**	**F-value**	**p-value**	**co-efficient**	**r^2**
Total	1, 3	0.22	0.68	0.008	0.1
Social	**1, 3**	**127.30**	**0.007**	**0.13**	**0.99**

4.5.3b *Macaca fuscata*

Table 4.8 shows partial correlation analyses for actual group size against play types in Japanese macaques, controlling for the effect of research effort in months. Partial correlation analyses show that total play is positively but not significantly, correlated with actual group size. There were too few observations of solitary locomotor, object, and social play to permit intra-specific statistical results.

Table 4.8. Partial correlation analyses of play type, research effort (mo) and actual group size in Japanese macaques

Play type	**DF**	**F-value**	**p-value**	**co-efficient**	**r^2**
Total	1, 4	3.80	0.12	0.17	0.49

4.5.3c *Papio anubis*

Table 4.9 shows partial correlation analyses for actual group size against play types in olive baboons, controlling for the effect of research effort in months. Partial correlation analyses show that total play is positively correlated with actual group size (Figure 4.14). This result is difficult to statistically quantify, given the small sample size. There were too few observations of solitary locomotor, object, and social play to permit intra-specific statistical analyses.

Table 4.9. Partial correlation analyses of play type, research effort (mo) and actual group size in olive baboons

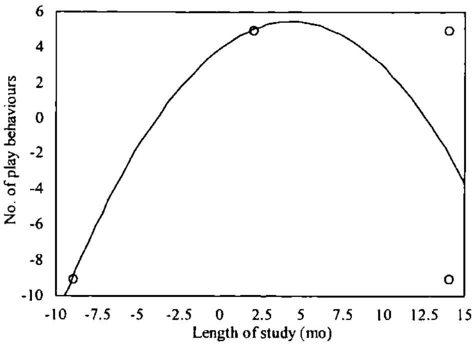
Play type	DF	F-value	p-value	co-efficient	r^2
Total	1, 2	-	-	0.58	1.0

4.5.4 Age class

Conducting intra-specific analyses on age class variations in play is problematic as there are few studies within the database that represent species replicates. Here, data for Japanese macaques and chimpanzees are presented. There is typically a scarcity of data in the literature that detail play rates for separate age classes, as most studies of play deal only with infants and/or juveniles. However, individually, most studies report decreasing amounts of play with increasing age (e.g. Fairbanks 2000).

4.5.4a *Macaca fuscata*

Table 4.10 details regression analyses for age class and play category in Japanese macaques. There were too few replicate matches to permit intra-specific analysis on solitary, object, and social play. Similarly, insufficient data exist to conduct analysis on any age class other than juveniles. Total play is positively, but not significantly correlated with the number of juveniles in a group. The amount of total play performed by juveniles (juvenile play) is positively, but not significantly correlated with the number of juveniles in a group. When actual group size is controlled for, juvenile play is negatively, but not significantly, correlated with the number of juveniles in the group.



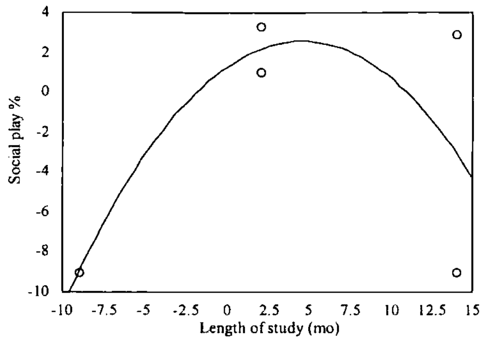
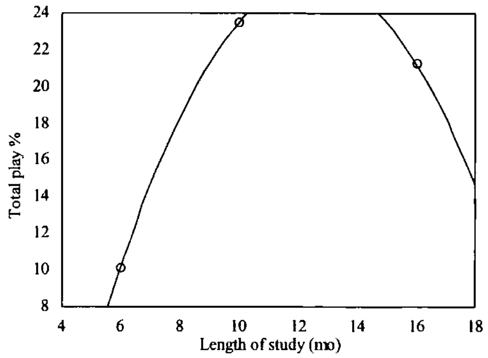


Fig. 4.9 Second-order polynomial regression of research effort in months on number of play behaviours in *Colobus badius*

Fig. 4.10 Second-order polynomial regression of research effort in months on social play in *Colobus badius*



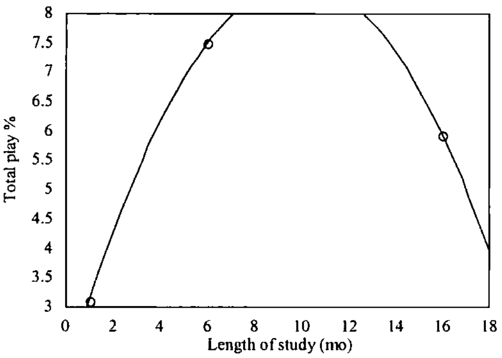
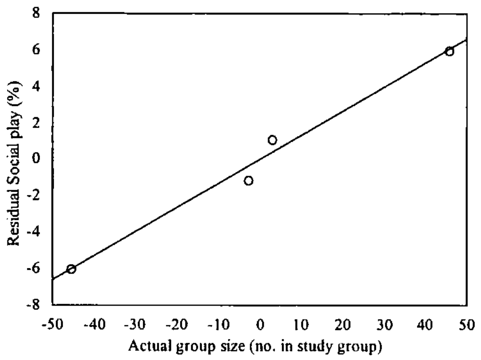


Fig. 4.11 Second-order polynomial regression of research effort in months on total play in *Macaca fuscata*

Fig. 4.12 Second-order polynomial regression of research effort in months on total play in *Papio anubis*



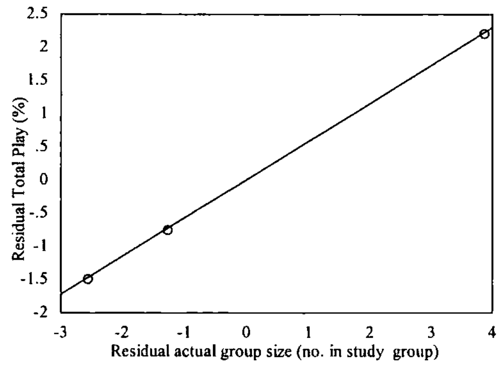


Fig. 4.13 Partial regression of social play on actual group size (no. in study group) in *Colobus badius*

Fig. 4.14 Partial regression of social play on actual group size (no. in study) in *Papio anubis*

Table 4.10. Regression and partial correlation analyses of play type and age class in Japanese macaques

Age class (No. in group)	**Play type**	**DF**	**F-value**	**p-value**	**co-efficient**	**r^2**
Juveniles	Total	1, 2	1.20	0.47	0.12	0.55
	Juvenile	1, 1	1.17	0.47	0.12	0.55
	~ Juvenile	1, 1	0.83	0.52	-18.39	0.45

~ controlled for actual group size

4.5.4b *Pan troglodytes*

Chimpanzees were the only species to yield sufficient data replicates for intra-specific analyses on age class with play variables. The number of adults in a species' group is positively, but not significantly, correlated with the amount of total play, solitary locomotor, object or social play exhibited by the group as a whole. In controlling for actual group size, the number of adults in a group is positively, but not significantly correlated with the amount of play exhibited by adults, expressed as a time budget. In controlling for the number of infants in the group, adult play is positively, but not significantly correlated with the amount of play expressed by adults; the degree of correlation however, is somewhat reduced, suggesting that infant number is but one factor driving adult play.

The number of juveniles in a group is positively but not significantly correlated with total play, and negatively but not significantly correlated with solitary locomotor play. There were too few matches of object play, and social play with number of juveniles to conduct intra-specific analyses. Interestingly, the number of juveniles in a group appears to correlate negatively, although not significantly, with the amount of play exhibited by juveniles. In controlling for actual group size, there is still a negative, although non-significant correlation between juvenile number and juvenile play. There were too few observations to control for infant number. In controlling for adult number there is a negative but non-significant correlation between number of juveniles and juvenile play.

The number of infants in a group is negatively but not significantly correlated with the amount of total and social play exhibited by the group. There were too few observations of solitary locomotor play to permit intra-specific analyses. Object play was positively, but not significantly, correlated with infant number. Infant number was negatively but not significantly correlated with the amount of infant play observed, and this effect holds when adult number was controlled for. In controlling for actual group size, infant number was positively but not significantly correlated with the amount of infant play observed.

Table 4.11 Regression and partial correlation analyses of play type and age class in chimpanzees

Age class (No. in group)	Play type	DF	F-value	p-value	co-efficient	r²
Adult	Total	1, 4	0.17	0.69	0.76	0.04
	Solitary	1, 2	0.02	0.89	0.34	0.01
	Object	1, 2	2.10	0.28	2.35	0.51
	Social	1, 2	1.38	0.36	1.78	0.41
	~Adult	1, 3	5.31	0.10	0.11	0.63
	#Adult	1, 3	0.44	0.55	0.06	0.13
Juveniles	Total	1, 3	0.04	0.86	0.01	0.01
	Solitary	1, 2	0.03	0.88	-0.15	0.03
	Object+	-	-	-	-	-
	Juvenile	1, 3	1.01	0.39	-0.94	0.25 ~
	Juvenile	1, 3	0.22	0.67	-0.51	0.07
	# Juvenile+	-	-	-	-	-
	¬ Juvenile	1, 2	0.26	0.69	-93.03	0.21
Infant	Total	1, 5	0.19	0.68	-0.49	0.04
	Solitary+	-	-	-	-	-
	Object	1, 3	3.44	0.16	0.83	0.53
	Social	1, 2	0.25	0.70	-3.65	0.20
	Infant	1, 2	0.004	0.96	-0.74	0.002
	~Infant	1, 2	0.003	0.96	1.07	0.002
	¬ Infants	1, 2	0.10	0.78	-4.96	0.05

+ Too few observations; ~ controlled for actual group size; # controlled for no. of infants; ¬ controlled for number of adults

4.5.5 Sex class

4.5.5a *Macaca fuscata*

Table 4.12 below shows regression analyses of sex parameters on play category in Japanese macaques. There were insufficient data to conduct intra-specific analyses for solitary, object, and social play behaviour. The amount of play performed by males (male total play) was the only play type to show a significant correlation, when controlled for actual group size; thus male total play was negatively and significantly correlated with the number of males in a group (Figure 4.15), although the sample size is very small. Attempts to split the sex parameters into age classes were only possible for juvenile males, and no significant correlations were observed.

Table 4.12. Regression and partial correlation analyses for age and sex parameters in Japanese macaques.

Sex Parameter	**Play type**	**DF**	**F-value**	**p-value**	**co-efficient**	**r^2**
No. males	Total	1, 2	0.53	0.60	0.06	0.35
	~Total	1, 2	0.82	0.53	-0.35	0.45
	Male play	1, 1	0.07	0.84	-0.03	0.06
	~Male play	1, 1	437.23	**0.03**	**-0.60**	**0.99**
No. females	Total	1, 2	0.79	0.54	0.05	0.44
	~Total	1, 2	0.82	0.53	-0.44	0.45
	Female play+	-	-	-	-	-
Split by age class:						
No. males	Total	1, 2	0.84	0.45	0.36	0.30
(juvenile)	~ Total	1, 2	0.22	0.68	0.22	0.10
	Male play	1, 2	0.11	0.78	0.15	0.05
	~ Male play	1, 2	3.44	0.98	-0.009	1.72
	Juvenile play	1, 2	0.88	0.52	0.19	0.47
	~ Juvenile play	1, 2	0.88	0.50	0.19	0.48

+ Too few observations; ~ controlled for actual group size

4.5.5b *Pan troglodytes*

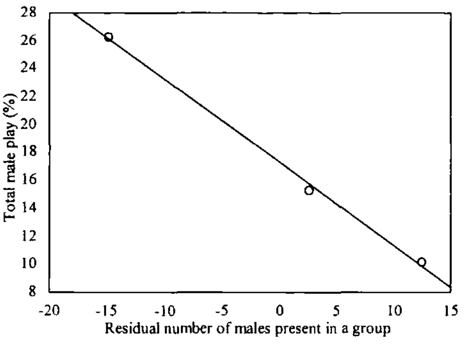
Table 4.13 shows regression analyses of sex parameter on each play category in chimpanzees. Raw regressions are shown alongside those that have been controlled for group size. The number of males in a group is positively, but not significantly correlated with all play types in chimpanzees. This trend does not appear quite so uniform when based on the number of females in a group, however none of the correlations are statistically significant. When these analyses are split by age class, only the number of adult females in a group is significantly correlated with solitary play when controlled for group size; the relationship is a negative one (Figure 4.16).

Table 4.13. Regression and partial correlation analyses for play type and sex parameters in chimpanzees.

Sex Parameter	Play type	DF	F-value	p-value	co-efficient	r^2
No. males	Total	1, 3	4.83	0.12	2.22	0.62
	~Total	1, 3	0.37	0.59	1.56	0.11
	Solitary	1, 2	0.75	0.48	1.85	0.27
	~Solitary	1, 2	3.66	0.19	4.52	0.65
	Object	1, 2	3.72	0.30	2.11	0.79
	~Object	1, 2	7.09	0.23	3.33	0.88
No. males	Social	1, 2	9.10	0.09	2.86	0.82
	~ Social	1, 2	3.35	0.21	3.97	0.63
	Male play	1, 2	0.61	0.58	0.51	0.38
	~Male play	1, 2	81.59	0.07	1.17	0.99
No. females	Total	1, 3	2.04	0.25	0.70	0.40
	~ Total	1, 3	0.37	0.57	-1.56	0.11
	Solitary	1, 2	0.06	0.83	-0.24	0.03
	~ Solitary	1, 2	3.66	0.19	-4.52	0.65
	Object	1, 2	0.03	0.89	0.11	0.03
	~Object	1, 2	7.09	0.23	-3.33	0.88
	Social	1, 3	0.26	0.65	0.21	0.08
	~Social	1, 3	5.47	0.10	-4.05	0.65
	Female play	1, 2	0.03	0.89	0.02	0.03
	~Female play	1, 2	4.58	0.27	-0.38	0.82
Split by age class:						
No. males	Total	1, 4	0.01	0.92	-0.09	0.003
(adult)	~ Total	1, 4	1.36	0.30	1.23	0.25
	Solitary	1, 2	0.78	0.47	3.82	0.28
	~Solitary	1, 2	0.78	0.47	3.84	0.28
	Object	1, 2	0.27	0.69	2.53	0.21
	~Object	1, 2	7.09	0.23	6.92	0.88
	Social	1, 3	0.08	0.79	0.30	0.03
	~Social	1, 3	2.07	0.25	1.80	0.41
	Adult play	1, 2	2.78	0.34	0.49	0.74
	~ Adult play	1, 2	0.12	0.78	0.24	0.11
	Male play	1, 2	1.52	0.34	-0.52	0.43
	~Male play	1, 2	0.08	0.79	-0.26	0.04
No. females	Total	1, 4	1.37	0.31	2.07	0.26
(adult)	~Total	1, 4	0.96	0.38	-3.81	0.19
	Solitary	1, 2	0.03	0.87	-0.41	0.02
	~Solitary	**1, 2**	**5559.89**	**0.0002**	**-22.55**	**1.0**
	Object	1, 2	0.04	0.87	0.34	0.04
	~Object	1, 2	7.09	0.22	-10.18	0.88
	Social	1, 2	0.38	0.60	1.16	0.16
	~Social	1, 2	4.23	0.17	-16.58	0.68
	Adult play	1, 2	32.45	0.11	1.50	0.97
	~Adult play	1, 2	0.12	0.78	3.18	0.11
	Female play	1, 2	0.11	0.79	0.08	0.10
	~Female play	1, 2	4.58	0.27	2.07	0.82

Sex Parameter	**Play type**	**DF**	**F-value**	**p-value**	**co-efficient**	**r^2**
No. males (juveniles)	Total	1, 2	3.66	0.19	-0.61	0.65
	~Total	1, 2	2.85	0.23	-1.51	0.59
	Solitary	1, 2	0.003	0.97	0.12	0.003
	~Solitary	1, 2	9.93	0.19	-8.53	0.91
	Object+	-	-	-	-	-
	Social	1, 2	1.51	0.34	-0.79	0.43
	~Social	1, 2	0.07	0.82	-0.56	0.03
	Juvenile play	1, 2	24.82	0.13	-4.32	0.96
	~Juvenile play	1, 2	0.24	0.71	-7.64	0.19
	Male play	1, 3	1.22	0.35	0.46	0.29
	~Male play	1, 3	0.43	0.56	0.74	0.13
No. females (juveniles)	Total	1, 4	4.18	0.11	0.54	0.51
	~Total	1, 4	5.47	0.07	0.79	0.58
	Solitary	1, 2	0.06	0.85	-0.31	0.05
	~Solitary	1, 2	9.93	0.19	-2.46	0.91
	Object+	-	-	-	-	-
	Social	1, 2	7.20	0.23	-1.08	0.88
	~Social	1, 2	1.60	0.43	-1.75	0.62
	Juvenile play	1, 2	121.35	0.06	-2.59	0.99
	~Juvenile play	1, 2	1.60	0.42	-1.75	0.62
	Female play	1, 2	11.80	0.18	0.35	0.92
	~Female play	1, 2	0.07	0.83	0.18	0.07
No males (infants)	Total	1, 2	1.74	0.32	9.74	0.47
	~Total	1, 2	0.05	0.84	8.97	0.03
	Solitary	1, 2	0.66	0.56	-10.00	0.40
	~Solitary	1, 2	5.31	0.26	-54.10	0.84
	Object+	-	-	-	-	-
	Social	1, 2	0.003	0.96	0.79	0.003
	~Social	1, 2	8.58	0.21	-49.40	0.90
	Infant play	1, 2	1.01	0.50	-27.60	0.50
	~Infant play	1, 2	3.11	0.33	-125.68	0.76
	Male play	1, 2	0.16	0.76	-1.54	0.14
	~Male play	1, 2	81.59	0.07	-15.22	0.99
No. females (infants)	Total	1, 2	3.15	0.22	8.95	0.61
	~Total	1, 2	1.24	0.38	7.27	0.38
	Solitary+	-	-	-	-	-
	Object+	-	-	-	-	-
	Social+	-	-	-	-	-
	Infant play	1, 2	5.12	0.26	15.86	0.84
	Female play+	-	-	-	-	-

+ Too few observations; ~ controlled for actual group size



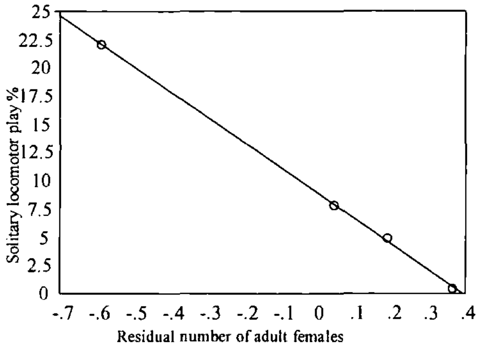


Fig. 4.15 Partial correlation of total male play, group size, and number of males in a group in *Macaca fuscata*

Fig. 4.16 Partial correlation of solitary play, actual group size, and number of adult females in *Pan troglodytes*

4.5.6 Space per individual

The following analyses attempt to identify the effect that captive space may have on the exhibition of play within species.

4.5.6a *Macaca fuscata*

Table 4.14 shows regression analyses of total play on space per individual in captive Japanese macaques. There were too few data to conduct intra-specific analyses on solitary, object, and social play. Total play is positively but not significantly correlated with increasing space in Japanese macaques. In controlling for group size a similar result is observed.

Table 4.14. Regression and partial correlation analyses of total play on space per individual in Japanese macaques

Play type	DF	F-value	p-value	co-efficient	r^2
Total	1, 2	0.45	0.57	0.24	0.18
~Total	1, 2	0.61	0.52	0.27	0.23

~ controlled for actual group size

4.5.6b *Pan troglodytes*

Table 4.15 shows regression analyses of total play on space per individual in captive chimpanzees. There were too few data to conduct intra-specific analyses on solitary, object, and social play. Total play is positively but not significantly correlated with increasing space in chimpanzees. In controlling for group size a similar result is observed.

Table 4.15 Regression and partial correlation analyses of total play on space per individual in chimpanzees

Play type	DF	F-value	p-value	co-efficient	r^2
Total	1, 3	1.16	0.36	0.05	0.28
~Total	1, 3	2.18	0.24	0.06	0.42

~ controlled for actual group size

4.5.7 Developmental trajectory

The following graphs (Figures 4.17-4.27) plot the developmental trajectory of play across the juvenile period in a number of different species.

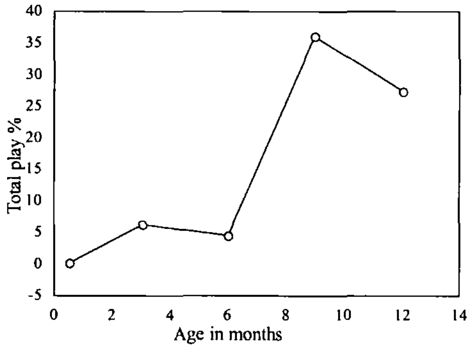


Fig. 4.17 ***Alouatta palliata***

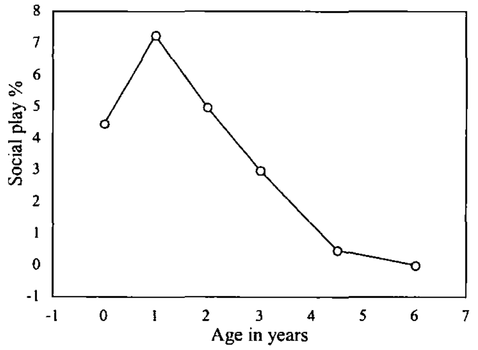


Fig. 4.18 ***Cercopithecus aethiops***

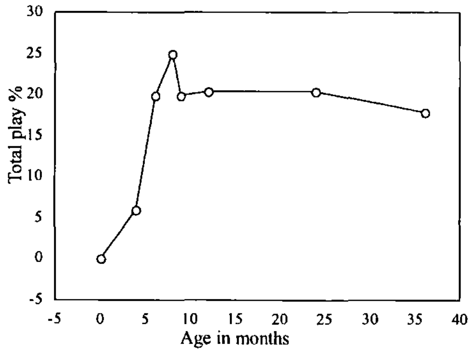


Fig. 4.19 ***Gorilla gorilla***

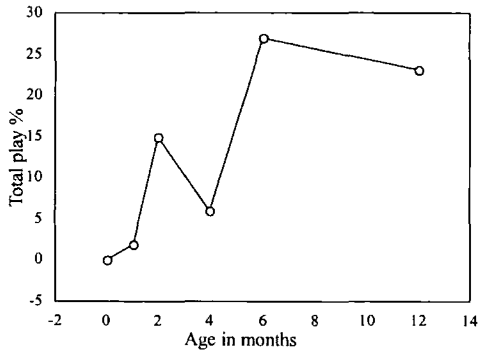


Fig. 4.20 ***Macaca arctoides***

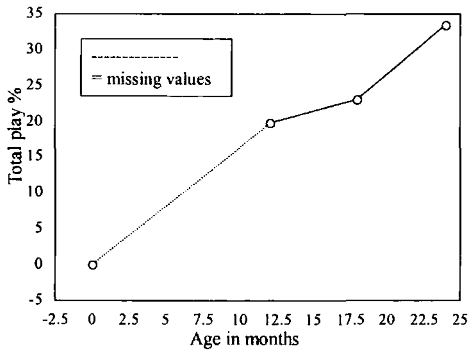


Fig. 4.21 ***Macaca fuscata***

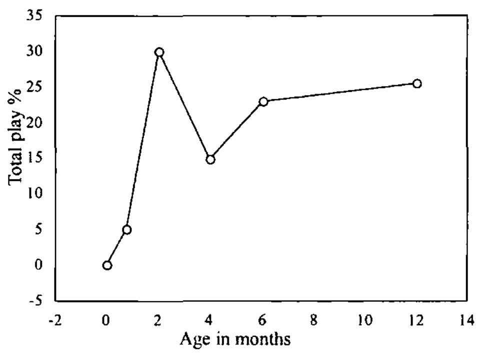


Fig. 4.22 ***Macaca mulatta***

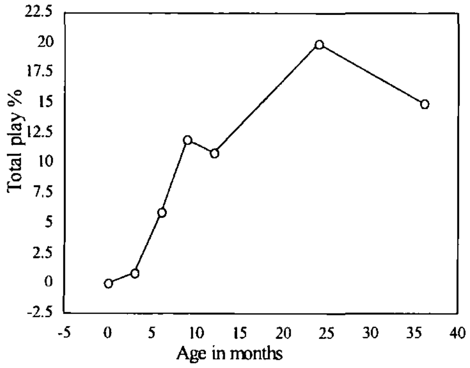


Fig. 4.23 ***Pan troglodytes***

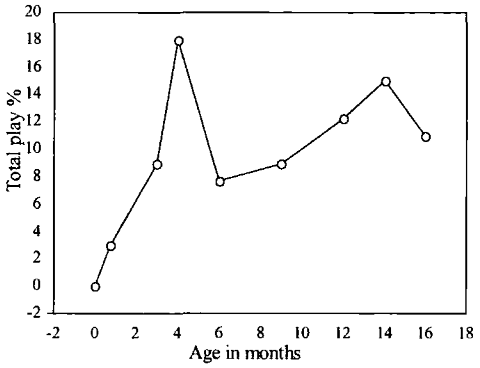


Fig. 4.24 ***Papio anubis***

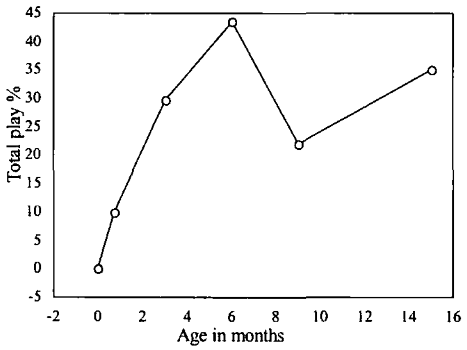


Fig. 4.25 ***Papio cynocephalus***

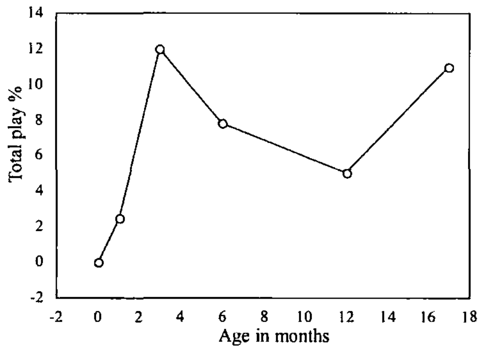


Fig. 4.26 ***Papio hamadryas***

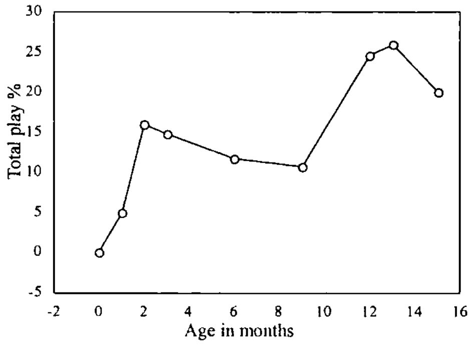


Fig. 4. 27 ***Saguinus fuscicollis***

Figs. 4.17-4.27. Developmental trajectory of total play in selected primates.

Age at weaning: *A. palliata*, 21 mo; *C. aethiops*, 8.5 mo; *G. gorilla*, 52 mo; *M. arctoides*, 9 mo; *M. fuscata*, unknown; *M. mulatta*, unknown; *P. troglodytes*, 48 mo; *P. anubis*, 14 mo; *P. cynocephalus*, 17 mo; *P. hamadryas*, unknown; *S. fuscicollis*, 3 mo.

4.5.8 Daily fluctuations

Play is sensitive to environmental variables, and its frequency fluctuates during the day. The following figures (Figures 4.28-4.35) detail intra-specific variation in daily play frequency trajectory in selected primate species. A summary of primates as an order appears in the Appendix.

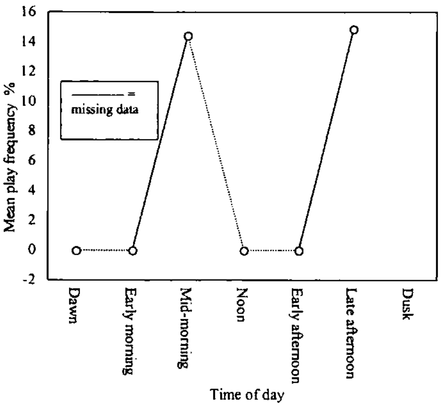


Fig. 4.28 ***Cebus apella***

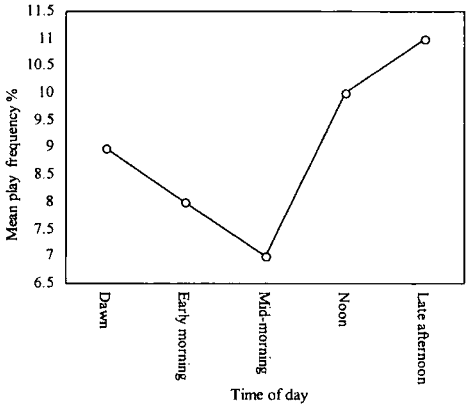


Fig. 4.29 ***Cercocebus atys***

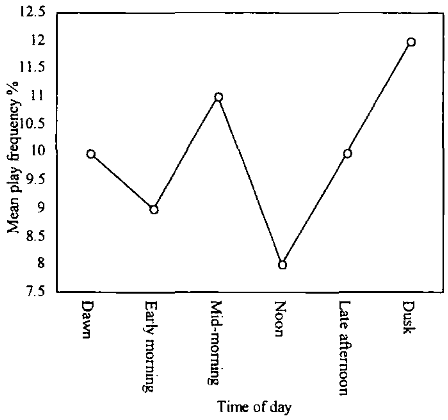


Fig. 4.30 ***Macaca arctoides***

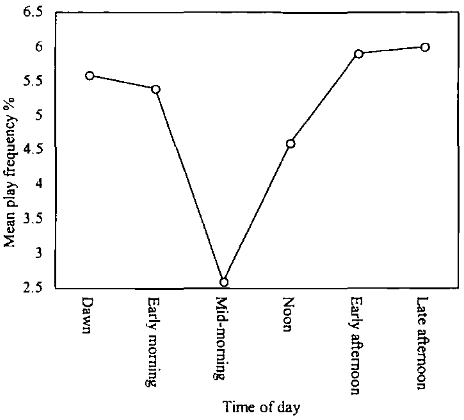


Fig. 4.31 ***Macaca mulatta***

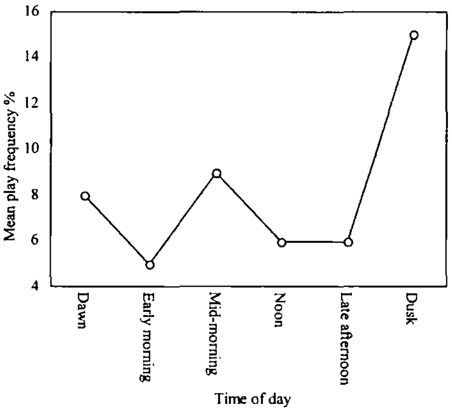


Fig. 4.32 ***Macaca nemestrina***

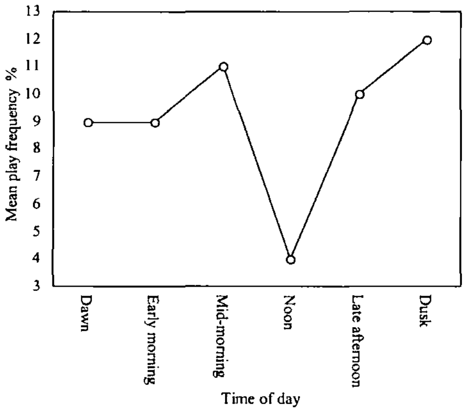


Fig. 4.33 ***Macaca nigra***

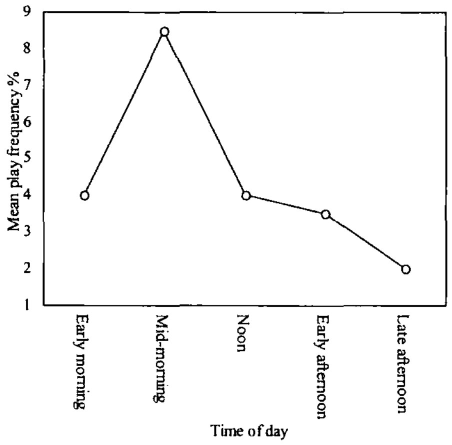


Fig. 4.34 ***Macaca sylvanus***

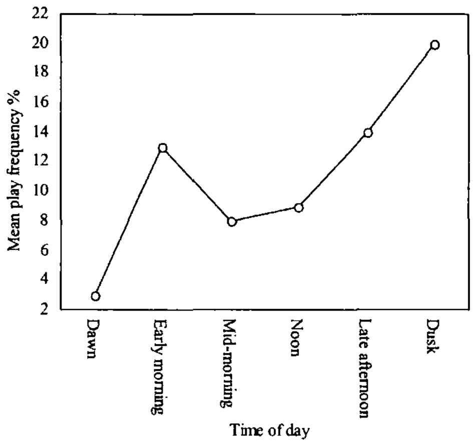


Fig. 4.35 ***Theropithecus gelada***

Figs 4.28-4.35 Average daily fluctuation in play frequency in selected primates.

4.6 Discussion

4.6.1 Research effort

The hypotheses predict that as a study increases in length, the number of play behaviours observed in that species will increase to a certain point, after which the relationship asymptotes as a species' behavioural repertoire becomes fully observed. This is certainly the case among the studies on red colobus monkeys analysed here, although the result is not significant for any of the other species focused upon within this chapter. Although these results are not necessarily specific to the exhibition of play, this analysis allows us to control for research effort. These results may reflect the nature of each study, and the extent to which the literature is reported, rather than being a definitive insight to a species' behavioural repertoire for play or any other given behaviour.

As with the number of different behaviours within a species' play repertoire, it is also likely that the amount of play (as a time budget) will show a similar trend: the longer the study, the more instances of a particular behaviour are likely to be reported. Again, these results are significant only within red colobus monkeys, and only for the exhibition of social play behaviour.

4.6.2 Group size

Actual group size (the total number of individuals within each study group) is positively and significantly correlated with social play in red colobus monkeys and olive baboons, but negatively and significantly correlated with object and social play in chimpanzees, and with no significant association in Japanese macaques. In the independent contrasts analyses in Chapter 6, mean species group size was only positively and significantly correlated with social play in primates and carnivores; the results showed that social group sizes, such as clique size, were better predictors of play frequency than the overall mean group size. Intra-specifically however, these results suggest that in species with very large group sizes, such as red colobus monkeys and olive baboons, with mean group sizes of 34 and 50, respectively (Barton 1999; Dunbar 1992), group size is important with regards to the time budget for play, but that in species with relatively smaller group sizes in comparison, such as chimpanzees (28 [Barton 1999]) the reverse is true. The result for Japanese macaques is interesting, as in the wild they live in large groups of around 36 (Barton 1999) and up to 194 (Rowe 1996); the largest group size in my collated data reached well in excess of this figure, at 316 individuals (Rostal & Eaton 1983). The correlation between group size and play in the results however, was non-significant (although positive). It may be the case that very large groups offer the capacity for increased clique sizes (for example), and that the overall group size is merely a function of this. Similarly, the larger the group, the increased likelihood of infants and juveniles, which would arguably increase the amount of play behaviour observed. In social species, such as primates, it is likely that social changes will create fluctuations in the exhibition of behaviour, and play may be affected thus. Merrick (1977) reports that following the death of an adult female, play frequency fell to its lowest point in a group of captive chimpanzees. Similarly, socially directed behaviour in a captive group of sloth bears (*Ursus ursinus*) decreased in the presence of an unfamiliar adult male (Forthman & Bakeman 1992).

4.6.3 Age class

It may be that group size alone is not a good general predictor of play frequency. The literature suggests that it is juveniles and infants that exhibit the most play, and thus perhaps it is the age composition of the group members that is important. However, when group composition was tested for, in terms of age class for individuals in each group, no significant results emerged for either Japanese macaques or for chimpanzees. Interestingly, even the number of individuals in each age class did not predict the amount of play performed by that age class (e.g. juvenile play was not significantly correlated with number of juveniles in chimpanzees). Explanations for this are unclear, although it suggests that there is a further factor at work within the expression of play in these species. Small sample sizes may also play a rôle in this result.

4.6.4 Sex class

Age alone does not appear to explain play frequencies at an intra-specific level in the primate species focused upon here. As the literature repeatedly reports that males are more playful than females, the analyses seek to evaluate to what extent this may be true for intra-specific comparisons. Social play is likely to be the play type that is most explained by the sex composition of a group in primates, given the tendency of males to engage in rough-and-tumble play (Meaney et al. 1985). In Japanese macaques, despite the small sample size, it is interesting to note that the number of males in a group negatively predicts the amount of play exhibited by males, suggesting that different group dynamics or demographics are more important to play than simply number. However, when splitting the number of males and the amount of play into age-class categories, there were no significant correlations for Japanese macaques. A similar result is seen in chimpanzees, where age and sex class splits do not appear to explain play variance. Indeed, the only significant result is a negative correlation between solitary play and the number of adult females present in a group.

Given the nature of play, and its liability to fall into sex-specific and age-specific groupings, it is expected that within species, this relationship would hold. These results suggest that this is not necessarily the case, although explanations for this remain unclear. One potential problem with these intra-specific analyses is the extremely small sample sizes, and future research should aim to test these relationships across a wider number of species replicates.

4.6.5 Space per individual

If group composition in terms of age and sex cannot sufficiently explain play variance within a species, it is necessary to consider other external factors that may be influential. Play has been shown to be sensitive to the effects of space and confinement (Fagen 1981; Burghardt 1984; Schapiro & Mitchell 1986; Jensen et al 1998; Jensen 1999, 2001). For this reason, a parameter for space per individual was analysed with total play. There are positive, although non-significant correlations between space per individual and total play in Japanese and rhesus macaques, and also in chimpanzees, indicative of no real association between these variables.

Explanations for these results are unclear. There are conflicting reports in the literature claiming that small or isolated enclosures negatively affect normal behaviour and reduce play frequencies in captive animals (Blackshaw et al. 1997; Herskin & Jensen

2000). However, studies on pigs have shown that individuals housed in large enclosures may play less than those in smaller pens (Apple & Craig 1992). With larger sample sizes, the intra-specific results in this chapter may have welfare implications, although the sample sizes in these analyses remain rather too small to be convincing correlations in either direction in this case. As stress is a factor most likely to decrease play (McCune 1992; Carlstead et al. 1993), it may be the case that it is the way in which the enclosure is enriched that proves more of a predictor of play, be it high quality environmental enrichment that increases play through the potential to stabilise social groups (Carlstead & Shepherdson 1994; [this is also the case with playground designs for children, see Barbour 1999]), or alternatively a lack of environmental enrichment increasing play as displacement behaviour (Apple & Craig 1992). Further investigation of these and similar results may potentially provide information pertinent to animal welfare, although more work is required to address these issues in more depth.

4.6.6 Developmental trajectory

The developmental trajectory plots in this chapter typically show two peaks in play frequency; one soon after play begins in infancy, and one later in the juvenile period. The first peak is usually followed by a rapid decline in play behaviour, which eventually increases to bring about the second peak in play activity just prior to weaning age. After this period, play declines steadily with the onset of adulthood. These patterns have been reported throughout the theoretical and empirical literature on play behaviour (e.g. Fagen 1993; Byers & Walker 1995). Indeed, the patterning of play during the juvenile period has been used to hypothesise that mammalian play has evolved to enhance the developing neuro-muscular system during sensitive periods (Byers & Walker 1995; Fairbanks 2000). For some of the species detailed in this chapter, available data on play rates throughout juvenility are not available for a period long enough to cover the second peak, or weaning age. However, it is worth noting that play peaks in baboons appear to tie in with time at which they lose their natal coats (Altmann 1998).

There are insufficient data to detail developmental trajectories for different types of play in primate species, although Fairbanks (2000) has done so with vervet monkeys. She concludes that solitary play begins early in infancy, being quickly replaced by social play as the most common form of play; social play peaks at around 12 months in vervets, and declines steadily to adult levels towards the end of the juvenile period. Object play usually begins later and decreases in frequency with increasing age. It appears that play trajectories can be measured in tandem with dental eruption and midlactation; social play peaks tend to coincide with the eruption of the first molar, and decline to adult levels by the emergence of the third molar (Fairbanks 2000). These patterns remain consistent across primate species, thus giving further credence to the argument that play serves important functions in mammalian development. Play is not timed to maximise physical functions that would benefit an animal for training purposes (the getting into shape hypothesis, Byers 1998; Byers & Walker 1995), but play is timed with neuromuscular plasticity, thus it seems highly likely that the timing of play behaviour in mammals has evolved to permanently influence the CNS during the juvenile period (Fairbanks 2000). Further studies should aim to delineate the developmental timing of different play categories across species, in an attempt to understand more the clearly the functions that different forms of play have in modifying neural pathways before adulthood.

4.6.7 Daily fluctuations

The frequency of play fluctuates over the course of the day, and peaks in activity are usually reported during the early part of the day and towards the end of the day and at dusk, when daily temperatures are lowest. Although the actual patterning of daily play activity is different from species to species, the general trends are similar. Future studies should aim to test the degree to which species living at different latitudes differ in their typical daily play patterns, and the extent to which seasonality affects this patterning.

4.7 Summary

Intra-specific analyses here indicate that there is indeed much variation in play between different species, but that it is not always clear what factors are driving these changes within species, based on analysis of species replicates for parameters such as group size, age- and sex class, and habitat space. It is likely that some key elements, such as group composition, co-drive the exhibition of play within species with an external variable, such as an environmental correlate. However, given the paucity of suitable data, and data-matches, intra-specific analyses here prove difficult and inconclusive. Further empirical studies should aim to identify these factors in the field and report the data, and comparative and intra-specific studies should collate and analyse these data, hopefully with larger sample sizes. Alternatively, it may be that each species is programmed to play according to its *typical* group size, environment, etc., and thus little or no correlation will be found across conspecific populations.

Chapter 5:

Play & Life-History Patterns

5.1 Introduction

This chapter will focus on how life-history variables are correlated with each category of play behaviour, and what this might indicate about behavioural evolution in primates and carnivores. Partridge & Harvey (1988) define life-histories as "*the probabilities of survival and the rates of reproduction at each stage in the life span*". The diversity of life-histories across taxa is variable, but limited (Harvey et al. 1987) and is often determined by habitat stability (Partridge & Harvey 1988) and body size (Harvey & Clutton-Brock 1985). For the study of play then, it is therefore important to understand the ways in which play distribution is related to different life-history strategies (Bekoff 1989b).

5.1.1 Reproduction and gestation

Body size is a variable that is strongly connected to life-history parameters in mammals; indeed, in primates, body weight may explain up to 80% of this variation (Ross & Jones 1999). It is certainly the case that an animal is constrained by its size in terms of reproduction and the way in which it can experience and utilise the surrounding environment (Ross & Jones 1999). It has also been argued that brain growth, rather than body size, constrains variables such as gestation length in mammals (Sacher & Staffeldt 1974); this is thought to be because neural tissue grows much more slowly than other somatic tissues, and thus there is a correlation between gestation length and neonate brain size (Harvey & Clutton-Brock 1985). In primates, gestation length varies between 60 and 250 days, and birth weight between 10 and over 2000 g (Harvey & Clutton-Brock 1985). Carnivores too, exhibit diversity in their reproduction, both in terms of behaviour, and in output. Much of this variation is due to differences in body size (Bekoff et al. 1984). The difficulty, as with the other variables, is that there is often a paucity of suitable studies from which to glean life-history data (Harvey & Clutton-Brock 1985); this is especially true of carnivores, where most families other than the Canidae are underrepresented (Bekoff et al. 1984).

Reproductive variables, as well as correlating with body size (Ross & Jones 1999), may also correlate with habitat or lifestyle. In carnivores, the extent of aquatic living in certain species may be important; true marine species usually produce a single precocial neonate, and this pattern is true of pinnipeds, cetaceans, sirenians, and the only true marine carnivore, the sea otter (*Enhydra lutris*). Other aquatic carnivores such as freshwater otters (lutrines) typically bear litters of 4-6 (Estes 1989). Reports exist of sea-otters giving birth to twins, however, only the strongest of the twins will be weaned by its mother, and the other twin is usually abandoned (Jameson & Bodkin 1986; Estes 1989). Habitat and genetic diversity and distribution may also affect reproductive output in terms of finding suitable mates. Indeed, this is a problem exacerbated in males of both wild and captive populations of cheetahs (*Acinonyx jubatus*), lions (*Panthera leo*), and Florida panthers (*Puma concolor coryi*) with the condition of teratospermia. This condition is characterised by a high proportion of abnormal sperm per ejaculate, thus female ova are often not fertilised. Teratospermia is believed to have arisen due to a lack of genetic diversity in local populations (Wildt et al. 2001).

As with socio-ecological factors such as group size, carnivore and primate life-histories are affected by diet. In canids for example, relatively larger (although fewer) offspring are born to typically omnivorous species, such as crab-eating foxes (*Cerdocyon thous*), than to exclusive carnivores such as coyotes (*Canis latrans*) (Bekoff et al. 1984). It has been hypothesised that this is due in part to the relationship between food preferences and reproductive effort: omnivores may experience fewer threats to reproductive success as they can monopolise a greater supply of food sources throughout the year (e.g. Smithers 1971), thus more likely to enable stasis of body fat which facilitates longer gestation and lactation periods, and play; whereas in times of food scarcity, exclusive meat-eaters might experience more marked difficulty in maintaining nutritional levels (Bekoff et al. 1984). Alternatively, it may be that large and exclusive carnivores exhibit higher levels of playfulness in comparison with smaller omnivorous species, as they require increased hunting experience prior to leaving the natal group (Bekoff et al. 1984). In this case, we should expect to see exclusive carnivores exhibiting more object play.

5.1.2 Precocial vs. altricial

Animals exhibit differing degrees of neonatal development, in terms of thermoregulation, nutrition, locomotion, and sensory development, and the extent to which this development varies, is described in terms of altricial and precocial young (Derrickson 1992). There is generally a lack of behavioural development data in ethological literature, especially for carnivores (Bekoff 1989b), and thus it is important to distinguish between altricial and precocial species where possible, in the study of animal behaviour.

In mammals, altricial species are typically those that are relatively undeveloped and helpless at birth, and thus reliant on maternal effort to impart warmth and food for survival (Derrickson 1992). Altricial species typically produce small-bodied offspring in large litters; most brain development occurs postnatally, so although neonate brains are small at birth, by adulthood their brains have developed to a comparable size as the brains of other mammals of a similar body size (Bennett & Harvey 1985). Precocial mammalian species are typically those that are well developed as neonates, and that can achieve independence quickly. Precocial species give birth to heavier neonates, in smaller litters, and over a longer gestation period, and thus are relatively well developed at birth; they do however tend to reach full adult mass at a slower rate than do altricial species (Derrickson 1992) and thus may present a longer juvenile period, which would potentially increase the opportunity to engage in play behaviour. Precocial species typically have reduced levels of postnatal brain growth in comparison with altricial species, having higher levels of foetal brain growth, and thus precocial species have a larger neonatal brain weight than do altricial neonates (Bennett & Harvey 1985). Humans are an exception to this rule in that they have extensive pre- and post-natal neural development (Harvey & Clutton-Brock 1985; Key 2000).

The altricial-precocial scale is very much a continuum, with some species being relatively more altricial or precocial than others (Burghardt 1988). The ancestral mammalian condition is likely to have been for a relatively small body size with altricial neonates (Derrickson 1992). Indeed, the majority of extant mammals are altricial at the genera and species levels, but precocial neonates are present in many orders (Derrickson 1992). In canids, for example, relative female body size is a good indicator of altriciality; larger females give birth to larger litters of smaller neonates who are relatively altricial; in contrast, smaller females produce fewer and more precocial offspring (Moehlman 1989). In this vein, the degree to which a species produces precocial or altricial infants is also indicative of other aspects of life-history and socio-ecology. Species in which neonates are altricial tend also to be species with a high degree of territoriality, and in some cases, a prevalence of infanticide. Female territoriality is common among some fissipeds and some strepsirhines, who also give birth to relatively non-mobile altricial young. This is in contrast to pinnipeds and haplorhine primates, whereby female territoriality is usually reduced or absent, and neonates are mobile altricial or precocial (Woolf 1997). Allometric analyses indicate that there is a positive and significant relationship between neonate weight, litter weight, and maternal body weight (Moehlman 1986; Ross & Jones 1999). Thus in the analyses in this chapter, body size, and maternal body size have been partialled out using residual regression. Fissiped carnivores, marsupials, and insectivores are typically altricial (Bennett & Harvey 1985) and are born with limited locomotor abilities, nominal visual, acoustic, and olfactory functions, and a long period of maternal dependence during which infants become "socialised" (Bekoff 1977) and develop motor and social skills (Bekoff 1989b). Pinnipeds, primates, chiropterans, artiodactyls, perissodactyls, proboscideans, and cetaceans are typically precocial (Bennett & Harvey 1985). Primates, for example, are relatively more mature at birth than other altricial mammals such as rats, cats, and dogs. However, in spite of this high level of precocial physical development, primates are sometimes considered *behaviourally* altricial, being relatively mobile, but reliant on maternal input for milk, warmth, and safety (Nicholson 1987; Wolff 1997). By contrast, in birds and reptiles, altricial species have larger brains, but that are smaller at hatching, than do precocial species (Bennett & Harvey 1985). In birds, precocial species grow at 25% the rate of altricial species (Derrickson 1992).

5.1.3 The effect of habitat

Ecological variables are known to affect life-history diversity, and habitat variation is a key factor affecting life-histories (Harvey & Clutton-Brock 1985; Partridge & Harvey 1988). Species that occupy open grasslands (e.g. African wild dogs, *Lycaon pictus*) tend to produce relatively smaller offspring than woodland (e.g. culpeo, *Dusicyon culpaeus*; cougar, *Puma concolor*) or forest-dwelling species (e.g. dhole, *Cuon alpinus*; ocelot, *Leopardus pardalis*) (Bekoff et al. 1984). Again, this may be due to dietary diversity with increasingly forested habitats facilitating a wider array of food sources (Kleiman & Eisenberg 1973). Gittleman (1984) found that forest-dwelling and aquatic mustelids such as minks and otters respectively, reach sexual maturity later in comparison with open grassland or woodland species such as badgers (*Meles meles*). This longer period of juvenility might explain the apparent playfulness of such species. Conversely, social species tend to occupy open habitats in larger groups (Gittleman 1989), which may act in predator avoidance, as well as providing an increased need to engage in play.

5.1.4 Longevity

Perhaps the best predictor of life-history variation is that of mortality, where species with lower longevity tend to reach maturity sooner, than in comparison with naturally long-lived species; thus those with a high adult mortality rate quite literally "live fast and die young" (Promislow & Harvey 1990). Mammals with a long life-span, tend to reach sexual maturity later, and produce precocial young, after a long gestation period; this is especially true of primates (Ross & Jones 1999; Alvarez 2000). Other mammals with a higher rate of adult mortality conversely tend to have a shorter natural lifespan, with a high birth rate, and give birth to altricial young (Ross & Jones 1999). Unsurprisingly then, body size is a further factor in mammalian life-spans, with larger species usually far outliving smaller ones; there is one notable exception to this within pinnipeds however, with the largest species, the elephant seal (*Mirounga angustirostris*), being rather short-lived (Estes 1989). Among carnivores, the problems of genetic diversity in extant populations (Wildt et al. 2001) may also be represented by longevity data; reproductive rates, juvenile weight, sexual maturation, and lifespan are all seriously reduced by the deleterious effects of inbreeding, and may be especially prevalent in social canids such as wolves (*Canis lupus*) (Laikre & Ryman 1991).

5.2 Methods

The data on primate body size (g) are taken from a compilation in Barton (1999), and carnivore body size from Deaner et al. (in press), Gittleman (1986), Bininda-Emonds (2000) and Oftedal & Gittleman (1989). The data for primate life-history variables are taken from Barton (1999), Ross & Jones (1999), Deaner et al. (in press), Harvey et al. (1987), and additionally from Rowe (1996), and Sacher & Staffeldt (1974). Carnivore life-history data are taken from Gittleman (1989), Oftedal & Gittleman (1989), Mead (1989), and Deaner et al. (in press). The data on each type of play behaviour were collected from the existing primate and carnivore behaviour literature, as detailed in Chapter 2. I used the method of independent contrasts (Felsenstein 1985; Harvey & Pagel 1991) with the primate phylogeny based on Purvis (1995), and the carnivore phylogeny from Bininda-Emonds et al. (1999). The analyses were conducted using the CAIC computer software programme (Purvis & Rambaut 1995), using the CRUNCH option for continuous variables, and the BRUNCH option for dichotomous variables. Statistical analyses of the output from CAIC were carried out using StatView versions 4.0 and 5.0. Regressions were set through the origin (Purvis & Rambaut 1995). For the purposes of these analyses, the data have been log-transformed, rendering them suitable for standard regressions (Freckleton 2000; Purvis & Rambaut 1995).

As life-history variables are highly correlated with body size, the statistical analyses, unless otherwise indicated, were corrected for body size; this was done by regressing body size (independent variable X) on a dependent variable (Y) (such as gestation length) to get the residual; the residual was then used as the independent variable in a regression of X on the play category variable Y. The effect of this is to partial out the effect of body size from the analysis.

Bonferroni procedure was used to adjust the statistical significance at a 5% significance level (Moore & McCabe 1999). The equation for Bonferroni procedure is:

$$\alpha / k$$

Where α is the protection level, or "cut-off" point for significance, and k is the number of tests in the sample. For regression analyses that meet statistical significance prior to

Bonferroni corrections, the graphs are presented here to be illustrative of a likely effect, given that sample sizes are often small; this is especially true of analyses on carnivore play and life-history variables in this chapter.

5.3 Hypotheses

The following hypotheses are presented for play in primates and carnivores with regard to life-history determinants. The null hypothesis, H_0, states that there will be no association between play behaviour and the life-history variable in question. Below, alternative hypotheses, H_a, are proffered.

1. Body size will correlate with social, but not non-social, play.

As body size appears to be a confounding variable in most life-history traits (e.g. Bekoff & Byers 1985; Burghardt 1988; Pagel & Harvey 1993), which in turn may have an affect on development and behavioural output, it is likely that play behaviour too will be confounded by body size. This is likely to be due to metabolic constraints (see Chapter 6) as well as a play-preference for similar sized players (Fagen 1981). Very small mammals are seldom reported to play; for example, in marsupials, the smallest mouse-like species play very simply and in low amounts, whereas the larger species play far more complexly and devoting a greater proportion of their daily time budget to play (Fagen 1981: 81-82). Such differences in play output are unclear, although it may be concerned with the relative degree of precociality or altriciality, or with prey-status, that is, the extent to which the species is more or less likely to be a predator or prey species. Indeed, larger species are more likely to be diurnal and gregarious, especially in primates (Harvey et al. 1987), and thus relatively larger species may have evolved a mechanism to allow play more readily than smaller, nocturnal and solitary species. Socio-ecological and neurological parameters will be dealt with in subsequent chapters. In any case, the extremes of body size may be limiting in terms of energy requirements and play output (Burghardt 1988).

It is possible that sexual dimorphism may correlate with social play, assuming that significant differences in body size are reflective of male-male competition, for example. Additionally, relative body size is likely to affect interspecific play, as differing body sizes between the two species may lead to their play becoming unstable (Fagen 1981). However, in these analyses, it is unlikely that body size will show a correlation with the dichotomous variable of whether or not a species engages in interspecies play, as the body size of the other species is not included here.

2. Play will be strongly associated with relative development.

It is predicted that the mode of development, in terms of the altricial-precocial distinction, will be a strong predictor of the type and amount of play that is exhibited. Thus, young that are precocial are predicted to be those that are most playful (Burghardt 1988) as their bodies and brains are more developed at birth than those of their altricial counterparts. Species with large neonate weight, small litters, and parental care are more likely to have evolved under conditions requiring behavioural flexibility, which is argued to have given rise to behaviours such as exploration and play (Bekoff & Byers 1985). Relatively more precocial species also tend to have larger relative brains, with higher encephalisation quotients (E.Q.); E.Q is also strongly correlated with life-history variables such as longevity and delayed sexual maturity, as well as with information storage (Eisenberg 1981). It is therefore likely that species born with a relatively long gestation period will be those that are relatively most playful. Similarly, and by extension, species with a higher relative birth weight, and smaller litter size (indicators of precociality) will also exhibit higher frequencies of play. Conversely, it might be the case that more altricial species require play in order to wire up their brains during their extended postnatal brain development.

Play usually rises to its peak just prior to weaning at which point it begins its continual decline towards the end of the juvenile period and the beginning of sexual maturity (Fairbanks 2000). It is likely that by the time of weaning, an individual has developed much of its body and brain, and thus its need to play becomes gradually reduced. It is predicted that in precocial species, play will occur earlier than in relatively more altricial species, although the peak of play activity during development may be the same in altricial species. The play peak plots will determine to what extent this is the case.

3. Play will be associated with reproductive markers.

Play is predicted to be associated with reproduction in terms of development, and the timing of an individual's first offspring. The period of lactation is also predicted to correlate with play time. This is true of mothers and neonates, who will engage each other in play during the period of nutritional dependency, and additionally for potential siblings, who may engage in play with their infant relation. Inter-birth interval (IBI) is also predicted to be a good measure of play in terms of development, as younger females typically have a longer IBI than relatively older females (Ross & Jones 1999). If this is true, then perhaps it suggests that younger adult females may play more, in terms of mother-infant playful interactions. Indeed, Pagel & Harvey (1993) suggest that selection pressures act on body size, and in primates, this has resulted in a later age at maturity, and reduced adult mortality. Such factors have led to a longer juvenile period (Ross & Jones 1999). If it is so that individuals that use this period to their adaptive advantage, by gaining behavioural experience, subsequently improve their biological fitness, then it can be argued that play during this time also has adaptive benefits.

4. Longevity may predict patterns of play.

It is predicted here that species that live longer, will also be those to be most playful. This is partly due to longevity correlating with certain other traits associated with relative precociality, such as a relative late onset of sexual maturity and relatively large brain size, as well as energetic traits such as a low to medium metabolic rate (Hofman 1993). It is thus expected that the longer an animal lives, the more social it is likely to be, and thus the more (social) play it is likely to engage in. It should be noted that other life-history variables correlate with brain size (e.g. Martin 1989), although body size may be a more suitable key variable (e.g. Key 2000; cf. Deaner et al. in press), and thus for the purposes of these analyses, it is body size that will generally be corrected for with regard to life-history variation. Chapter 7 will deal with brains and play, and Chapter 6 with energetic constraints.

5.4 Data

Table 5.1 details continuous life-history variables for primates. Table 5.2 details continuous carnivore life-history variables. Further information on data categories are detailed in Chapter 2.

Table 5.1. Continuous life-history variables for primates

Species	**Gestation• (days)**	**Neonatal • weight (g)**	**Litter□ size (years)**	**Age at □ weaning (years)**	**Juvenile* period (years)**	**Age at • sexual maturity (mo)**	**Age at 1st ∇ reproduction (mo)**	**Lactation* period (mo)**	**IBI□ (years)**	**Maximum∇ life-span (years)**
Allenopithecus nigroviridis	-	-	-	-	-	-	-	-	-	-
Alouatta palliata	187	480.0	1	1.73	-	45.0	43.2	-	1.88	20.0
Ateles geoffroyi	229	426.0	1	2.25	3.37	48.0	60.0	25.03	2.66	27.3
Callicebus moloch	-	-	1	0.16	-	-	36.0	-	1.00	10.0
Callithrix jacchus	148	28.0	2.1	0.25	1.25	12.0	18.0	-	0.52	12.0
Cebus albifrons	154*	234.0	1	0.75	3.27	43.1	48.0	-	1.5	44.0
Cebus apella	160	248.0	1	-	-	-	66.0	8.71	1.79	44.0
Cebus capucinus	162*	230.0	1	-	-	-	48.0	16.98	1.6	46.9
Cebus olivaceus	-	-	1	2.00	-	-	-	-	2.17	-
Cercocebus albigena	177	425.0	1	1.00	-	48.0	49.2	-	2.12	32.7
Cercocebus atys	167	-	1	-	-	-	56.4	-	1.08	27.0
Cercopithecus aethiops	163	314.0	1	1.00	4.0	30.0	42.0	6.69	1.33	31.0
Cercopithecus diana	-	450.0	1	1.00	-	-	64.8	-	1.00	34.8
Cercopithecus hamlyni	-	-	1	-	-	-	-	-	-	-
Cercopithecus mitis	140	402.0	1	1.91	4.01	62.0	51.6	-	3.92	20.0
Cercopithecus neglectus	182	260.0	1	1.00	-	48.0	48.0	-	1.62	22.0
Colobus badius	-	-	1	2.16	-	-	49.0□	-	2.12	-
Colobus guereza	-	445.0	1	1.07	-	-	56.4	-	1.00	22.3
Erythrocebus patas	163	-	1	0.58	2.42	33.0	36.0	8.49	1.00	21.6
Gorilla gorilla	256	2110.0	1	2.75	7.29	78.0	118.2	29.99	3.83	50.0

Species	Gestation• (days)	Neonatal • weight (g)	Litter□ size (years)	Age at □ weaning (years)	Juvenile* period (years)	Age at • sexual maturity (mo)	Age at 1st ∇ reproduction (mo)	Lactation* period (mo)	IBI□ (years)	Maximum∇ life-span (years)
Hylobates lar	205	410.5	1	2.00	7.31	108.0	111.6	24.49	2.69	31.5
Hylobates syndactylus	231	517.0	1	-	-	-	108.0	-	3.00	35.0
Lemur catta	135	88.2	1.2	0.29	1.72	-	24.0	-	1.50	27.1
Macaca arctoides	175	-	1	-	-	30.0	42.0	-	1.48	30.0
Macaca fascicularis	162	346.0	1	1.15	2.71	-	46.8	7.60	1.07	37.1
Macaca fuscata	173	503.0	1	1.00	-	-	66.0	-	1.50	33.0
Macaca mulatta	167	481.0	1	1.00	3.5	34.0	45.0	6.39	1.00	29.0
Macaca nemestrina	167	473.0	1	1.00	2.92	35.0	47.3	7.78	1.11	26.3
Macaca nigra	176	455.0	1	-	-	-	57.6	-	1.48	-
Macaca radiata	162	404.0	1	1.00	-	-	-	-	1.00	30.0□
Macaca silenus	-	-	1	1.00	-	-	-	-	1.38	38.0□
Macaca sinica	-	-	1	0.85	-	-	-	-	1.50	-
Macaca sylvanus	164‡	-	1	-	-	46.0	57.6	-	1.00	22.0
Mandrillus sphinx	173	613.0	1	0.96	3.14	-	60.5	10.09	1.46	29.1
Nycticebus coucang	193	49.3	1	0.49	-	-	-	-	1.00	14.5
Pan troglodytes	228	1756.0	1	4.00	9.0	118.0	122.4	55.97	5.50	53.0
Papio anubis	180	1068.0	1	-	-	-	-	20.0	1.16	-
Papio cynocephalus	175	854.0	1	1.00	4.50	51.0	73.0	15.0	1.75	-
Papio hamadryas	172	443.0†	1	1.00	5.11	-	-	18.71	2.00	-
Papio ursinus	187	-	1	-	-	-	-	28.97	-	-
Pithecia pithecia	163	-	1	-	-	-	25.2	-	1.58	13.8
Pongo pygmaeus	260	1728.0	1	1.12	8.56	84.0	128.4	41.97	6.5	57.3
Presbytis entellus	168	-	1	1.25	2.17	42.0	51.0	8.30	1.68	25.0

Species	**Gestation▪ (days)**	**Neonatal ▪ weight (g)**	**Litter□ size (years)**	**Age at □ weaning (years)**	**Juvenile* period (years)**	**Age at ▪ sexual maturity (mo)**	**Age at 1st ∇ reproduction (mo)**	**Lactation* period (mo)**	**IBI□ (years)**	**Maximum∇ life-span (years)**
Pygathrix nemaeus	165	-	1	-	-	-	-	-	1.36	-
Saguinus fuscicollis	149	40.0	2	0.25	-	-	-	-	1.00	-
Saguinus midas	127	36.0	2	0.19	1.81	20.0	24.0	-	0.55	13.3
Saguinus oedipus	145	43.2	1.9	-	-	18.0	22.8	-	0.58	13.5
Saimiri sciureus	170	195.0	1	0.14	-	-	30.0	-	1.17	21.0
Theropithecus gelada	170	464.0	1	1.23	-	49.5	48.0	-	1.00	19.3

▪ Harvey et al. (1987); * Deaner et al. (in press); ‡ Rowe (1996); □ Ross & Jones (1999); ∇ Barton (1999); † Sacher & Staffeldt (1974)

Table 5.2 Continuous life-history variables for carnivores

Species	**Gestation+ (days)**	**Birth ‡ weight (g)**	**Litter ‡ size (days)**	**Age at * weaning (days)**	**Age at ✧ independence (days)**	**Age at 1st * conception (days)**	**IBI * (mo)**	**Maximum * captive lifespan (years)**
Acinonyx jubatus	91.0*	287.5	3.8	108.9	464	645.5	18.0	-
Ailuropoda melanoleuca	140.0	104.8	1.5	179.8	-	2312.1	12.0	18.0
Arctocephalus australis	365.0	-	-	-	-	-	-	-
Canis latrans	61.52*	225.0	6.2	98.0	-	364.8	12.0	-
Cerdocyon thous	56.0	140.0	3.1	90.0	-	364.7	8.0	-
Crocuta crocuta	109.9*	1500.0	2.0	390.0	916	912.0	17.0	23.0
Felis silvestris	67.0*	137.10	3.0✧	84.0	140	313.3	6.0	-
Haliochoerus grypus	345.0	-	-	-	-	-	-	-
Helogale undulata	-	-	4.0✧	-	-	-	-	-
Lontra canadensis	305	-	3.0✧	93.0	-	729.5	-	-
Mustela putorius	41.0	-	5.0✧	-	-	-	12.0	-
Mustela vison	57.5	-	-	-	-	419.8	12.0	-
Panthera leo	105.4*	1650.0	2.6	150.0	1075	1621.8	25.0	18.0
Phoca vitulina	*300.0*	-	-	-	-	-	-	-
Selenarctos thibetanus	216.0	-	2.0✧	119.1	337	1185.8	-	33.0
Speothos venaticus	65.01*	-	-	-	-	-	-	-
Ursus americanus	225.0	285.0	2.5	167.8	483	10839.3	27.0	22.5
Ursus arctos	210.0	1000.0	2.0	729.0	645	1336.6	30.0	25.3
Thalarctos maritimus	265.5	641.6	1.9	-	821	1733.8	24.0	34.0

+ Mead (1989); * Deaner et al. (in press); ‡ Oftedal & Gittleman (1989); ✧ Gittleman 1989

5.5 Results

First, bivariate regressions of contrasts of each play category and body size are presented, with graphs. Thereafter, results are presented for each play category on life-history variables, controlling for body size (partial correlation analysis), and graphs are only presented for significant results. Statistics are presented for each section where there is a significant correlation, and results for the non-significant statistics appear in the Appendix. It should be noted that where sufficient data are available, results for both primates and carnivores are analysed and presented; however, due to a lack of play data, many carnivore analyses are apparently "missing". A summary of the results is presented in Table 5.21 at the end of this section.

5.5.1 Primate body size

Table 5.3 details bivariate regression analyses of contrasts for each play category on body size in primates. Mean body size is positively and significantly correlated with total play (Figure 5.1). Mean body size is not significantly associated with solitary locomotor play (Figure 5.2); one outlier has been removed from the result, as indicated by the CAIC programme (see Chapter 2), although this does not change the overall trend of the graph. Mean body size is positively correlated with object play although the result falls short of significance (Figure 5.3); one outlier has been removed from the analyses as indicated in the CAIC programme. Mean body size is not significantly associated with social play (Figure 5.4).

Table 5.3 Bivariate regression analyses of play category on mean body size in primates

Play category	DF	F-value	p-value	co-efficient	r^2
Total	**1, 38**	**12.93**	**0.009**	**0.68**	**0.26**
Solitary	1, 19	0.16	0.70	0.15	0.009
Object	1, 10	3.68	0.08	0.37	0.27
Social	1, 22	0.03	0.85	0.003	0.001

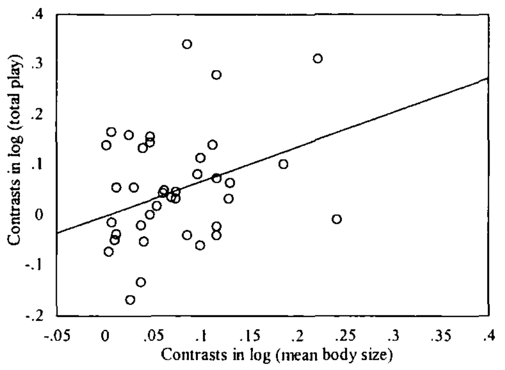


Fig. 5.1 Regression plot of log (total play) on log (body size) in primates

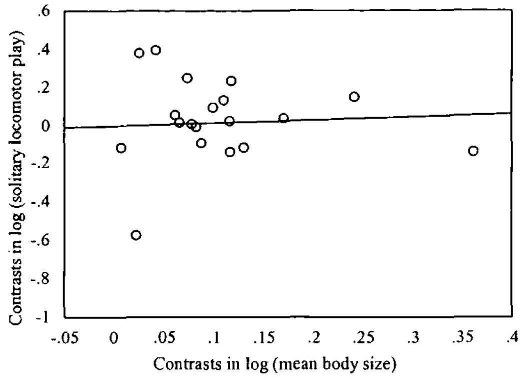


Fig. 5.2 Regression plot of log (solitary locomotor play) on log (body size) in primates

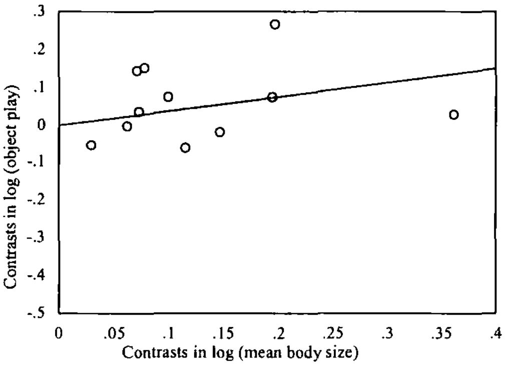


Fig. 5.3 Regression plot of log (object play) log (body size) in primates

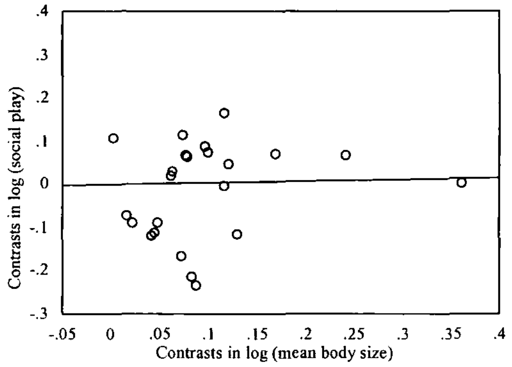


Fig. 5.4 Regression plot of log (social on play) on log (body size) in primates

5.5.2 Carnivore body size

Table 5.4 details bivariate regression analyses of contrasts for each play category on mean body size in carnivores. Mean body size is negatively and significantly correlated with total play (Figure 5.5); however, Bonferroni correction renders this result non-significant. Mean body size is not significantly associated with solitary locomotor play (Figure 5.6), although insufficient sample size renders a statistical result impermissible. Mean body size is not significantly correlated with object play (Figure 5.7), or with social play (Figure 5.8).

Table 5.4 Bivariate regression analyses of play category on mean body size in carnivores

Play category	DF	F-value	p-value	co-efficient	r^2
Total	**1, 12**	**5.34**	**0.04**	**-0.33**	**0.31**
Solitary	1, 2	0.22	0.68	0.26	0.10
Object	1, 4	0.86	0.41	0.39	0.18
Social	1, 8	0.14	0.91	0.02	0.002

Bonferroni 0.013 = n.s.

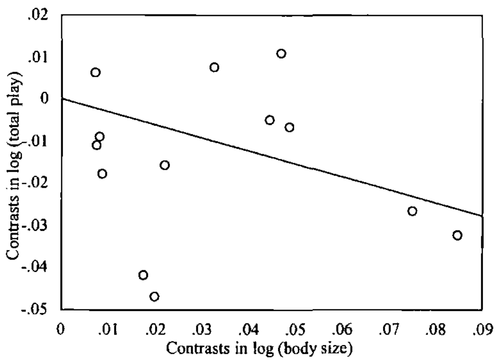


Fig. 5.5. Regression plot of log (total play) play) on log (body size) in carnivores

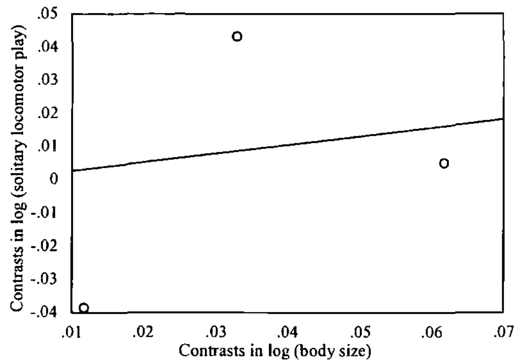


Fig. 5.6. Regression plot of log (total on log (body size) in carnivores

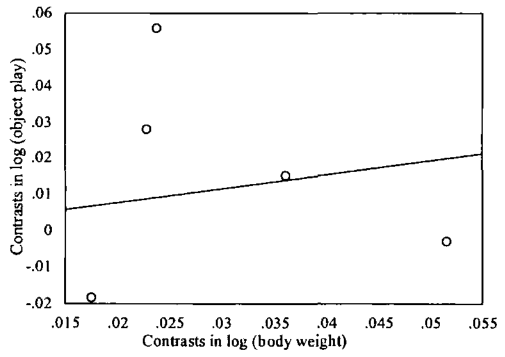


Fig. 5.7 Regression plot of log (object play) on log (body size) in carnivores

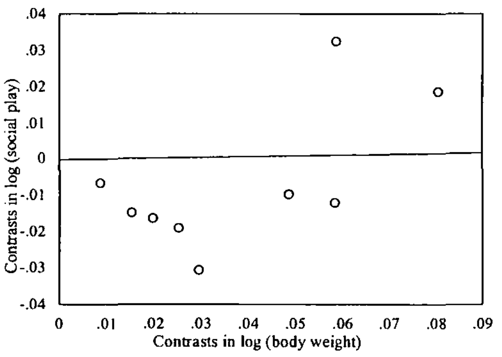


Fig. 5.8 Regression plot of log (social play) on log (body size) in carnivores

5.5.3 Carnivore female body weight

Table 5.5 details bivariate regression analyses of contrasts for each play category on mean female body weight in carnivores. Female body size is negatively and significantly correlated with total play (Figure 5.9), however Bonferroni correction renders this result non-significant. Female body size is not associated with either solitary locomotor play (Figure 5.10), object play (Figure 5.11), or social play (Figure 5.12).

Table 5.5 Bivariate regression analyses of play category on female body size in carnivores

Play category	DF	F-value	p-value	co-efficient	r^2
Total	**1, 11**	**6.08**	**0.03**	**0.27**	**0.36**
Solitary	1, 3	0.19	0.71	0.25	0.09
Object	1, 4	0.58	0.49	0.35	0.13
Social	1, 8	0.10	0.76	0.05	0.01

Bonferroni 0.013 = n.s

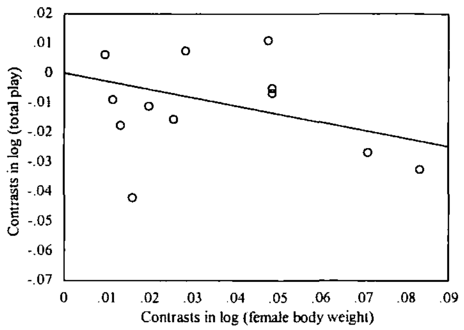


Fig. 5.9. Regression plot of log (total play) on log (female body size) in carnivores

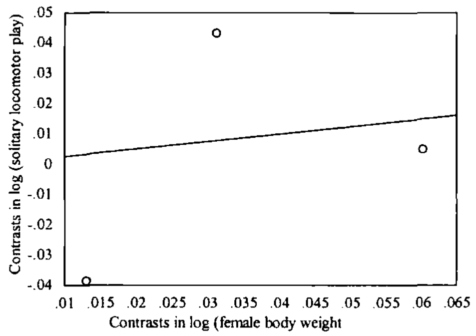


Fig. 5.10. Regression plot of log (solitary locomotor play) on log (female body size) in carnivores

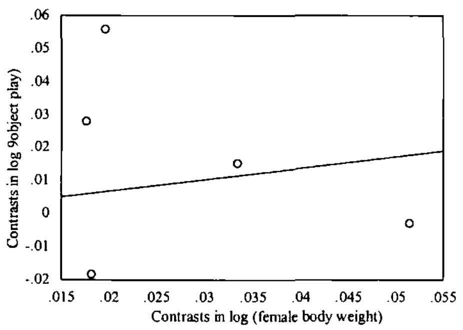


Fig. 5.11 Regression plot of log (object play) on log (female body size) in carnivores

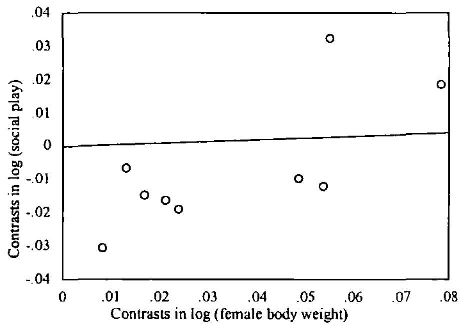


Fig. 5.12 Regression plot of log (social play) on log (female body size) in carnivores

5.5.4 Gestation period

Partial correlation analyses are used throughout the following sections to remove the effect of body size. This was done by regressing the dependent variable (e.g. gestation period) on body size (independent variable); these residuals were then regressed against each play category. Partial correlation analyses of contrasts for each play category in primates revealed a positive but non-significant relationship. Table 5.6 details partial correlation analyses of contrasts for each play category on gestation length in carnivores. Gestation length is not significantly correlated with total, solitary locomotor, or object play. Gestation period is however positively and significantly correlated with social play in carnivores (Figure 5.13).

Table 5.6. Partial correlation analyses of play type on gestation length in carnivores controlling for female body size

Play type	DF	F-value	p-value	co-efficient	r^2
Total	1, 12	0.05	0.83	0.12	0.004
Solitary	1, 2	9.75	0.09	1.97	0.83
Object	1, 4	0.01	0.92	0.11	0.003
Social	**1, 7**	**11.34**	**0.01**	**1.21**	**0.62**

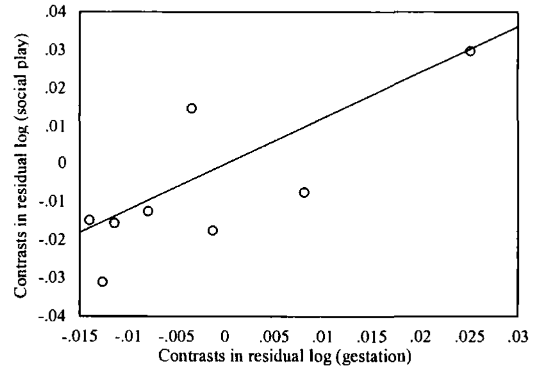


Fig. 5.13 Partial correlation plot of log (social play) on log (gestation period) in carnivores

5.5.5 Birth weight in primates

Table 5.7 shows the results of partial correlation analyses of contrasts for each play category on birth weight in primates, removing the effect of body size. Birth weight is not significantly associated with total, solitary, or object play in primates. Birth weight is however, positively and significantly correlated with social play in primates (Figure 5.14).

Table 5.7. Partial correlation analyses of play category on birth weight in primates, controlling for body size

Play type	DF	F-value	p-value	co-efficient	r^2
Total	1, 29	0.16	0.69	0.12	0.005
Solitary	1, 16	1.98	0.18	1.30	0.11
Object	1, 8	0.92	0.37	0.29	0.10
Social	**1, 16**	**6.84**	**0.002**	**0.55**	**0.30**

Partial correlation analyses were similarly conducted of contrasts for each play category on birth weight in carnivores. None of the play categories were significantly correlated with birth weight in carnivores.

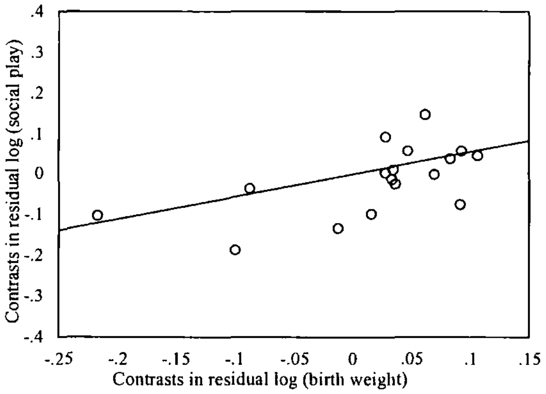


Fig. 5.14 Partial correlation plot of log (social play) on log (birth weight) in primates

5.5.6 Litter size

Partial correlation analyses of contrasts for each play category on litter size in primates show no significant correlation.

Table 5.8 shows partial correlation analyses of contrasts for play category on litter size in carnivores, controlling for body size. Litter size is not significantly correlated with solitary locomotor, object or social play. Litter size is however negatively and significantly correlated with total play in carnivores (Figure 5.15).

Table 5.8. Partial correlation analyses of play type on litter size in carnivores, controlling for female body weight

Play type	**DF**	**F-value**	**p-value**	**co-efficient**	**r²**
Total	**1, 9**	**57.34**	**<0.0001**	**-2.58**	**0.86**
Solitary+	-	-	-	-	-
Object	1, 2	7.20	0.11	-4.47	0.78
Social	1, 4	0.41	0.56	-0.90	0.09

+ Too few observations

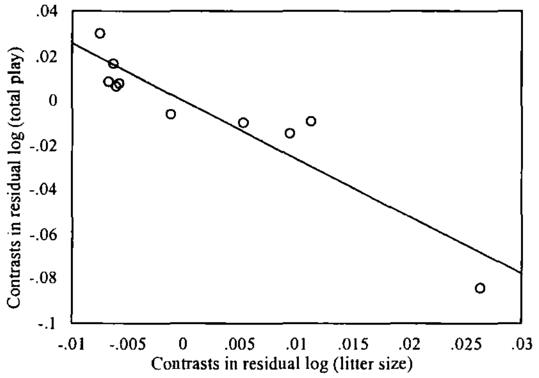


Fig. 5.15 Partial correlation plot of log (total play) on log (litter size) in carnivores

5.5.7 Age at weaning

Table 5.9 details partial correlation analyses of contrasts for each play category on weaning age in primates, controlling for body size. Age at weaning is negatively and significantly associated with total play (Figure 5.16). Age at weaning is not significantly associated with solitary locomotor, object of social play.

Table 5.9. Partial correlation analyses of play category age at weaning in primates, controlling for body size

Play type	**DF**	**F-value**	**p-value**	**co-efficient**	**r^2**
Total	**1, 15**	**16.46**	**0.001**	**-1.10**	**0.52**
Solitary	1, 7	1.04	0.34	-1.15	0.13
Object	1, 3	0.35	0.59	-0.38	0.11
Social	1, 8	0.09	0.77	0.19	0.01

Partial correlation analyses of contrasts for each play category on age at weaning in carnivores, controlling for body size shows no significant correlation.

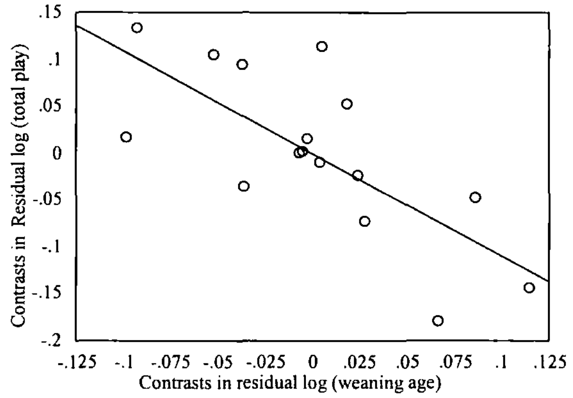


Fig. 5.16. Partial correlation plot of log (total play) on log (age at weaning) in primates

5.5.8 Juvenile period in primates

Table 5.10 details results of partial correlation analyses of contrasts for each play category on juvenile period in primates, controlling for body size. Juvenile period is positively and significantly correlated with total play (Figure 5.17). Juvenile period shows no significant associated with any other play category.

Table 5.10 Partial correlation analyses of play category on juvenile period in primates, controlling for body size

Play type	DF	F-value	p-value	co-efficient	r^2
Total	**1, 15**	**12.89**	**0.002**	**0.28**	**0.46**
Solitary	1, 7	0.99	0.35	1.90	0.12
Object	1, 3	5.05	0.11	2.64	0.63
Social	1, 8	0.07	0.80	0.03	0.008

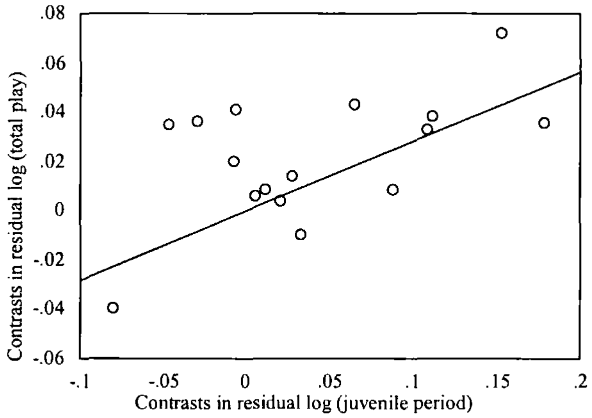


Fig. 5.17. Partial correlation plot of log (total play) log (juvenile period) in primates

5.5.9 Age at independence in carnivores

Table 5.11 shows the results of partial correlation analyses of contrasts for each play category on age at independence in carnivores, controlling for body size. Partial correlation of total play on age at independence shows a negative and significant result (Figure 5.18). Partial correlation of social play on age at independence shows no association. There were too few observations of solitary locomotor play and object play to permit a statistical result.

Table 5.11 Partial correlation analyses of play category on age at independence in carnivores, controlling for body size

Play type	DF	F-value	p-value	co-efficient	r^2
Total	**1, 7**	**17.52**	**0.004**	**-0.55**	**0.72**
Solitary+	-	-	-	-	-
Object+	-	-	-	-	-
Social	1, 3	0.08	0.88	-0.40	0.03

+ Too few observations

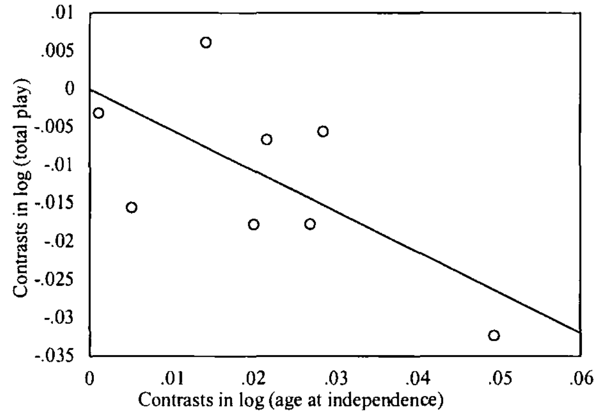


Fig. 5.18. Partial correlation plot of log (total play) on log (age at independence) in carnivores

5.5.10 Age at first conception in carnivores

Table 5.12 shows the results of partial correlation analyses of contrasts for each play category on age at first conception in carnivores, controlling for female body weight. Age at first conception is not significantly correlated with total, solitary locomotor, or social play. Age at first conception in carnivores is however positively and significantly correlated with object play, although there are too few observations to permit statistical analysis.

Table 5.12 Partial correlation analyses of play category on age at first conception in carnivores, controlling for female body weight

Play type	DF	F-value	p-value	co-efficient	r^2
Total	1, 8	0.02	0.91	0.04	0.002
Solitary+	-	-	-	-	-
Object+	**1, 2**	**673.18**	**0.001**	**3.20**	**0.99**
Social	1, 4	0.38	0.57	0.09	0.09

+ Too few observations

5.5.11 Age at first reproduction in primates

Table 5.13 details partial correlation analyses of contrasts for each play category on age at first reproduction in primates, controlling for body size Age at first reproduction is positively and significantly correlated with both total and social play (Figures 5.19 and 5.20). However, after Bonferroni correction, neither of these results ate significant. Age at first reproduction shows no significant association with solitary locomotor or object play.

Table 5.13. Partial correlation analyses of play category on age at first reproduction in primates, controlling for body size

Play type	DF	F-value	p-value	co-efficient	r^2
Total	**1, 31**	**5.26**	**0.03**	**0.95**	**0.15**
Solitary	1, 16	0.31	0.59	1.21	0.02
Object	1, 9	0.03	0.86	0.17	0.003
Social	**1, 20**	**4.05**	**0.05**	**1.19**	**0.17**

Bonferroni 0.013 = n.s

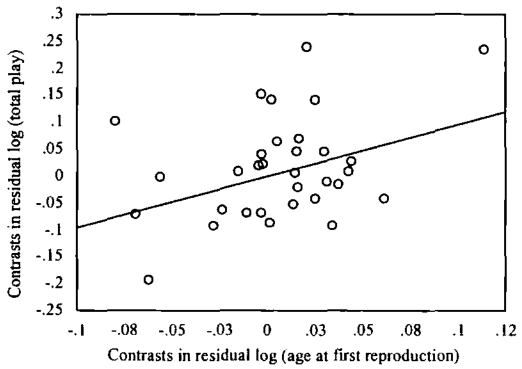


Fig. 5.19. Partial correlation plot of log (total play) on log (age at first reproduction) in primates

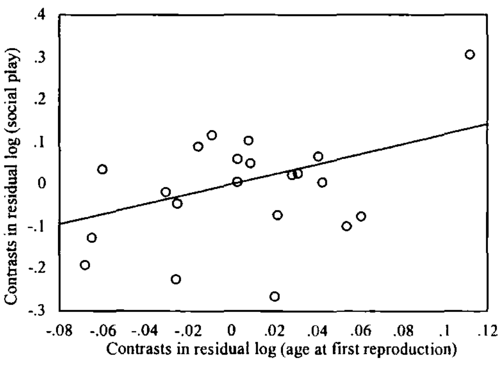


Fig. 5.20. Partial correlation plot of log (social play) on log (age at first reproduction) in primates

5.5.12 Lactation period in primates

Table 5.14 shows the results of partial correlation analyses of contrasts for each play category on lactation period in primates, controlling for body size. Lactation period is positively and significantly correlated with total play (Figure 5.21). Lactation period shows no significant association with solitary locomotor, object play, or social play.

Table 5.14. Partial correlation analyses of play category on age at lactation period in primates, controlling for body size

Play type	DF	F-value	p-value	co-efficient	r^2
Total	**1, 13**	**6.05**	**0.03**	**0.88**	**0.32**
Solitary	1, 6	1.53	0.26	1.08	0.20
Object	1, 2	0.24	0.67	0.29	0.11
Social	1, 7	1.80	0.22	0.55	0.21

Bonferroni 0.013 = n.s

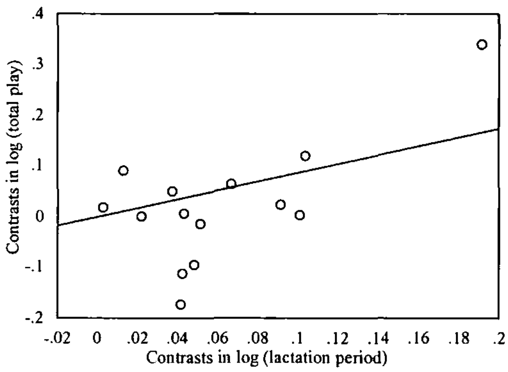


Fig. 5.21 Partial correlation of log (social play) on log (lactation period) in primates

5.5.13 Inter-birth interval (IBI)

Table 5.15 shows partial correlation analyses of contrasts for each play category on inter-birth interval in primates, controlling for body size Inter-birth interval is positively and significantly correlated with total and object play (Figures 5.22 and 5.23). There was no such association between inter-birth interval and solitary locomotor, or social play.

Table 5.15 Partial correlation analyses of play category on inter-birth interval in primates, controlling for body size

Play type	DF	F-value	p-value	co-efficient	r^2
Total	**1, 37**	**18.48**	**0.0001**	**1.55**	**0.33**
Solitary	1, 19	1.66	0.21	1.75	0.08
Object	**1, 11**	**5.67**	**0.03**	**1.76**	**0.34**
Social	1, 23	1.44	0.24	0.55	0.06

Bonferroni 0.013 = Object play n.s

Table 5.16 shows partial correlation analyses of contrasts for each play category on inter-birth interval in carnivores, controlling for body size. Partial correlation of total play on inter-birth interval shows a negative and significant correlation (Figure 5.24), after Bonferroni correction however, this result is not significant. There was no association object or social play and inter-birth interval. There were too few observations of solitary locomotor play to permit a statistical result.

Table 5.16 Partial correlation analyses of play category on inter-birth interval in carnivores, controlling for body size

Play type	DF	F-value	p-value	co-efficient	r^2
Total	**1, 8**	7.29	**0.03**	**-1.01**	**0.48**
Solitary+	-	-	-	-	-
Object	1, 2	0.07	0.83	1.52	0.07
Social	1, 4	0.001	0.97	0.03	2.4

+ Too few observations; Bonferroni 0.013 = n.s

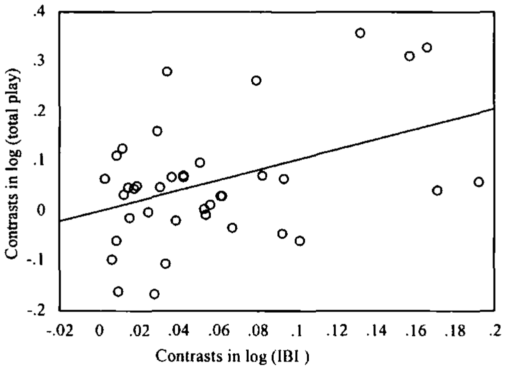


Fig. 5.22 Partial correlation plot of log (total play) on log (IBI) in primates

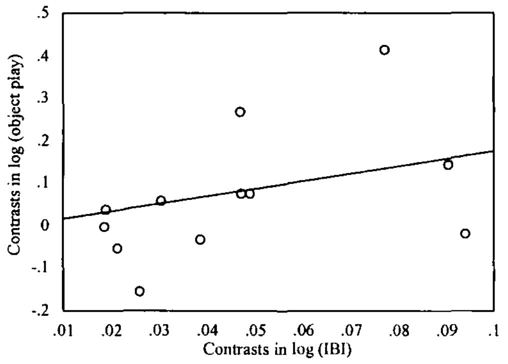


Fig. 5.23 Partial correlation plot of log (object play) on log (IBI) in primates

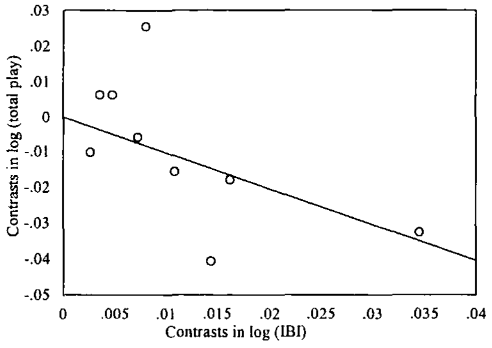


Fig. 5.24 Partial correlation plot of log (total play) on log (IBI) in carnivores

5.5.14 Maximum lifespan

Table 5.17 shows the results of partial correlation analyses of contrasts for each play category on maximum lifespan in primates, controlling for body size. Maximum lifespan shows a positive and significant correlation with both solitary locomotor play and social play (Figures 5.25 and 5.26), after Bonferroni correction however, these results are non- significant. Maximum lifespan is not significantly associated with total play or object play.

Table 5.17. Partial correlation of play category on maximum lifespan in primates, controlling for body size

Play type	DF	F-value	p-value	co-efficient	r²
Total	1, 32	0.36	0.55	0.29	0.01
Solitary	**1, 18**	**6.50**	**0.02**	**4.22**	**0.27**
Object	1, 10	0.24	0.64	0.44	0.02
Social	**1, 20**	**5.29**	**0.03**	**1.70**	**0.21**

Bonferroni 0.013 = n.s

Lifespan is one life-history variable that has been shown to correlate very strongly with brain size (Deaner et al. in press). Thus, partial correlation analyses were also run to remove the effect of adult brain size in primates. Table 5.18 details the results of partial correlation analyses of contrasts for each play category on maximum lifespan in primates, controlling for brain size. Total play was not significantly associated with maximum life span in primates. Object play was negatively but non-significantly correlated with maximum lifespan in primates. Solitary locomotor-rotational play, and social play however, were positively and significantly correlated with maximum life span in primates after the effect of brain size was removed from the analyses (Figures 5.27-5.28). However, Bonferroni correction renders the result for social play non-significant.

Table 5.18 Partial correlation of play category on maximum lifespan in primates, controlling for brain size

Play type	DF	F-value	p-value	co-efficient	r^2
Total	1, 32	0.02	0.90	-0.06	4.85
Solitary	**1, 18**	**8.03**	**0.01**	**5.22**	**0.31**
Object	1, 10	1.87	0.20	-1.56	1.57
Social	**1, 19**	**4.78**	**0.04**	**2.13**	**0.20**

Bonferroni 0.013 = social play n.s

Maximum lifespan is not significantly associated with total play or social play in carnivores. There were too few observations of solitary locomotor play and object play to permit a statistical result. Unfortunately, there were too few observations to permit partial correlation analyses removing the effects of brain size for all play categories except total play. Partial correlation analysis of total play on maximum lifespan in carnivores shows no association.

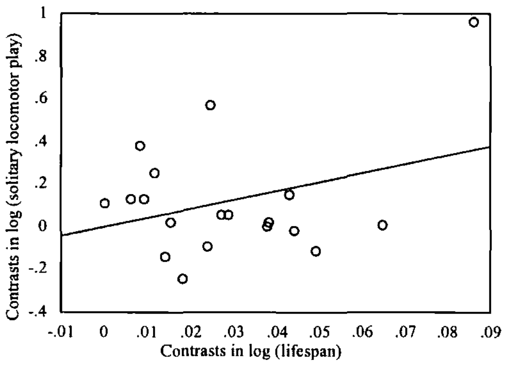


Fig. 5.25 Partial correlation plot of log (solitary locomotor play) on log (maximum lifespan) in primates

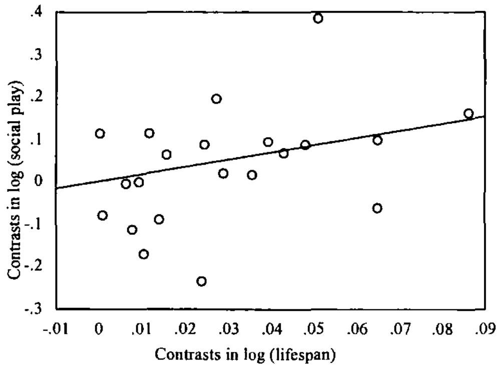
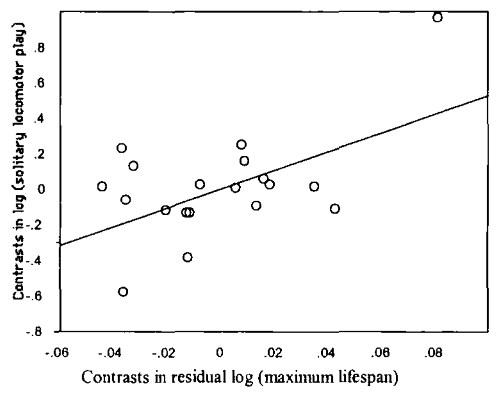


Fig. 5.26 Partial correlation plot of log (social play) on log (maximum lifespan) in primates



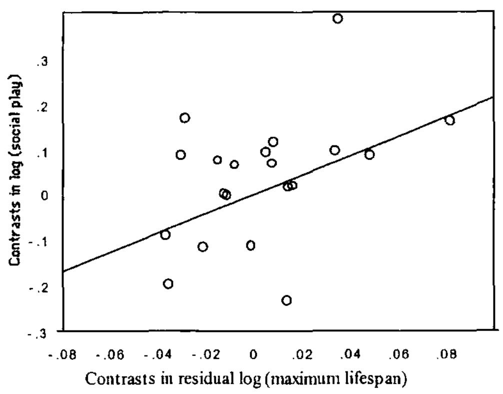


Fig. 5.27 Partial correlation plot of log (solitary locomotor play) on log (maximum lifespan) in primates

Fig. 5.28 Partial correlation plot of log (social play) on log (maximum lifespan) in primates

5.5.15 Play peaks

Play is subject to peaks of activity during the juvenile period (Fairbanks 2000). Table 5.19 shows partial correlation analyses of weaning age and relative neonatal body size (neonate size controlled for maternal body size) on the onset and developmental peaks in the play of primates. Regression analyses show a negative and significant correlation between relative neonatal body weight on month at which play first appears (Figure 5.29). Developmental trajectories for individual species are presented in Chapter 4.

Table 5.19 Partial correlation analyses of weaning age and neonatal body weight on developmental onset and peak-frequency of play in juvenile primates

Timing	DF	F-value	p-value	co-efficient	r^2
Age at weaning on:					
Month play appears	1, 11	0.94	0.35	0.41	0.08
Month at 1st play peak	1, 6	0.04	0.85	0.58	0.006
Month at 2nd play peak	1, 3	0.001	0.97	0.003	4.68
Neonatal body weight on:					
Month play appears	**1, 8**	**11.65**	**0.009**	**-0.17**	**0.59**
Month at 1st play peak	1, 5	0.17	0.69	0.75	0.03
Month at 2nd play peak	1, 3	0.48	0.54	-0.13	0.14

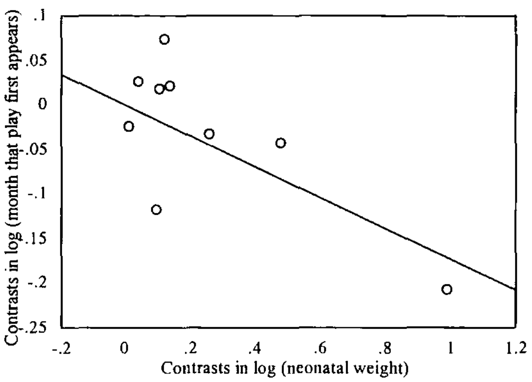


Fig. 5.29 Partial correlation plot of log (neonatal body weight) on log (age at the first appearance of play (mo)) in primates

5.5.16 Dichotomous variables

The following one sample analyses (t-test) testing for significant evolutionary change in body size relative to the transitions in the dichotomous variables.

Table 5.20 T-tests on changes in body size with transitions in dichotomous play variables

Variable	**Mean**	**DF**	**t-value**	**p-value**	**Significance?**
Adult play	-0.01	13	-0.60	0.56	N.S
Adult male play	-0.03	11	-1.18	0.26	N.S
Adult-adult play	0.002	16	0.08	0.94	N.S
Sex play	0.003	17	0.12	0.90	N.S
SSD	-0.03	13	-1.03	0.32	N.S
SSP	-.001	11	-0.02	0.98	N.S
SAD	0.01	12	0.40	0.69	N.S
SAP	-0.005	8	-0.14	0.89	N.S
Sibling	0.06	4	1.42	0.23	N.S
Relatedness	-0.07	5	-1.35	0.24	N.S
Dominance	0.02	3	0.25	0.82	N.S
Vocalisation	-0.02	10	-0.62	0.55	N.S
Dyadic	**0.06**	**2**	**52.39**	**0.01**	*
Polyadic	0.04	8	1.19	0.27	N.S
Interspecific	0.03	3	0.35	0.75	N.S
Place	-0.03	5	-1.05	0.34	N.S

* p = <0.05; Bonferroni 0.003, thus N.S.

Table 5.21 Summary of results of life-history variables on each category of play in primates and carnivores

Life-history variable	Play category: significant correlation?			
	Total	Solitary locomotor	Object	Social
Body size	✓+ ✓-	× ×	× ×	× ×
Female body size	✓+	×	×	×
Gestation period	× ×	× ×	× ×	× ✓+
Birth weight	× ×	× ×	× ×	✓+ ×
Litter size	× ✓-	× ×	× ×	× ×
Age at weaning	✓- ×	× -	× ×	× ×
Juvenile period	✓+ -	× -	× -	× -
Age at independence	- ✓-	- ×	- ×	- ×
Age at first conception	- ×	- -	- ✓+	- ×
Age at sexual maturation	× -	× -	× -	× -
Age at first reproduction	✓+ -	× -	× -	✓+ -
Lactation period	✓+	×	×	×

Life-history variable	Play category: significant correlation?			
	Total	Solitary locomotor	Object	Social
	-	-	-	-
Inter-birth interval	✓+	✗	✓+	✗
	✓-	-	✗	✗
Maximum lifespan	✗	✓+	✗	✓+
	✗	-	-	✗

✓ = significant, ✗ = not significant, + = positive correlation, - = negative correlation/no data; Symbols: **Black** = primates, Red = carnivores.

5.6 Discussion

5.6.1 Body size

These results indicate that body size is positively and significantly correlated with total play in primates, suggesting that increases in total play over evolutionary time have co-evolved with increases in body size. Interestingly, the reverse trend is seen in carnivores, where both mean body size, and female body size, are negatively and significantly correlated with total play (except that Bonferroni correction renders this actually non-significant). These results may be explained by reproductive influences. In carnivores, larger females give birth to relatively altricial young; this is a byproduct of carrying larger litters of smaller, less well-developed, neonates (Moehlman 1989). The hypothesis predicts that precocial species are more playful than altricial ones. Primates, with relatively larger brains, typically give birth to precocial infants, with well-developed brains. Primates therefore, are less likely to be constrained by body size in terms of altriciality, and thus with increasing body sizes and larger relative brains, are also more playful. Indeed, raw and unconstrasted play category values from the literature tend to suggest that primates spend more time in play than do carnivores. We might expect to see body size correlate with social play, if social play functions in social assessment and fighting practice. The lack of a relationship here may be suggestive of a seemingly innate trend towards choosing evenly-matched partners in terms of size. The largest carnivores, such as bears, also tend to be those species that are more solitary (see Chapter 6). Species that are habitually solitary are less likely to find the need or opportunity to engage in play (especially social play) to the extent to which relatively more social species do. Additionally, large body size acts as an anti-predator mechanism (Key 2000). In carnivores, species that are large and solitary may be better able to avoid predation through sheer size, thus potentially limiting the rôle that play appears to offer in terms of honing physical skills. Body size is correlated with group size, and Chapter 6 will address these issues in more detail.

5.6.2 Reproductive effects

As with body size, reproductive effects appear to be important in the expression of play behaviour. Body size, for example, appears to affect the relationship of gestation length to play. In primates, although the trend is a positive one, none of the play categories show a significant correlation when regressed against gestation length. In carnivores, when the confounding effect of body size is removed from the analysis, there is a positive and significant correlation between social play and gestation length. This suggests that increases in gestational period have been correlated with increases in social play over evolutionary time. This again seems to be indicative of the level of development of carnivore neonates. A relatively longer relative gestation time is associated with an increased level of precociality among neonates. This may be crucial, especially in terms of social play, as precocial young are better equipped to engage in social interactions far sooner than relatively more altricial young. This trend may be similar for primates, although the lack of significance of the result suggests that another factor is at work, possibly brain size.

The relationship between birth weight and play is interesting. In primates, the results appear to fit the hypothesis, and a positive and significant relationship is found between social play and birth weight, suggesting that evolutionary increases in birth weight correlate with increases in the amount of social play exhibited. More importantly, this relationship holds when the effects of body size are removed, thus rendering the result true of relative birth weight in primates. It is likely that this too, is indicative of relative development, with relatively larger neonates being relatively more precocial and hence more able to play, especially in terms of social play behaviours.

The results for play type and litter size corroborate the association between precociality and play. In carnivores, the results reveal a negative and significant correlation between litter size and play in carnivores, even when body size is controlled for. This indicates that as litter size has increased, play has decreased in frequency. Again, this appears to add further support to the hypothesis that the degree to which an animal is altricial or precocial has huge impacts on behavioural development. In carnivores, the larger the litter, the smaller the offspring, and the more altricial the neonates (Moehlman 1989). Carnivore litter sizes vary widely, and thus may be a good indicator of life-history and behavioural variation. In primates, the variation in number of offspring is far more limited. Most species bear a single and precocial neonate, with twins being the norm in callitrichids (e.g. Dunbar 1995b; Windfelder 2000). Thus, litter size is unlikely to be a significant variable in the exhibition of primate play, although intra-specific analyses may delineate the importance more specifically (see Chapter 4). This may explain the non-significance of the result for litter size and play in primates.

5.6.3 Weaning and sexual maturity

As an individual approaches the end of infancy and into the period of weaning and juvenility, play remains a prominent behaviour although the rate at which it occurs begins to decline towards the onset of adolescence and sexual maturity (Fairbanks 2000). Results here show no significant correlation between play budgets and age at weaning in either carnivores or primates. However, when the effects of juvenile period are removed from the analyses, age at weaning shows a negative and significant relationship with total play in primates. This suggests that as age at weaning becomes later relative to the total length of the juvenile period, the tendency to engage in play behaviour declines. This might be explained by the frequent sharp decline in play of many species specifically at weaning age (e.g. vervet monkeys, *Cercopithecus aethiops*, Fairbanks 2000). This might be due to parent-offspring conflict during the transition from a maternal milk diet, to a more solid diet (Nicholson 1987). The distress of this conflict, coupled with the need to become more independent at this time, might best explain the negative relationship between play and weaning in primates. There is no correlation between weaning age and play in carnivores.

With the onset of weaning, the juvenile period, as opposed to that of infancy, begins. The juvenile period is as the dominant period of play behaviour in primates (Freeman & Alcock 1973; Fagen 1981; Hayaki 1983; Eaton et al. 1986; Pereira & Fairbanks 1993a, b; Bloomsmith et al. 1994). Thus, the hypothesis states that the longer the juvenile period, the greater potential exists for the exhibition of playful behaviour. The results here concern primates, as there are no data available for the length of the juvenile period in carnivores. These findings reveal that the juvenile period is positively and significantly correlated with social play in primates; and when the effects of weaning age are removed, the juvenile period is positively and significantly correlated with total play in primates. These results thus support the hypothesis, as with the selection for an extended juvenile period, there have been increases in the amount of play exhibited. Juvenile primates have been selected for an extended juvenile period (Joffe 1997) during which social learning occurs, and the body, brain, and social relationships are developed, modified, and perfected in readiness for independent adult life (Byers 1999). It is therefore likely that play serves to facilitate these developments during the period when the brain and body are relatively plastic; indeed the trajectory of play during this period maps closely onto the shift towards maturity, with increasing independence limiting the prevalence of play (Fairbanks 2000). It is important to note that because females reach sexual maturity far earlier than their male counterparts (e.g. Dunbar 1979), males ostensibly have a longer pre-adult phase during which to prepare for adulthood. Thus, males tend to devote significantly more time to play than do females.

5.6.4 Birth and lactation

Although Bonferroni correction renders the relationship actually non-significant, we see a trend towards a positive correlation between age at first reproduction and both total and social play in primates. Explanations for this finding may be that females who reach sexual maturity somewhat later after a relatively longer juvenile period may have had more opportunity, or more need, in which to engage in play before becoming mothers. These individuals are likely to have had increased opportunities for social interactions, including play, and this may better equip them for adulthood. Play-mothering is a behaviour that occurs in some primates during adolescence (Lancaster 1971); this may enable experience of pseudo-mothering behaviours, especially in species that attain adulthood quickly. Additionally, new mothers may begin to increase their social play output at this time, after the cessation of play at the time of sexual maturity, by engaging in mother-infant playful behaviours with their offspring.

A similar trend, and pattern of significance is seen for lactation period in primates. Lactation period is positively and significantly correlated with total play in primates (prior to Bonferroni correction), suggesting that there is a trend for longer lactation periods being selected for, thus the propensity to engage in playful behaviours also increased. This may add further support to the hypothesis that the degree of postnatal development is vital to the expression of playful behaviours, although the result here is actually not significant. Lactation periods are indicative of the amount of time an infant remains dependent on its mother, and primates may suckle their young for up to 4.5 years (e.g. in chimpanzees). This dictates the period of infancy, dependence and relative development, which in turn may influence the potential to engage in play.

Again, prior to Bonferroni correction, IBI is positively and significantly correlated with total play and object play in primates, suggesting that the wider the gap between births, the greater likelihood of total and object play being exhibited. In carnivores, the reverse trend is true, with IBI being negatively and significantly correlated with total play, suggesting that as IBI has increased, the exhibition of total play has declined. This is likely to be connected to relative development and maturity rates, which differ between primates and carnivores. That these results fall short of significance may be due to small sample sizes.

Primates, by mammalian standards, have rather unusual life-histories, having long periods of growth, juvenility, and life expectancy, and a late onset of maturity and reproduction. Primates therefore, appear to have co-evolved traits for long life history, social complexity, and cognition (Key 2000). Conversely, carnivores tend to be more representative of the "typical" mammalian trend. If we are to understand the evolution of play in these two orders, then it is necessary to understand their life-history adaptations. Litter size is a variable that can be closely associated with diet. Species that give birth to small litter sizes tend also to be those that have an omnivorous diet. Conversely, species that give birth to larger litters tend to be those with a more carnivorous diet (Bekoff & Byers 1985). These factors might be associated with play in one of two ways. Omnivorous species tend to be those with longer gestation and lactation periods. It is thought that omnivores are better equipped to store and stabilise body fat enabling a more precocial life history and one that is adapted to surviving periods of famine. Under these conditions, we should expect omnivorous species to be relatively more playful than species is reliant on a more exclusive diet (Bekoff & Byers 1985). This is because play is so susceptible to changes in environmental conditions (Fagen 1981). Relatively more omnivorous species, with their long life histories and fewer precocial offspring, are also most likely to exhibit social complexity and socially cohesive groups, as well as demonstrating cognitive abilities (Key 2000). Conversely, it may be argued that large and exclusive carnivores play more to gain hunting experience; in this case we should expect to see significantly more object play amongst exclusive carnivores (Bekoff & Byers 1985). Indeed, relatively larger species also tend to be those with the longest lifespan. Such species are typically more prone to precociality, and thus more likely to be not only playful, but also to exhibit complexity in their play (Bekoff & Byers 1985). Play may therefore have evolved under conditions of behavioural flexibility due to changing environments, and that have selected for larger brains, and social groups.

5.6.5 Longevity

Maximum lifespan is positively and significantly correlated with both solitary locomotor play, and social play in primates. This relationship is borne out when both body size and brain size are partialled out of the analyses. Thus, the selection for longevity correlated with the selection for an increased amount of both solitary locomotor play and social play. This relationship does not however hold for carnivores, where there is a negative, but non-significant correlation with play. The sample size for these analyses are however, very small. We should expect play to correlate with lifespan, given that the most long lived species tend also to be those that give birth to precocial neonates, with longer periods of juvenility, during which the brain is permanently modified by playful behaviour (Bekoff & Byers 1985; Byers & Walker 1995; Fairbanks 2000). In captive situations, where species tend to live beyond the age of their wild counterparts, play is also a behaviour seen more frequently. This is due to the reduction of energetic constraints on finding food, shelter, and mates, and fighting disease and infection. One of the problems in using longevity data is that species that are not common in captivity will be assigned lower estimates of maximum lifespan (Deaner et al. in press).

Longevity is also strongly correlated with body size, which may act as an anti-predator mechanism (Harvey et al. 1987). It may be the case that relatively larger species, and thus those with the longest lives, and precocial neonates, are also those that can better afford to play, as they are also likely to be diurnal and group-living (gregarious). Indeed, it seems that long life, large brains, and large bodies have been co-selected over evolutionary time. It may be that complex behaviours are only possible where the CNS is fully mature; thus evolutionary increases in brain size not only delays sexual and physiological maturation, but in doing so facilitates a longer juvenile period during which the CNS is honed and complex behaviours mastered (Fairbanks 2000; Deaner et al. in press). Given the time frame of such maturation, the onset of play behaviour, and the results shown in this chapter, it seems reasonable to suppose that play too, has co-evolved with these adaptations for longer life and augmented cognitive abilities.

5.6.6 Play peaks

The results here suggest that across primates, neonatal body weight, more so than weaning age, is a good predictor of the developmental onset of play. This adds further weight to the hypothesis that relatively more precocial species are more playful than relatively more altricial ones, as precocial species are equipped to be playful very soon after birth. There are no significant results to suggest that weaning age predicts later peaks in play frequency. Fairbanks (2000) has shown that molar eruption is a good predictor of play peaks in juvenile primates.

5.7 Summary

Many life-history variables are demonstrated to have an effect on play behaviour in these analyses. Play behaviour appears to have co-evolved with the selection for large bodies, large precocial neonates in small litters, long-life histories, diurnality, social group living, and a large relative brain size. The strongest contingent in the exhibition of play, appears to be the extent to which a species bears altricial or precocial neonates. Play is most prominent in species that are relatively more precocial, and thus more well-developed at birth and with a longer period of postnatal infant and juvenile development in which to hone their bodies, brains, and behaviours to suit the conditions of the population. Under these conditions, play has evolved to be widespread and complex. Play is highly susceptible to environmental and social influences, and Chapter 6 will focus on the ways in which socio-ecology fits in with life-history in the evolution and exhibition of play behaviour in primates and carnivores.

Chapter 6:

Play & Socio-ecology

6.1 Introduction

In the previous chapter, life-history variables were analysed with regard to play behaviour, and inferences drawn about the evolution of play. Life-history variables are often strongly related to ecology, especially in terms of the constraints of diet on body size (e.g. Harvey et al. 1987), and the influence on group dynamics (Dunbar 1988: 55). Thus in turn, body size constrains life-history. Here, the focus is upon how socio-ecological factors are correlated with each category of play behaviour and what this might indicate about behavioural evolution in primates and carnivores. The play behaviour of any given species is likely to be especially associated with socio-ecology, in terms of environment, diet, and social organisation (Poole 1985). Both primates and carnivores offer an excellent basis for comparative studies of socio-ecology, given the variation within and between the species of each order in terms of habitat, diet, and social and behavioural traits (Bekoff et al. 1984; Bekoff 1989b; Lee 1999). The extent to which variation in play is related to variation in habitat and resources in largely unknown (Berger 1979; Bekoff 1989b), but it seems likely that play experience will be affected by diet and food distribution in the environment (Lee 1984). This chapter aims to shed some light on this from a comparative perspective.

6.1.1 Sociality

Most mammals are solitary (Poole 1985). Indeed, most carnivores are solitary, often only consorting with conspecifics for the purposes of mating (Sandell 1989). Primates are typically considered social, but do however comprise a great diversity of social strategies, including species that are group living, pair-bonded, and also solitary (Smuts et al. 1987; Rowe 1996; see also section 6.1.2 below). In comparison, only approximately 10-15% of carnivore species are habitually group-living (Gittleman 1989). However, studies of play appear to be heavily skewed towards canids, presumably due to the fact that canids include many species that are diurnal and live in social groups (Bekoff et al. 1984), and thus more easily observed, but also to the fact that some have relatively large brains, and often display food-sharing behaviours as well as tolerating, and even apparently caring for, sick adult group mates (Moehlman 1989).

There are clear advantages and disadvantages to living in groups, and several hypotheses exist for the evolution of group living. The benefits of group-living might include protection from predators (Elgar 1989; Fichtel & Kappeler 2002; Hass & Valenzuela 2002; Stanford 2002), access to mates and reproductive success (McNutt 1996), co-operative hunting (Mitani et al. 2002), especially with large prey (Stander 1992), effective group foraging (Rita et al. 1997; Zhang et al. 1999), enhanced opportunities for care-giving (Dunbar 1988: 106), and defence of resources (food; mates; suitable habitat) (Wrangham 1980; Krebs & Davies 1993; Johnson et al. 2001). Conversely, the costs to group-living might entail the transfer of parasites (Poulin 1991), competition for resources (both within and between groups) (Sterck et al. 1997), and visibility to predators (e.g. Poole 1985). Smaller species, or species that occupy open habitats, are typically most likely to exhibit forms of group defence, as they are more likely to be conspicuous to predators (Gittleman 1989). Group size is often dependent on ranging area and food availability. Thus in lions (*Panthera leo*), for example, pride size depends on territory range, which in turn is determined by the availability of prey. Numbers may vary from a few members, to prides of over 40 (Bothma & Walker 1999). In both primates and carnivores, variation in group size emerges in the form of units; there may be differences between overall group size, feeding groups where individuals share the same food source simultaneously, foraging or hunting groups where individuals form bands in search of food (Gittleman 1989), and there may be further distinctions in coalition group sizes, such as primary social partners (clique size), and overall social network sizes (Kudo & Dunbar 2001). As multi-level societies complicate the analysis of group size, it is important to consider these different levels of sociality in the study of behaviour, as they all yield different values.

6.1.2 Breeding strategy, mating system, and social organisation

Social organisation, as well as mating and breeding strategies, are also key factors in group-living, and systems vary widely across mammalian taxa, not least in carnivores and primates where several very different systems of social organisation are in place (Poole 1985). The mating and social systems of a species are likely to affect the way in which that species plays (Fagen 1981). Adult play, for example, might be more common in solitary species, whereby play may be used as a mechanism to overcome unfamiliarity (Pellis & Iwaniuk 1999a). In species where there is reduced paternal contribution to raising offspring, there is reduced female competition for males, and this is associated with polygyny, an adult sex ratio biased towards females, and male dispersal (Parental investment and sexual selection theory: Trivers 1972); this is typically true of smaller bodied carnivores (Moehlman 1989), and such species may exhibit higher levels of male-male play. Conversely, in species with larger litters of altricial neonates, male investment may be increased, and female competition for males might also increase as females cannot afford to share male investment with other females, and monogamy is more likely (Trivers 1972). In larger canids for example, co-operative male-female hunting, group defence, obligate monogamy, and "helpers at the den", are relatively frequent (Moehlman 1989).

Fissipeds (terrestrial carnivores) comprise species with very different mating and rearing systems, and include species that are basically solitary with overlapping male and female territories, such as bears and most felids; species with a system of dispersed harems, which includes many species of mustelids; canids, that are usually monogamous (Moehlman 1989), but often exhibit temporary monogamy (e.g. foxes, *Vulpes vulpes*); permanent monogamy whereby there is one breeding pair within a pack (e.g. jackals, *Canis aureus*); and those that live in permanent social groups or packs with clearly defined dominance hierarchies (e.g. wolves, *Canis lupus*) (Bekoff et al. 1984; Poole 1985; Gittleman 1989). Solitary species may only consort with conspecifics for the purposes of mating (e.g. leopard, *Panthera pardus*; caracal, *Caracal caracal*, Bothma & Walker 1999) and in this vein may exhibit opportunistic mating strategies (Poole 1985); other solitary species may be very hostile to species conspecifics (e.g. aardwolf, *Proteles cristatus*, Bothma & Walker 1999). Some solitary species are highly territorial with both males and females defending a home range. Other species may be less territorial, or seasonally so (African hunting dog, *Lycaon pictis*, Bothma & Walker 1999). Alternatively, some species may show a mix of solitary and social group-living, often with typically solitary or nomadic males, and with females forming stable units with their dependent offspring and perhaps some siblings (e.g. cheetah, *Acinonyx jubatus*, Bothma & Walker 1999). Pinniped social organisation is determined largely by food availability and breeding sites, as they come ashore to breed; those with the largest group sizes tend to be highly polygynous, whereas those with small or dispersed groups have a tendency toward monogamy (Poole 1985).

Primates too exhibit a great diversity in social organisation and breeding systems. Strepsirhines (Family: Lorisidae, Galagonidae, Cheirogaleidae, Megaladapidae, Lemuridae) are typically nocturnal and solitary, with the exception of some lemurs, which are cathemeral or diurnal (Doyle & Martin 1979; Tattersall 1987; Curtis & Zaramody 1999). Some males defend territories that encompass the territories of nearby females, exhibiting dispersed polygyny, whereas others are nomadic and have loose and overlapping ranges (Poole 1985). Although females may exhibit solitary foraging, due to wide food dispersal, the females of many species will group together in sleeping sites (e.g. grey mouse lemur, *Microcebus murinus*; fat-tailed dwarf lemur, *Cheirogaleus medius*; Demidoff's bush baby, *Galagoides demidoff*, Charles-Dominique & Bearder 1979; Poole 1985; Radespiel & Zimmerman 2001). Indris (*Indri indri*), in contrast exhibit monogamy, and ring-tailed lemurs (*Lemur catta*) support both male and female dominance hierarchies, with overall female dominance, and aggressively defend large territories (Jolly 1966; Sauther et al. 1999). Some gregarious sakis, uacaris (Pitheciinae), and some lemurs (Lemuridae) may also be monogamous (Rowe 1996).

Amongst haplorhines, species that exhibit typical monogamy tend to live in pairs or family units and are often highly territorial (e.g. marmosets, *Callithrix* spp.; gibbons, *Hylobates* spp. Dunbar 1995b, c; Bartlett 1999). Polygynous species tend to live in social groups, as a male's defence of his harem requires female-female tolerance (e.g. mountain gorilla, *Gorilla gorilla berengei*, Stoinki et al. 2001). Males often leave their natal group with the onset of adulthood to form male-bands, competing with one another for alpha status when attempting to join an established group (e.g. Hanuman langurs, *Semnopithecus entellus*, Hrdy 1977; Sommer & Mendoza-Granados 1995).

Alpha males usually cannot obtain and defend two harems simultaneously, due to the intolerance of the females towards members of the opposing harem (Poole 1985); however, juvenile offspring of different harems will often play when they encounter one another (Dolhinow 1972). Highly social multimale-multifemale groups or troops also exist, and may exhibit male or female dominance hierarchies (e.g. ring-tailed lemur, *Lemur catta*; chimpanzee, *Pan troglodytes*, Stanford 1998) or fission-fusion communities (bonobo, *Pan paniscus*, Indani 1991; spider monkeys, *Ateles* spp, Symington 1990). Dominance is usually positively correlated with age in these species, although lower-ranking males might compete for dominance ranking (Poole 1985). In such social systems, various mating strategies may be employed at different times: opportunistic mating, promiscuous mating, mate-guarding of an oestrous female, or affiliative and sexual bonding where the pair actively avoid other males (Goodall 1975; Poole 1985).

6.1.3 Habitat and dietary influences

Group-living and dietary habitats are typically linked, both in terms of nutritional value and in distribution; group-living may offer advantages in finding both a quantity and diversity of food, but a disadvantage in terms of intra-group competition (Kruuk 1972; Gittleman 1989). Food that is dispersed but high in quality tends to be exploited by solitary species, whereas species in social groups may show an advantage in gaining food that is unpredictably dispersed (Krebs & Davies 1993). Habitat richness in terms of food dispersal is one element likely to affect the exhibition of play behaviour (Sommer & Mendoza-Granados 1995); play diminishes when food distribution is scattered, as individuals transfer play time to foraging time (Baldwin & Baldwin 1974, 1976). Factors such as metabolism may have an effect on the play behaviour of these species (Burghardt 1988). The rate at which an individual can exploit environmental resources is governed by daily energy requirements (Nagy et al. 1999), and thus energetic constraints are likely to be a factor in play variability. Martin (1984a, b) has shown that in domestic cats, play accounts for 9% of the daily time budget and approximately 4% of an individual's daily energy expenditure under favourable conditions, so diet may constrain metabolic rate. Sharpe et al. (2002) showed that long-term nutritional status was positively correlated with social play frequency in wild meerkats (*Suricatta suricatta*). It has been shown that brain size and metabolism are correlated in mammals (Armstrong 1983), as are metabolism and ranging patterns and sociability (Martin 1981); these studies however, treated species as independent data points (Barton 1999). Conversely, McNab & Eisenberg (1989) and Barton (1999) claim that there actually exists fairly little evidence for a strong relationship between brain size and metabolic rate, as some variables affect metabolic rate without affecting the brain. Yet primates for example, may allocate 9-20% of their metabolism to the brain; in other mammals the figure stands closer to 5% (Bennett & Harvey 1985). More importantly, variation in metabolism can usually be explained by differences in body size and phylogeny, although factors such as diet, seasonality, temperature, and so on, may also contribute to this variance (Nagy 1994). Furthermore, it should be borne in mind that both body size and group size are often interrelated variables in mammalian orders, and may be also associated with energetic consumption and the availability of food sources (Gittleman 1989). This trend is not necessarily true of all orders however, and does not seem to be a strong factor in carnivore grouping systems; this may be due to the diversity of carnivore species with a greater percentage of large-bodied species (e.g. bears) living typically solitary existences, whilst smaller species such as meerkats live in large packs (Gittleman 1989).

Play types are largely dictated by habitat preference in terms of the degree to which an animal is arboreal or terrestrial. Aquatic and sub-aquatic play appears in some carnivores, such as otters and sea otters (*Lutra canadensis*; *Enhydra lutris*), mink (*Mustela vison*), and leopard cats (*Felis viverrinus*), although data are typically scarce (Poole 1985). In fact, most carnivores are actually good swimmers, but not all can be termed aquatic; but even predominantly aquatic species such as otters and pinnipeds, spend a substantial proportion of their time on land (Estes 1989).

6.2 Methods

Primate group size and adult mean body weight data are taken from a compilation in Barton (1999); missing values from Barton (1999) are taken from the relevant chapters in Smuts et al. (1987), and additionally from Rowe (1996). Carnivore group size data are taken from Gittleman (1989), and Dunbar & Bever (1998) (see Appendix). The data for other continuous and dichotomous ecological variables (see Tables 6.1-6.4) are taken from Barton (1999), Ross & Jones (1999), and Deaner & Barton (2002). Other carnivore data are also taken from Gittleman (1989). The data on each play behaviour category were collected from the existing primate and carnivore behaviour literature, as detailed in Chapter 2. Food availability can affect social interactions, and thus it is important to differentiate at some level between species that are artificially fed and those that are not (Rowell 1972; Bekoff et al. 1984). In this case, distinctions will be drawn where possible between captive- and wild-studied groups. The method of independent contrasts is used here, conducted on the CAIC computer programme (see Chapter 2 for details). Outliers have been removed in instances where CAIC has flagged them, and are indicated in the accompanying text. Statistics are shown only where there is a significant correlation in the sample, unless otherwise indicated. Non-significant statistics are presented in the Appendix.

6.3 Hypotheses

The following hypotheses are presented for play in primates and carnivores with regard to socio-ecological determinants. The null hypothesis, H_0, states that there will be no association between play behaviour and the socio-ecological variable in question. Below, alternative hypotheses, H_a, are proffered.

1. Species in larger groups should play more than those in smaller groups.

Group size is a variable proposed to affect play behaviours (Fagen 1981); play behaviour is likely to occur at a higher frequency in groups that offer more opportunities to engage in play, in terms of increased access to suitable playmates. However, it is unlikely that effect of group size is merely a constraint on the number of potential partners. Species in larger groups tend also to have relatively larger brains (Dunbar 1992), and therefore play may be functionally related to sociality, as sociality requires more learning mediated by play. Thus, it might be predicted that the amount of play will be greater in larger groups, due to the need to develop and maintain the skills required in group-living. In this case, it is predicted that social play in particular will be more frequent in larger groups, as group-living might have evolved to be beneficial for social facilitation and learning (Gittleman 1989). Thus it is predicted that social play behaviours in particular will correlate most significantly with breeding or "social" group size than with feeding group size. In addition, it may be the case the social play is the most important category of play for social development in social species. Indeed, social groups not only offer the opportunity to play, but this may be buffered by a necessity to engage in social play. Given that social play has been shown to have its own trajectory, and recently even considered to have an entirely separate function from other play categories (Panksepp 1998; Fairbanks 2000), social play may be the most important play within social groups, and an area that merits close attention in relation to group life.

2. Group size correlates with number of partners in play interactions.

It might be expected that group size and polyadic play are associated, as a larger group potentially requires a greater level of social interaction that can be facilitated through social play. Additionally of course, larger groups provide a greater number of prospective play-partners; this is unlikely to be true of dyadic play, as engaging in play with only one partner is less likely to be dependent on an increased group size above a threshold cohort size of 2. However, group size may correlate with the availability of similarly-aged partners; in species such as gorillas, where the group sizes are relatively small, there will be less probability of like-aged play partners than in comparison with species such as baboons, that live in much larger groups and thus with a relatively high probability of same-aged play partners. Similar to the hypothesis that group size may affect polyadic play, is the hypothesis that group size will be important to the inclination and preference to engage in play with same-aged, and possibly also same-sex conspecifics. Primates typically prefer to play with like-aged players whenever there is the opportunity to do so (e.g. Brown 1988). A larger group might typically offer the opportunity for play with individuals, most importantly of the preferred age, and in addition, the preferred sex. It is unlikely that a larger group alone will explain preferences for play with siblings or other relatives in juvenile primates. Group size is therefore likely to predict play frequency, both due to the availability of partners, but more likely, that life in social groups requires increased levels of social cognition that may be mediated by engaging in social play at an early age.

3. Play is affected by ecological constraints.

It has been established that time spent playing declines under conditions where food supplies are depleted (e.g. Baldwin & Baldwin 1976), thus play is especially sensitive to nutritional requirements (Burghardt 1988). By this argument, it is expected that species with animal protein-rich diets, especially those with a varied dietary intake, will exhibit more play than those without such a diet (Bekoff et al. 1984; Burghardt 1988). Primates may actually have relatively low protein requirements, due to growth rates being spread over time, thus despite the possibility of exploiting protein-rich food patches, the necessity for protein is not augmented, especially when diets include leaves (Oftedal 1991). Although leaves are protein-rich in comparison with fruit, their calorific value is lower (e.g. Kool 1992; Merkel et al. 1999); leaves however, are more abundant than either fruit or prey, and thus easier to obtain. Folivorous species must spend much more time eating and digesting their food than do frugivorous or predator species, and may seek leaves that are relatively lower in fibre (digestion inhibitors) to compensate for the relatively lower metabolic rate of folivores in comparison with frugivores (Kool 1992; Yeager et al. 1997). Folivore digestion and lower metabolic rate may conceivably impose a constraint on activity levels (Dasilva 1992), which may include play time. In tandem with a relatively low metabolic rate, folivores (especially folivorous primates) also have a smaller relative brain size (Bennett & Harvey 1985). It is predicted that play will be most prominent in species with a relatively high metabolic rate, and a larger relative brain size (see Chapter 7) in comparison with species with a lower metabolic rate and smaller relative brain size. Thus play should be more prominent in frugivores or predator species, than in folivores. Furthermore, species that are more frugivorous or subsist on prey items should show a greater expression of play in their behavioural repertoire (e.g. Fagen 1981; Bekoff et al. 1984; Burghardt 1988; Burghardt 2001).

4. Play will be more frequent in captive animals than in wild animals.

Play seems to be reduced when more pressing survival behaviours are required, such as predator avoidance, foraging, or finding shelter (Fagen 1981). These constraints are effectively removed in a well-maintained and thoughtful captive environment (Markowitz 1979), thus "freeing-up" time during which an individual can engage in behaviours such as play (Burghardt 1988).

6.4 Data

Table 6.1 gives continuous socio-ecological variables for primates. Table 6.2 gives continuous socio-ecological variables for carnivores. Table 6.3 gives dichotomous socio-ecological variables for primates. Table 6.4 gives dichotomous ecological variables for carnivores. Where two or more play data replicates exist for any one species, a mean was taken to represent the species average in this type of play (Chapter 2).

Table 6.1. Continuous socio-ecological variables for primates

Species	**† Feeding group size**	**†Breeding group size**	**‡Clique size**	**‡Network size**	**†Home-range (km)**	**†Day range length**	**∊Leaves %**	**†Prey %**	**➡Fruit %**	**➡ BMR**	**† Growth rate**	**†Sex ratio**
Alouatta palliata	-	-	-	-	-	-	-	-	32.0	2000	-	-
Ateles geoffroyi	-	16.98	3.38	9.5	1.4	-	10.96	2.0	79.8	-	20	-
Callicebus moloch	-	-	-	-	-	-	-	-	53.7	-	-	-
Callithrix jacchus	-	-	-	-	-	-	-	-	22.0	-	-	-
Cebus albifrons	-	13.0	-	-	0.80	-	2.1	62.2	24.6	-	-	-
Cebus apella	-	-	2.38	8.0	-	-	-	-	52.0	-	-	-
Cebus capucinus	-	-	-	-	-	-	-	-	67.5	-	-	-
Cercocebus albigena	-	-	-	-	-	-	-	-	64.0	-	-	-
Cercocebus atys	-	-	-	-	-	-	-	-	79.0	-	-	-
Cercopithecus aethiops	-	-	1.47	4.7	-	-	-	-	71.0	-	-	-
Cercopithecus diana	-	-	2.20	4.0	-	-	-	-	41.4	-	-	-
Cercopithecus mitis	14.9	18.66	5.20	17.0	0.37	1.3	20.0	19.78	54.5	3391.5	18	3.70
Cercopithecus neglectus	-	-	-	-	-	-	-	-	77.0	-	-	-
Colobus badius	50.03	33.96	2.40	6.5	0.53	0.66	76.03	4.0	26.0	-	-	2.5
Colobus guereza	-	-	1.36	3.9	-	-	-	-	14.0	2978	-	-
Erythrocebus patas	20.0	35.48	2.86	6.2	52.0	2.5	12.1	13.02	75.0	-	-	1.0
Gorilla gorilla	10.0	10.0	-	-	6.51	0.4	92.9	1.0	3.0	-	-	-
Hylobates lar	3.9	4.0	-	-	0.49	1.70	221.3	12.50	60.0	-	31	-
Hylobates syndactylus	-	-	-	-	-	-	-	-	47.0	-	-	-
Lemur catta	-	-	2.06	15.0	-	-	-	-	54.0	-	-	-
Macaca arctoides	-	-	1.60	5.0	-	-	-	-	-	-	-	-
Macaca fascicularis	-	-	-	-	-	-	-	-	66.9	-	-	-

Species	**† Feeding group size**	**†Breeding group size**	**‡Clique size**	**‡Network size**	**†Home-range (km)**	**†Day range length**	**∈Leaves %**	**†Prey %**	**☛Fruit %**	**☛ BMR**	**† Growth rate**	**†Sex ratio**
Macaca fuscata	-	-	4.57	22.6	-	-	-	-	38.0	-	-	-
Macaca mulatta	-	-	2.56	8.5	-	-	-	-	63.0	2239	-	-
Macaca nemestrina	-	-	-	-	-	-	-	-	75.0	-	-	-
Macaca nigra	-	-	-	-	-	-	-	-	-	-	-	-
Macaca radiata	-	-	8.60	21.3	-	-	-	-	-	-	-	-
Macaca sinica	-	-	-	-	-	-	-	-	97.0	-	-	-
Macaca sylvanus	-	-	2.21	8.0	-	-	-	-	33.0	-	-	-
Mandrillus sphinx	-	-	-	-	-	-	-	-	-	-	-	-
Nycticebus coucang	1.0	1.0	-	-	-	-	1.0	30.97	60.0	272.6	-	-
Pan troglodytes	3.9	27.99	3.07	8.8	21.49	3.89	25.03	11.51	28.0	9000	19	1.90
Papio anubis	-	-	1.77	7.0	-	-	-	-	-	-	-	-
Papio cynocephalus	33.96	63.5	2.44	21.0	24.1	3.61	23.71	4.89	62.0	-	-	2.0
Papio hamadryas	-	-	4.83	17.0	-	-	-	-	88.0	-	-	2.0
Papio ursinus	34.0	63.53	2.00	7.0	24.0	3.59	23.74	4.9	73.0	-	-	-
Pithecia pithecia	2.99	2.9	-	-	5.0	-	7.9	-	92.0	-	16	-
Pongo pygmaeus	-	-	-	-	-	-	-	-	64.0	-	-	-
Presbytis entellus	-	-	3.46	9.0	-	-	-	-	52.0	-	-	-
Pygathrix nemaeus	2.0	9.3	-	-	0.97	-	-	-	-	-	-	-
Saguinus midas	-	-	-	-	-	-	-	-	69.0	-	-	-
Saguinus oedipus	-	-	-	-	-	-	-	-	-	-	-	-
Saimiri sciureus	6.98	40.27	-	-	2.5	-	5.99	74.9	28.0	677	14	-
Theropithecus gelada	-	-	1.70	4.9	-	-	-	-	26.0	-	-	-

† Deaner & Barton 2002; ‡ Kudo & Dunbar 2001; ☛ Barton 1999; ∈ Ross & Jones 1999.

Table 6.2. Continuous ecological variables for carnivores

Species	**Population* group size**	**Feeding* group size**	**Foraging* group size**
Acinonyx jubatus	1.0	1.0	1.0
Ailuropoda melanoleuca	1.0	-	-
Arctocephalus australis	-	-	-
Canis latrans	2.0	1.5	1.5
Cerdocyon thous	-	-	-
Crocuta crocuta	55.0	18.5	6.4
Felis silvestris	1.0	1.0	1.0
Haliochoerus grypus	-	-	-
Helogale undulata	10.0	1.0	1.0
Lontra canadensis	3.2	-	-
Mustela putorius	1.0	-	-
Mustela vison	1.0	-	-
Panthera leo	9.0	6.5	2.5
Phoca vitulina	-	-	-
Selenarctos thibetanus	1.0	-	-
Speothos venaticus	-	-	-
Ursus americanus	1.0	1.0	1.0
Ursus arctos	1.0	-	-
Thalarctos maritimus	1.0	1.0	1.0

* Taken from Gittleman (1989).

Table 6.3 Dichotomous ecological variables for primates

Species	**☜Activity Timing**	**†Stratification**	**☜◊Frugivory**	**†◊Folivory**	**Mating system**
Allenopithecus nigroviridis	0	1	1	1	0
Alouatta caraya	0	0	0	0	0
Alouatta palliata	0	0	0	0	0
Ateles geoffroyi	0	0	1	1	0
Callicebus moloch	0	0	1	1	1
Callithrix jacchus	0	0	1	1	1
Cebus albifrons	0	0	1	1	0
Cebus apella	0	0	1	1	0
Cebus capucinus	0	0	1	1	0
Cebus olivaceus	0	0	1	1	0
Cercocebus albigena	0	0	1	1	0
Cercocebus atys	0	1	1	1	0
Cercopithecus aethiops	0	1	1	1	0
Cercopithecus diana	0	0	1	1	0
Cercopithecus hamlyni	0	0	1	1	0
Cercopithecus mitis	0	0	1	1	0
Cercopithecus neglectus	0	1	1	1	0
Colobus badius	0	0	0	0	0
Colobus guereza	0	0	0	0	0
Erythrocebus patas	0	1	0	1	0
Gorilla gorilla	0	1	0	0	0
Hylobates lar	0	0	1	1	1
Hylobates syndactylus	0	0	1	1	1
Lemur catta	0	0	1	0	0
Macaca arctoides	0	1	1	1	0
Macaca fascicularis	0	0	1	1	0
Macaca fuscata	0	1	1	1	0
Macaca mulatta	0	1	1	1	0
Macaca nemestrina	0	1	1	1	0
Macaca nigra	0	1	1	1	0
Macaca radiata	0	1	1	1	0
Macaca silenus	0	0	1	0	0
Macaca sinica	0	1	1	1	0
Macaca sylvanus	0	1	1	0	0
Mandrillus sphinx	0	1	1	1	0
Nycticebus coucang	1	0	1	1	0
Pan paniscus	0	1	1	1	0
Pan troglodytes	0	1	1	1	0

Species	**☚Activity Timing**	**†Stratification**	**☚◆Frugivory**	**†◆Folivory**	**∞Mating system**
Papio anubis	0	1	1	1	0
Papio cynocephalus	0	1	0	1	0
Papio hamadryas	0	1	0	1	0
Papio ursinus	0	1	0	1	0
Pithecia pithecia	0	0	1	1	1
Pongo pygmaeus	0	0	1	1	0
Presbytis entellus	0	1	0	0	0
Pygathrix nemaeus	0	0	0	0	0
Saguinus fuscicollis	0	0	1	1	1
Saguinus midas	0	0	1	1	1
Saguinus oedipus	0	0	1	1	1
Saimiri sciureus	0	0	0	1	0
Theropithecus gelada	0	1	0	1	0

☚ Barton 1999; † Deaner & Barton 2002; ◆ Derived from Rowe 1996; ∞ Smuts et al. 1987

Activity timing: 0 = day, 1 = night; Usual stratification: 0 = arboreal, 1 = semi-terrestrial/terrestrial; Frugivory: 0 = non-frugivorous, 1 = frugivorous (over 50% diet from fruit); Folivory: 0 = folivorous (over 50% diet from leaves), 1 = non-folivorous; Mating system (usual): 0 = polygynous/promiscuous, 1 = monogamous

Table 6.4. Dichotomous ecological variables for carnivores

Species	**Activity pattern**	**Zonation**	**Diet**	**Vegetation**	**Prey size**
Acinoynx jubatus	0	0	0	0	0
Ailuropoda melanoleuca	1	0	1	0	-
Arctocephalus australis	-	1	1	1	0
Canis latrans	1	0	0	0	0
Cerdocyon thous	-	0	0	-	-
Crocuta crocuta	1	0	0	0	1
Felis silvestris	1	0	0	0	0
Haliochoerus grypus	-	1	1	1	-
Helogale undulata	0	0	1	0	0
Lontra canadensis	-	1	1	1	-
Mustela putorius	1	0	0	0	0
Mustela vison	1	0	0	0	0
Panthera leo	1	0	0	0	1
Phoca vitulina	-	1	1	1	-
Selenarctos thibetanus	1	0	0	0	1
Speothos venaticus	-	0	0	-	-
Ursus americanus	0	0	0	0	-
Ursus arctos	1	0	0	0	-
Thalarctos maritimus	0	0	0	-	-

From Gittleman 1989.

Activity pattern: 0 = diurnal, 1 = nocturnal/arrhythmic/crepusular; Zonation: 0 = terrestrial/terrestrial and occasionally arboreal, 1 = aquatic; Diet: 0 = carnivorous (flesh-eater)/omnivorous, 1 = insectivorous/piscivorous/frugivorous and folivorous; Vegetation (primary habitat): 0 = open grassland/forest/woodland, 1 = aquatic; Prey size: 0 = small, 1 = medium-large.

6.5 Results

First, bivariate regressions of contrasts for each play category and group size are presented, with graphs. Thereafter, results are presented for each play category on socio-ecological variables, controlling for group size (partial correlation analysis), and graphs are only presented for significant results. Statistics are presented for each section where there is a significant correlation, and results for the non-significant statistics appear in the Appendix. It should be noted that where sufficient data are available, results for both primates and carnivores are analysed and presented; however, due to a lack of play data, many carnivore analyses are apparently "missing". A summary of the results is presented in Table 6.28 at the end of this section.

6.5.1 Primate mean group size

Table 6.5 details bivariate regression analyses of contrasts for each play category on mean group size in primates. Mean group size is positively and significantly correlated with total play (Figure 6.1). Group size is not significantly correlated with solitary locomotor play or with object play (Figures 6.2 and 6.3). Group size is positively and significantly correlated with social play (Figure 6.4).

Table 6.5 Bivariate regression analyses of play category on mean group size in primates

Play type	DF	F-value	p-value	co-efficient	r^2
Total	**1, 41**	**4.87**	**0.03**	**0.31**	**0.11**
Solitary	1, 20	0.35	0.56	0.08	0.02
Object	1, 14	0.002	0.96	-0.20	1.30
Social	**1, 23**	**6.29**	**0.01**	**0.56**	**0.22**

Bonferroni = 0.013, total play n.s.

These results therefore indicate, as predicted, an association between group size and social play, but no association between group size and non-social play categories.

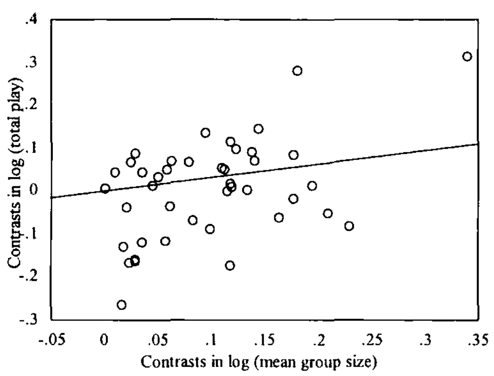


Fig. 6.1 Regression plot of log (total play) on log (group size) in primates primates

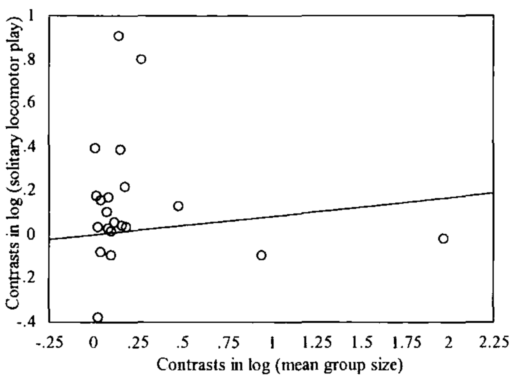


Fig. 6.2 Regression plot of log (solitary locomotor play) on (group size) in

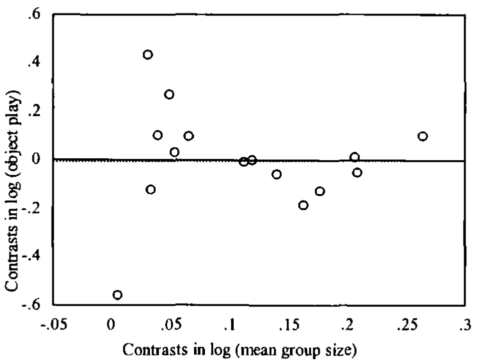


Fig. 6.3 Regression plot of log (object play) play) on log (group size) in primates

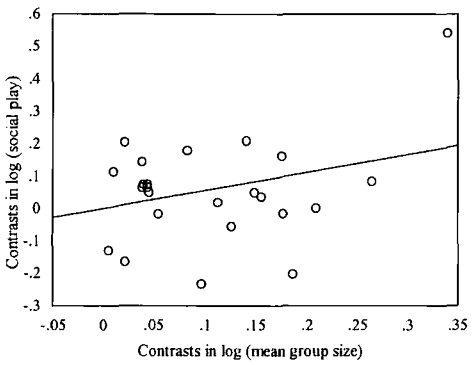


Fig. 6.4 Regression plot of log (social on log (group size) in primates

6.5.2 Carnivore mean group size

Table 6.6 details bivariate regression analyses of contrasts for each play category on mean group size in carnivores. Mean group size is not significantly associated with total play (Figure 6.5); one outlier has been removed as indicated by the CAIC programme. There were too few observations of solitary locomotor play and object play to permit a statistical result. Mean group size is positively correlated with social play, although the result does not reach significance (Figure 6.6).

Table 6.6 Bivariate regression analyses of play category on mean group size in carnivores

Play type	**DF**	**F-value**	**p-value**	**co-efficient**	**r^2**
Total	1, 5	0.08	0.78	-0.11	0.02
Solitary+	-	-	-	-	-
Object+	-	-	-	-	-
Social	1, 3	2.71	0.20	1.09	0.47

+ Too few observations

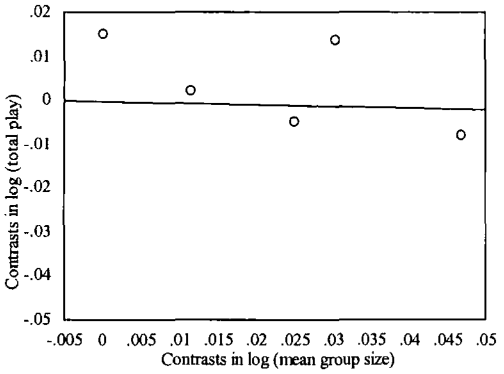


Fig. 6.5 Regression plot of log (total play) on log (mean group size) in carnivores

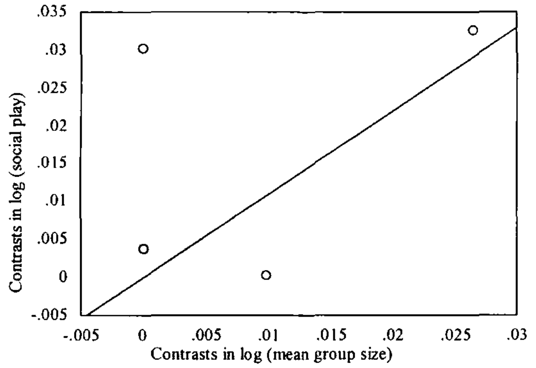


Fig. 6.6 Regression plot of log (social play) on log (mean group size) in carnivores

6.5.3 Breeding group size in primates

Table 6.7 shows the results of bivariate regression analyses of contrasts for each play category on breeding group size in primates. Regressions of total, solitary, and object play on breeding group size do not show any significant correlations. Regression of social play on breeding group size shows a positive and significant correlation (Figure 6.7); however, Bonferroni correction renders this result non-significant.

Table 6.7 Bivariate regression analyses of play category on breeding group size in primates

Play type	**DF**	**F-value**	**p-value**	**co-efficient**	**r^2**
Total	1, 9	0.72	0.42	0.25	0.07
Solitary	1, 4	2.06	0.25	0.79	0.41
Object	1, 3	0.03	0.88	0.14	0.02
Social	**1, 7**	**6.20**	**0.04**	**0.58**	**0.47**

Bonferroni = 0.013, n.s.

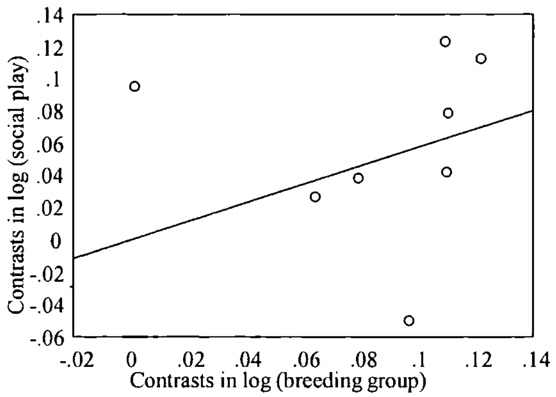


Fig. 6.7. Regression plot of social play on log (breeding group) size in primates

6.5.4 Population group size in carnivores

Table 6.8 shows the results of bivariate regression analyses of contrasts for each play category on population (maximum) group size in carnivores. Population group size is not significantly correlated with total or object play. There were too few observations of solitary play to permit a statistical result. Population group size is however positively and significantly correlated with social play (Figure 6.8). The relationship in Figure 6.8 is entirely driven by one point however; a larger sample size would enable a more detailed understanding of this relationship.

Table 6.8 Bivariate regression analyses of play category on population group size in carnivores

Play type	**DF**	**F-value**	**p-value**	**co-efficient**	**r^2**
Total	1, 8	0.47	0.51	-0.16	0.06
Solitary+	-	-	-	-	-
Object	1, 3	1.30	0.37	0.73	0.39
Social	**1, 4**	**17.70**	**0.01**	**1.12**	**0.82**

+ Too few observations

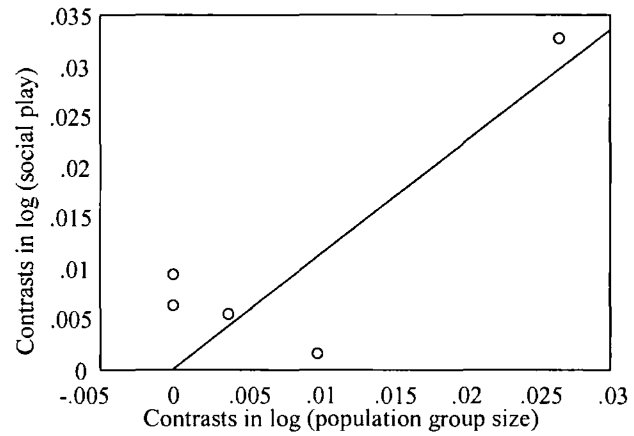


Fig. 6.8. Regression plot of log (social play) on log (population group size) in carnivores

6.5.5 Clique group size in primates

Table 6.9 shows the results of bivariate regression analyses of contrasts for each play category on clique size in primates. Regressions of total, solitary and social play on clique size show positive and significant correlations (Figures 6.9-6.11); however, Bonferroni correction renders the results for total and solitary play non-significant. Regression of object play on clique size does not show any association. The results for both total play and social play on clique size are displayed having removed one outlier as indicated in the CAIC analyses.

Table 6.9 Bivariate regression analyses of play category on clique size in primates

Play type	**DF**	**F-value**	**p-value**	**co-efficient**	**r^2**
Total	**1, 15**	**5.72**	**0.03**	**0.65**	**0.28**
Solitary	**1, 8**	**5.70**	**0.04**	**0.49**	**0.44**
Object	1, 3	0.39	0.58	6.25	0.12
Social	**1, 12**	**6.41**	**0.01**	**0.50**	**0.35**

Bonferroni = 0.013, total and solitary play n.s.

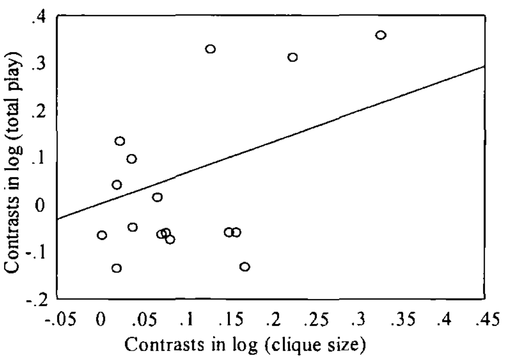


Fig. 6.9 Regression of log (total play) on log (clique size) in primates

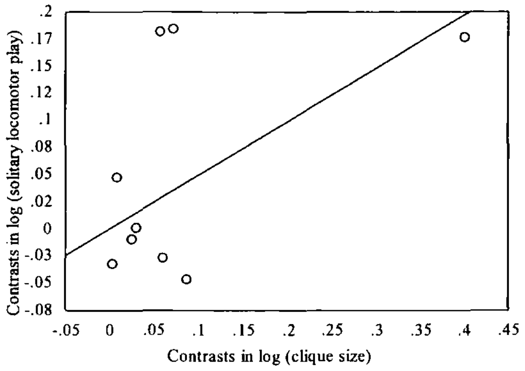


Fig. 6.10 Regression of log (solitary locomotor play) on log (clique size) in primates

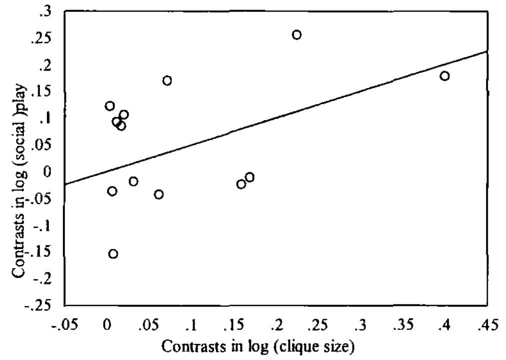


Fig. 6.11 Regression of log (social play) on log (clique size) in primates

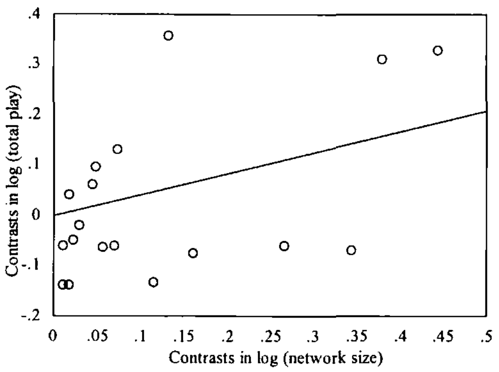
6.5.6 Network size in primates

Table 6.10 shows the results of bivariate regression analyses of contrasts for each play category on network size in primates. Regressions of total, solitary and social play on network size show positive and significant correlations (Figures 6.12-5.14); however, Bonferroni correction renders the results for total and solitary play non-significant. Regression of object play on network group size however, does not show any association. The results for social play and clique size (Figure 6.14) are displayed having removed one outlier as indicated in the CAIC analyses.

Table 6.10 Bivariate regression analyses of play category on network group size in primates

Play type	DF	F-value	p-value	co-efficient	r²
Total	**1, 17**	**5.231**	**0.04**	**0.42**	**0.24**
Solitary	**1, 8**	**5.76**	**0.04**	**0.41**	**0.42**
Object	1, 3	0.22	0.67	-1.31	0.07
Social	**1, 12**	**5.87**	**0.01**	**0.42**	**0.33**

Bonferroni = 0.013, total and solitary play n.s.



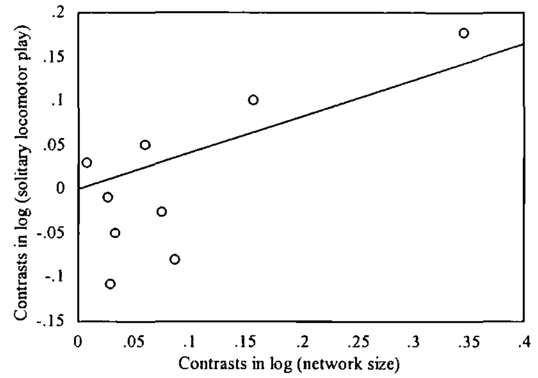


Fig. 6.12 Regression of log (total play) on log (network size) in primates

Fig. 6.13 Regression of log (solitary locomotor play) on log (network size) in primates

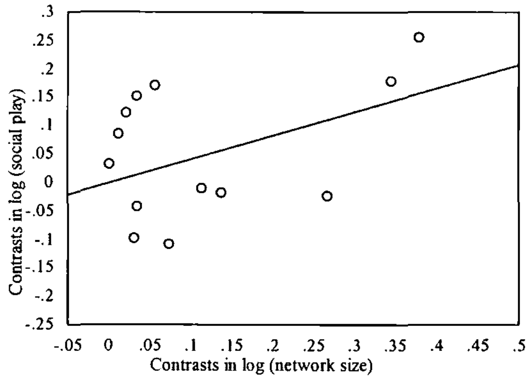


Fig. 6.14 Regression of log (social play) on log (network size) in primates

6.5.7 Home range size in primates

Home range size is a variable likely to be confounded by group size, thus the following analyses remove the effect of group size through partial correlation. Table 6.11 shows the results of partial correlation analyses of contrasts for each play category on home range size in primates, having removed the effect of group size by regression. Regressions of total and social play on home range size show a significant and positive correlation (Figures 6.15 and 5.16). Regression of solitary play on home range size does not reach the same significance, and there were too few observations of object play to permit a statistical result.

Table 6.11 Partial correlation analyses of play category on home range size in primates, controlling for group size

Play type	DF	F-value	p-value	co-efficient	r^2
Total	**1, 8**	**24.35**	**0.001**	**0.31**	**0.75**
Solitary	1, 3	4.27	0.17	1.01	0.68
Object+	-	-	-	-	-
Social	**1, 6**	**9.97**	**0.01**	**0.30**	**0.62**

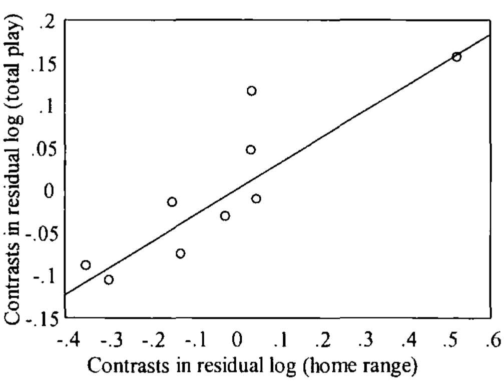
+ Too few observations.

A further variable likely to confound home range size is that of body size, thus the following partial correlation analyses remove the effect of body size. Table 6.12 shows the results of partial correlation analyses of contrasts for each play category on home range size in primates, controlling for body size. Regressions of total and social play on home range size show a significant and positive correlation (Figures 6.17 and 6.18). Regression of solitary play on home range size falls short of significance, and there were too few observations of object play to permit a statistical result.

Table 6.12 Partial correlation analyses of play category on home range size in primates, controlling for body size.

Play type	DF	F-value	p-value	co-efficient	r^2
Total	**1, 8**	**10.90**	**0.001**	**0.22**	**0.58**
Solitary	1, 3	11.23	0.07	0.60	0.85
Object+	-	-	-	-	-
Social	**1, 6**	**10.94**	**0.01**	**0.28**	**0.65**

+ Too few observations



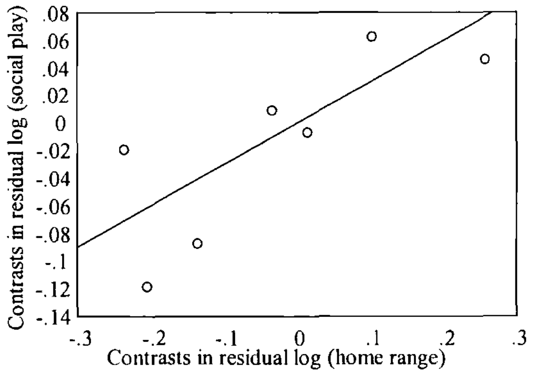
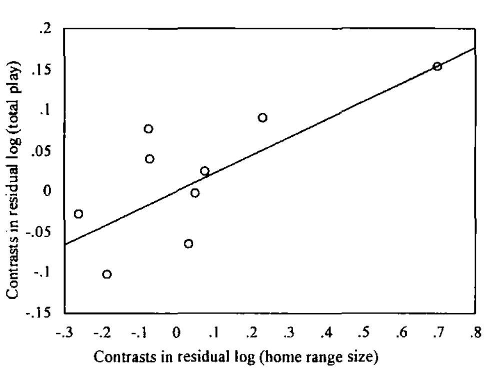


Fig. 6.15 Partial correlation of log (total play) on residual log (home-range size) controlling for group size in primates

Fig. 6.16 Partial correlation of log (social play) on residual log (home-range size) controlling for (group size) in primates



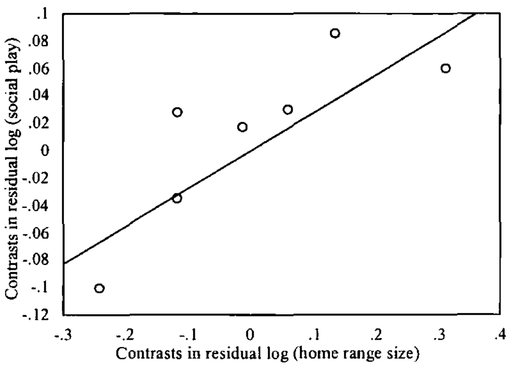


Fig. 6.17 Partial correlation of log (total play) on residual log (home-range size) controlling for body size in primates

Fig. 6.18 Partial correlation of log (social play) on residual log (home-range size), controlling for(body size in primates

6.5.8 Day range length in primates

Table 6.13 shows the results of bivariate regression analyses for contrasts of each play category on day range length in primates. Regression of total play on day range length shows a positive and significant correlation, with the removal of one outlier as indicated in the CAIC programme (Figure 6.19). Regression of social play on day range length does not show such a correlation. There were too few observations of either object play or solitary locomotor play to test for a statistical correlation. Unfortunately, there were rather too few contrasts to partial out the effects of either group size or body size from these analyses.

Table 6.13 Bivariate regression analyses of play category and day range length in primates

Play type	DF	F-value	p-value	co-efficient	r^2
Total	**1, 4**	**13.91**	**0.01**	**1.13**	**0.78**
Solitary+	-	-	-	-	-
Object+	-	-	-	-	-
Social	1, 4	1.35	0.31	0.36	0.25

+ Too few observations

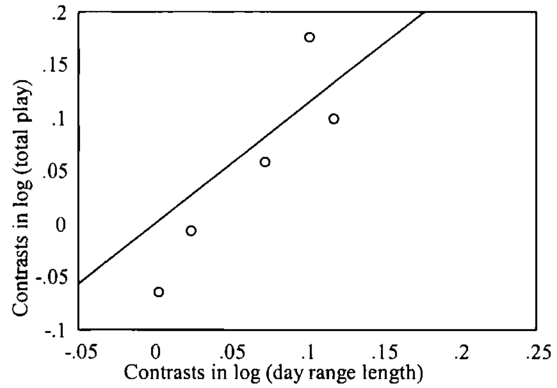


Fig. 6.19. Regression of log (total play) on log (day range length) in primates

6.5.9 BMR (Basal metabolic rate) in primates

Bivariate regression analyses were conducted for contrasts of each play category on BMR in primates. There were too few observations of solitary locomotor, object and social play to test for a statistical correlation. Regression of total play on BMR does not show a significant correlation.

However, as BMR is likely to be confounded by body size, the following partial correlation analyses remove this effect. Table 6.14 shows the results of partial correlation analyses of contrasts for each play category on BMR, removing the effect of body size. All results show a stronger correlation, having removed the effect of body size, however, it is only social play that is positively and significantly correlated with BMR in primates (Figure 6.20).

Table 6.14 Partial correlation analyses of play category on BMR in primates, controlling for body size

Play type	**DF**	**F-value**	**p-value**	**co-efficient**	**r^2**
Total	1, 4	3.75	0.15	3.65	0.56
Solitary	1, 3	6.04	0.13	9.38	0.75
Object+	-	-	-	-	-
Social	**1, 3**	**95.21**	**0.002**	**3.59**	**0.97**

+ Too few observations

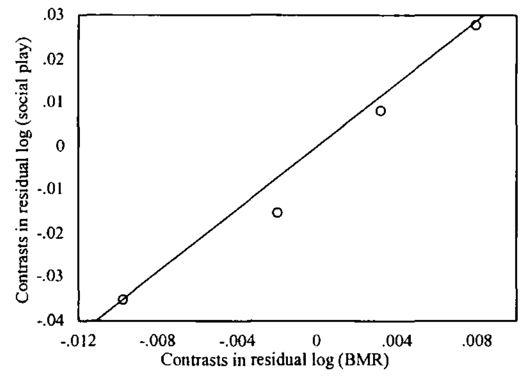


Fig. 6.20. Partial correlation of log (social play) on residual log (BMR) in primates, controlling for body size

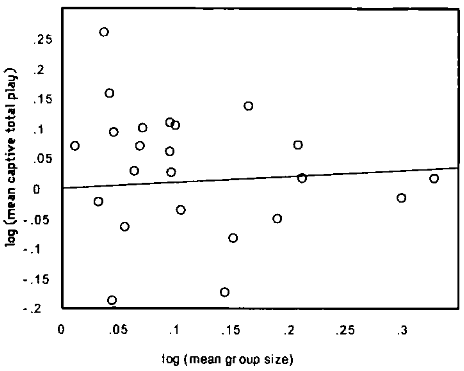
6.5.10 Captive and wild studies in primates

Table 6.15 shows regression analyses of contrasts of play on mean group size within each play category in primates. The results are split by whether a study is based in captive or wild observations. Graphs are detailed for all results to illustrate captive-wild comparison (Figures 6.21-6.27). Graphs on the left refer to captive studies, whilst those on the right refer to wild studies.

Table 6.15. Regression of mean group size on each play category, split by captive and wild studies in primates.

Play Category	**Captive/ wild?**	**DF**	**F-value**	**p-value**	**co-efficient**	**r^2**
Total	Captive	1, 23	0.38	0.54	0.097	0.02
	Wild	1, 14	0.001	0.97	0.008	1.09
Solitary	**Captive**	**1, 13**	**8.19**	**0.01**	**1.40**	**0.41**
	Wild	**1, 4**	**23.44**	**0.02**	**1.54**	**0.89**
Object	Captive	1, 7	4.69	0.07	0.53	0.44
	Wild+	-	-	-	-	-
Social	**Captive**	**1, 15**	**8.74**	**0.01**	**0.47**	**0.38**
	Wild	1, 5	0.34	0.59	0.71	0.08

+ Too few observations



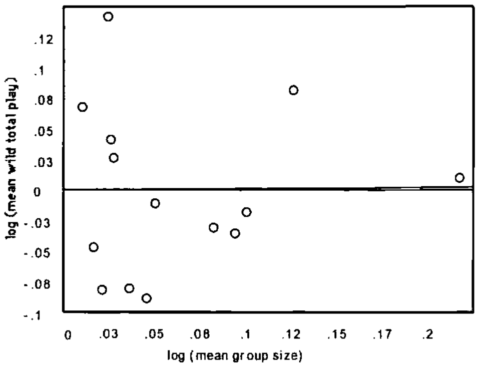
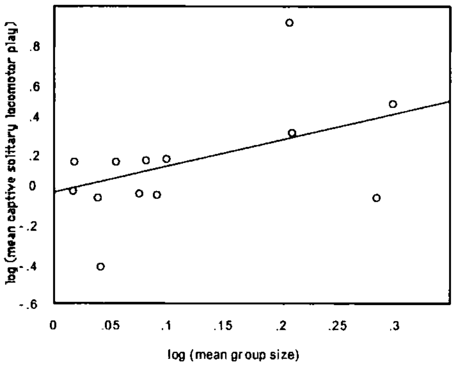


Fig. 6.21 Regression plot of contrasts of log (mean captive total play) on log (mean group size) in primates

Fig. 6.22 Regression plot of contrasts of log (mean wild total play) on log (mean group size) in primates



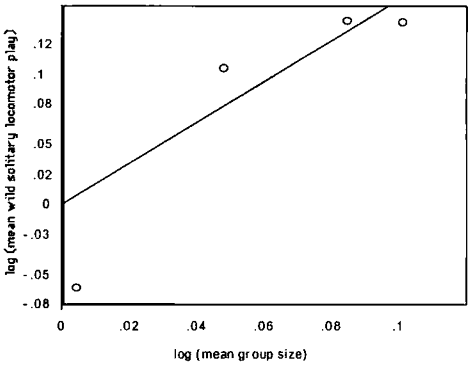


Fig. 6.23 Regression plot of contrasts of log (mean captive solitary locomotor play) on log (mean group size) in primates

Fig. 6.24 Regression plot of contrasts of log (mean wild solitary locomotor play) on on log (mean group size) in primates

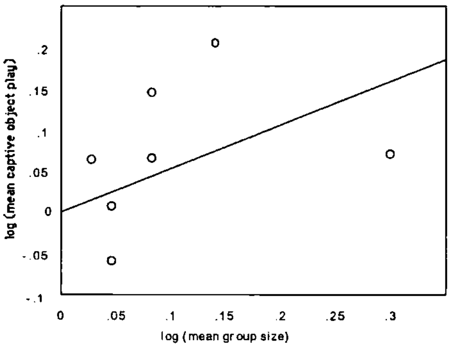


Fig. 6.25 Regression plot of contrasts in log (mean captive object play) on log (mean group size) in primates

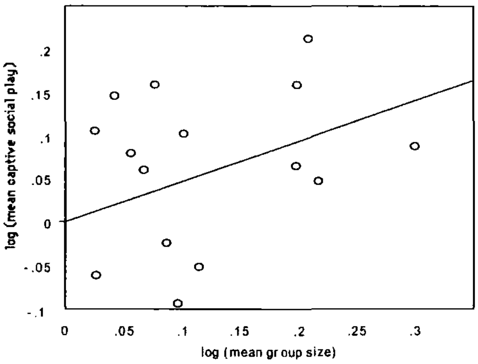


Fig. 6.26 Regression plot of contrasts of log (mean captive social play) on log (mean group size) in primates

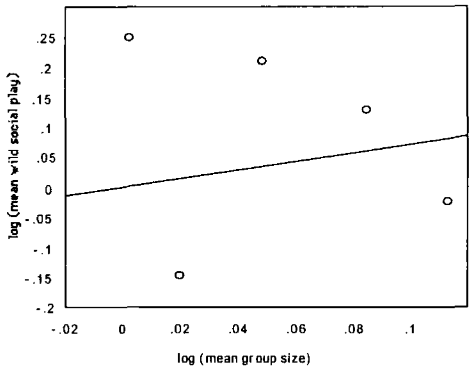


Fig. 6.27 Regression plot of contrasts of log (mean wild social play) on log (mean group size) in primates

6.5.11 No. of behaviours

The following set of analyses focus upon the number of different play behaviours recorded within a species' repertoire in primates, and control for research effort in months.

6.5.11a Group size

The following analyses focus on group size and number of behaviours controlling for research effort in months using the method of independent contrasts.

6.5.11ai Primates

Regression analyses of contrasts in the number of different play behaviours observed in a species' play repertoire against group size, controlling for research effort in months, reveals a positive correlation although falling short of significance (F (1, 16) = 3.32, p = 0.09, co-efficient = 0.33, r^2 = 0.17).

6.5.11aii Platyrrhines (New World primates)

Regression analyses of contrasts in the number of different play behaviours observed in a species' play repertoire against group size, controlling for research effort in months, reveals a positive, but non-significant correlation (F (1, 5) = 0.48, p = 0.52, co-efficient = 0.28, r^2 = 0.11).

6.5.11aiii Catarrhines (Old World primates and apes)

Regression analyses of contrasts in the number of different play behaviours observed in a species' play repertoire against group size, controlling for research effort in months, reveals a positive and significant correlation (F (1, 14) = 9.39, p = 0.008, co-efficient = 2.38, r^2 = 0.40) (Figure 6.45).

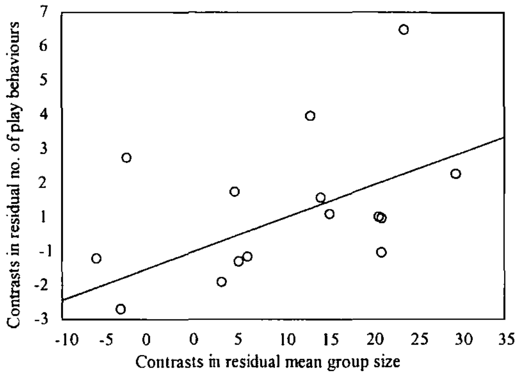


Fig. 6.28 Partial regression of mean group size on no. of play behaviours in the repertoire of catarrhines

6.5.12 Dichotomous variables

Table 6.16 shows one sample analyses (t-test) testing for significant evolutionary change in group size relative to the transitions in the dichotomous play variables in primates. Similar analyses with body size appear in Chapter 5.

Table 6.16 T-tests on changes in mean group size with transitions in dichotomous play variables in primates

Variable	Mean	DF	t-value	p-value	Significance?
Adult play	0.06	7	1.56	0.16	N.S.
Adult male play	-0.02	7	-0.53	0.61	N.S.
Adult-adult play	0.05	13	1.94	0.07	N.S.
Sex play	-0.02	14	-0.58	0.57	N.S.
SSD	0.03	14	0.98	0.34	N.S.
SSP	0.02	7	0.46	0.66	N.S.
SAD	-0.01	5	-0.35	0.74	N.S.
SAP	**-0.06**	**7**	**-2.57**	**0.04**	*
Sibling	-0.03	4	-0.99	0.37	N.S.

Variable	Mean	DF	t-value	p-value	Significance?
Relatedness	-0.04	5	-0.98	0.37	N.S.
Dominance	-0.003	3	-0.08	0.94	N.S.
Vocalisation	0.03	6	0.80	0.45	N.S.
Polyadic	0.06	3	2.79	0.07	N.S.
Interspecific	0.04	3	1.26	0.29	N.S.

* $p = < 0.05$; Bonferroni: 0.004, thus N.S.

Only one of the results detailed above is significant at $p < 0.05$. After making a Bonferroni adjustment (Moore & McCabe 1999), this result is non-significant.

As regression analyses showed the amount of play observed in a species to be predicted by social group variables, such as clique size and network size, and also home range size, Tables 6.17-6.27 show one sample analyses (t-test) testing for significant evolutionary change in these variables relative to the transitions in the dichotomous play variables in primates.

Table 6.17 T-tests on changes in mean clique size with transitions in dichotomous play variables in primates

Variable	Mean	DF	t-value	p-value	Significance?
Adult play	-0.03	6	-0.95	0.38	N.S.
Adult male play	0.005	4	0.31	0.77	N.S.
Adult-adult play	0.05	5	1.42	0.22	N.S.
Sex play	0.04	8	1.09	0.31	N.S.
SSD	0.01	7	0.89	0.40	N.S.
SSP	0.01	3	0.59	0.62	N.S.
SAD	-0.01	2	-0.15	0.91	N.S.
SAP	0.02	4	0.77	0.48	N.S.
Sibling+	-	-	-	-	-
Relatedness	-0.01	2	-2.75	0.11	N.S.
Dominance	0.02	2	0.64	0.58	N.S.
Vocalisation	0.01	3	0.94	0.42	N.S.
Dyadic+	-	-	-	-	-
Polyadic+	-	-	-	-	-
Parent play+	-	-	-	-	-
Place	-0.002	2	-0.09	0.94	N.S.
Interspecific+	-	-	-	-	-

+ Too few observations

Table 6.18. T-tests on changes in mean network size with transitions in dichotomous play variables in primates

Variable	Mean	DF	t-value	p-value	Significance?
Adult play	-0.03	6	-5.68	0.58	N.S.
Adult male play	0.003	4	0.20	0.85	N.S.
Adult-adult play	0.08	5	1.33	0.24	N.S.
Sex play	0.08	8	1.43	0.19	N.S.
SSD	0.41	7	0.66	0.53	N.S.
SSP	0.12	3	0.38	0.73	N.S.
SAD	0.01	2	0.80	0.57	N.S.
SAP	0.13	4	0.33	0.76	N.S.
Sibling+	-	-	-	-	-
Relatedness	-0.002	2	-0.09	0.93	N.S.
Dominance	0.02	2	0.44	0.70	N.S.
Vocalisation	0.02	3	1.18	0.32	N.S.
Dyadic+	-	-	-	-	-
Polyadic+	-	-	-	-	-
Parent play+	-	-	-	-	-
Place+	-0.003	2	-0.50	0.71	N.S.
Interspecific+	-	-	-	-	-

* $p = < 0.05$

Table 6.19. T-tests on changes in mean home range size with transitions in dichotomous play variables in primates

Variable	Mean	DF	t-value	p-value	Significance?
Adult play	0.17	3	1.93	0.15	N.S.
Adult male play	0.11	2	1.58	0.36	N.S.
Adult-adult play	0.11	2	1.72	0.34	N.S.
Sex play	-0.22	3	-0.16	0.88	N.S.
SSD	-0.03	5	-0.82	0.45	N.S.
SSP	0.08	2	1.37	0.40	N.S.
SAD+	-	-	-	-	-
SAP+	-	-	-	-	-
Sibling+	-	-	-	-	-
Relatedness	-0.01	2	-0.55	0.68	N.S.
Dominance+	-	-	-	-	-
Vocalisation	0.008	2	0.08	0.94	N.S.
Dyadic+	-	-	-	-	-
Polyadic	0.05	2	0.60	0.66	N.S.
Parent play+	-	-	-	-	-
Place+	-	-	-	-	-
Interspecific	0.06	2	0.39	0.74	N.S.

\+ Too few observations.

Tables 6.20-6.23 show tests for significant evolutionary change in play categories relative to the transitions in the dichotomous variables detailed below, where the hypothesised mean is equal to 0. As stratification is a variable likely to be confounded by group size, multiple regression analyses have been used here to remove such effects. Indeed, without controlling for group size, stratification shows a highly significant correlation with all play types, suggesting that group size accounts for most of the variance.

Table 6.20 Total play with dichotomous ecological variables in primates

Variable	Mean	DF	t-value	p-value	Significance?
Activity timing	-0.05	2	-15.91	0.04	N.S
Stratification	0.06	5	1.008	0.35	N.S
Frugivory	-0.06	15	-1.77	0.09	N.S
Folivory	-0.006	17	-0.30	0.77	N.S
Mating system	**0.06**	**4**	**5.15**	**0.001**	*

* p = < 0.05. Bonferroni = 0.01, activity timing n.s.

Table 6.21 Solitary play with dichotomous ecological variables in primates

Variable	Mean	D.F.	t-value	p-value	Significance?
Activity timing	0.75	2	3.00	0.20	N.S
Stratification	0.03	3	0.34	0.75	N.S.
Frugivory	-0.02	10	-0.82	0.43	N.S
Folivory	-0.02	10	-0.75	0.47	N.S
Mating system	-0.55	2	0.75	0.53	N.S

Table 6.22 Object play with dichotomous ecological variables in primates

Variable	Mean	D.F.	t-value	p-value	Significance?
Activity timing	0.001	2	0.005	0.99	N.S
Stratification	0.33	3	0.27	0.81	N.S
Frugivory	-0.10	5	-1.717	0.15	N.S
Folivory	0.05	8	0.78	0.46	N.S
Mating system	-0.14	2	-2.26	0.15	N.S

Table 6.23 Social play with dichotomous ecological variables in primates

Variable	Mean	D.F.	t-value	p-value	Significance?
Activity timing	-0.05	2	-1.71	0.34	N.S
Stratification	0.07	4	0.74	0.50	N.S
Frugivory	-0.02	11	-0.54	0.60	N.S
Folivory	-0.02	12	-0.60	0.56	N.S
Mating system	0.48	5	0.97	0.37	N.S

Tables 6.24-6.27 show tests for significant evolutionary change in play categories relative to the transitions in the dichotomous variables for carnivores detailed below, where the hypothesised mean is equal to 0.

Table 6.24 Total play with dichotomous ecological variables in carnivores

Variable	Mean	D.F.	t-value	p-value	Significance?
Activity pattern	4.63	6	0.06	0.96	N.S.
Zonation	-1.14	6	-0.02	0.98	N.S.
Diet	-0.001	6	-0.23	0.82	N.S.
Vegetation	-1.80	4	-0.02	0.99	N.S.
Prey size	-0.01	4	-0.14	0.89	N.S.

Table 6.25 Solitary play with dichotomous ecological variables in carnivores

Variable	Mean	D.F.	t-value	p-value	Significance?
Activity pattern+	-	-	-	-	-
Zonation	0.03	2	1.65	0.24	N.S.
Diet	0.02	2	1.66	0.24	N.S.
Vegetation+	-	-	-	-	-
Prey size+	-	-	-	-	-

+ Too few observations

Table 6.26 Object play with dichotomous ecological variables in carnivores

Var iable	Mean	D.F.	t-value	p-value	Significance?
Activity pattern	0.04	2	3.78	0.16	N.S.
Zonation	0.002	2	0.13	0.91	N.S.
Diet	0.02	2	14.15	**0.04**	*
Vegetation	-0.03	2	-0.13	0.92	N.S.
Prey size+	-	-	-	-	-

+ Too few observations; * p = <0.05, Bonferroni: 0.013, thus N.S.

Table 6.27 Social play with dichotomous ecological variables in carnivores

Variable	Mean	D.F.	t-value	p-value	Significance?
Activity pattern	-0.001	2	-0.13	0.91	N.S.
Zonation	0.01	4	1.39	0.24	N.S.
Diet	0.01	5	1.56	0.18	N.S.
Vegetation	0.02	3	3.39	**0.04**	*
Prey size+	-	-	-	-	-

+ Too few observations; * p = <0.05, Bonferroni 0.013, thus N.S.

6.6 Discussion

6.6.1 Sociality

Play frequency is likely to be not only increased in large groups, through an increased number of potential partners (Fagen 1981; Gittleman 1989), but also necessary in large groups, because of the need to develop social skills. Social complexity selects for social skills, mediated by large brains (and specifically larger neocortices) (e.g. Dunbar 1992, 1995a). A larger relative neocortex may require more play behaviour over the juvenile period to become properly "wired up". Thus, the performance of play behaviour supports the development of skills necessary for life in large groups. We therefore expect that species in larger groups will be those that are also most playful. The results in this chapter support this hypothesis for primates, in that group size correlates significantly with the amount of social play behaviour observed, suggesting that over the course of behavioural evolution, increases in group size were associated with increases in the amount of social play behaviour exhibited. The same trend is demonstrated for total play in primates, but the results fall short of significance after Bonferroni correction. There is a positive correlation between social play and group size in carnivores, although the result falls short of significance; possibly because of small sample sizes. However, with carnivore overall (maximum) population group size, the result is both positive and significant: the larger the (local) population group size, the greater the number of increased partners, and thus the increased likelihood and opportunity for (social) play. Again, the sample sizes for the carnivores analysed here are small, and thus caution is required in forming conclusions as to this relationship.

Table 6.28 Summary of results of socio-ecological variables on each category of play in primates and carnivores

Socio-ecological variable	Play category: significant correlation?			
	Total	Solitary locomotor	Object	Social
Mean group size	✓ +	✗	✗	✓ +
	✗	-	-	✗
Feeding group size	✗	✗	✗	✗
	✗	-	-	✗
Breeding group size	✗	✗	✗	✓ +
Population group size	✗	-	✗	✓ +
Clique size	✓ +	✓ +	✗	✓ +
Network size	✓ +	✓ +	✗	✓ +
Foraging group size	✗	-	-	-
Home range size (group)	✓ +	✗	-	✓ +
Home range size (body)	✓ +	✗	-	✓ +
Day range length	✓ +	-	-	✗
% leaves in diet	✗	✗	✗	✗
% prey items in diet	✗	✗	✗	✗
% fruit in diet	✗	✗	✗	✗
Sex ratio	✗	✗	✗	✗
BMR	✗	-	-	-
BMR (body)	✗	✗	-	✓ +
Growth rate	✗	-	-	✗

✓ = significant, ✗ = not significant, + = positive correlation, - = negative correlation/no data; Symbols: **Black** = primates, Red = carnivores.

As social groups often break off into smaller units for social and foraging purposes (Kudo and Dunbar 2001), it is expected that play, especially social play, will show an evolutionary relationship with more tight-knit social group units, such as clique size and network size, which is indeed what is shown in the results presented here. Play categories and feeding group sizes (number of individuals simultaneously collecting around a food source or kill) show no significant associations. However, feeding group size is not necessarily a relevant measure of partner availability or sociality. For example, it may be that adults control feeding group numbers. Additionally, infants and juveniles might not always be present in typical feeding groups. As the need to feed suppresses play behaviours (Fagen 1981), it seems unlikely that feeding group size will predict the amount of play behaviour expressed. None of the play categories showed an association in primates, and although carnivore data for this result pertain only to total play, no significant correlation emerged. The same trend thus links primate feeding group size, and carnivore feeding group and foraging group size, and possibly for similar reasons.

There is a positive and significant evolutionary correlation between breeding group size and social play in primates, however this falls short of significance when controlled for Bonferroni procedure. However, a trend is indicated for smaller social groups to be important to the exhibition of social play. Breeding groups, network sizes, and clique sizes are generally small and close-knit units, and thus may be an indicator of social bonds. In multi-level societies, these close-knit groupings represent the "true" social units, within which individuals have well-differentiated and stable long-term relationships (Kudo & Dunbar 2001). In species with especially large population sizes, such as baboons (*Papio* spp.), it is possible that these affiliative subgroups hold more sway in the exhibition of play, rather than overall group size, as it may be difficult to maintain social bonds with extremely large numbers of conspecifics. Indeed, amongst primates, it seems that clique size best predicts evolutionary increases in time spent playing. The results here indicate that total, solitary, and social play, are positively and significantly correlated with clique size in primates. The exception to this rule is object play, although the sample size is small. This result is interesting as clique size is formed of the individual's most common social partners (Kudo & Dunbar 2001), thus it is expected that the social kernel of the player's own network should be useful in predicting social behaviours, such as social play. Interestingly, before Bonferroni correction, clique size also correlates strongly with solitary locomotor play. This may be due to an increase in play behaviour in a general sense. As a juvenile's clique is likely to include its mother, there is limited argument for locomotor play acting in displays of competence to parents (Chiszar 1985). An almost identical trend is shown in primates for play and network size. This may be as network size is an expanded version of clique size, incorporating all major social partners (Kudo & Dunbar 2001).

Adult sex ratio does not appear to be a significant factor in the evolution of each play category. This is an interesting finding given that play assists in preparation for adult social behaviour, and that sex ratio correlates with mating systems and sexual competition. Sex differences and preferences for same-aged and same-sex partners in play are apparent in many species, although the dichotomous variables analysed here do not show any significant relationship with group size, clique size, network size or home range size. Socio-ecological variables are likely to affect and control the hormonal mechanisms of an individual. These in turn affect and control the exhibition of play. The results here can draw no positive conclusions regarding the relationships between such variables, although particularly small sample sizes in some analyses may be crucial. There is certainly a shortage of available data studies that detail these occurrences in field studies; future ethological work should aim to report such episodes where possible.

In primates, mating system is shown to be a variable significantly associated with the amount of total play. This is likely to be concerned with social structure. We would expect polygynous species to exhibit high rates of social play, due to the increased prevalence of male-male aggression in adulthood to compete for mates and resources. However, social play and mating structure are not significantly associated in the results from the dichotomous analyses here. It may be necessary to distinguish more explicitly the range of mating systems into more categories (e.g. dispersed polygyny, harem, promiscuity, etc.).

The results detailed in this chapter indicate the importance of sociality to the expression of social play behaviour. It is likely therefore, that the social play of relatively large brained taxa, or those with large neocortices, such as primates and carnivores, is necessary for successful group living. In order to be a "successful" member of the group, it is important to be able to react to social cues quickly, efficiently, and accurately. The same skills are required for a successful social play bout (Špinka et al 2001). In addition to honing the CNS during development (Fairbanks 2000), play, and especially social play, contributes to forming social bonds, learning social skills, and may even facilitate "socialisation" during infancy and juvenility (Bekoff et al. 1984). This is borne out by the evolutionary correlation between time spent in social play and clique and network group sizes, in that social play is especially prevalent among highly social units.

6.6.2 Habitat & Diet

It has been shown that species in richer habitats exhibit relatively greater amounts of play behaviour than species in poorer habitats (Sommer & Mendoza-Granados 1995). Species with a larger home range size are also likely to be those with a relatively larger group size, and possibly also larger relative brain sizes (see Chapter 5 and Chapter 7 for further discussion). Additionally, home range size and body mass should also be correlated as larger species require more energy (McNab 1963). It is therefore expected that species that occupy a larger home range are more playful. In such species, play may be a necessary behaviour, given that large home ranges are typically associated with lower environmental productivity and food density, and increased risk of predation. The factors have selected for a larger group size, especially in open habitats (Gittleman 1989), and as the results show, group size correlates with play time budgets. However, the results here show that there is a positive and significant correlation between home range size and time spent in total and social play behaviour in primates, which remains even after removing the confounding effects of group size and body size.

There was also a positive and significant relationship between total play and day range length in primates. Species or populations with an increased day range length tend also to spend more time travelling and foraging (Dunbar 1992). So this result is somewhat counter to the expectations of the idea of time and energy constraints. The result may reflect the positive correlation between group size and day range length (Dunbar 1992).

As habitat and nutritional richness appear to affect the exhibition of play behaviour (Fagen 1981; Burghardt 1984), it is predicted that access to (high-quality) food as well as primary food sources, will be important constraints on play behaviour, especially given that diurnal and frugivorous species typically have larger neocortical visual areas (Barton 1996) (Chapter 7 will look more closely at how the brain relates to play). However, the results here do not support such hypotheses when percentages of leaves, fruit, and prey items in the diet are considered. Non-significance is also reported for prey size and diet in carnivores, in the dichotomous variables analysed here. It was predicted that species with increased access to animal protein would exhibit more play, whilst species with a diet high in toxins (e.g. folivores) would be relatively less playful (Burghardt 1988). Although none of the results here are significant, the general trends in the data reveal that for all play categories, there is no association between play and percent of leaves in the diet, and mildly negative associations between percent of fruit and prey items in the diet. Thus, according to my results here, diet does not actually appear to be a good predictor of play prevalence. Growth rate is also affected by diet and metabolism, but does not appear to be an evolutionary factor in the evolution of play time budgets, which is an interesting result, given the evidence for precocial species being more playful in the results in Chapter 5. Explanations for this are unclear, although small sample size may again have an effect.

6.6.3 Metabolic rate

One difficulty here is the lack of data on basal metabolic rates (BMR) for the species analysed. However, the results show that social play is positively and significantly correlated with BMR in primates, controlling for the effect of body size, although the sample size is small. This is an important finding. Given the motor elements of most play behaviours, it seems intuitive that BMR should be a factor in the exhibition of play, even though play itself is almost certainly not performed for the purposes of exercise (Byers 1998b). Caution must still be taken given the small sample size; however, the strength of the relationship suggests that energy constraints are important in the expression of (social) play. Indeed, although the rate of energy consumed by play may typically be relatively low, like other behaviours and conditions such as thermoregulation and other activity patterns, it remains a metabolic expenditure and should affect an individual's daily energy requirement and metabolic rate (Nagy 1994). Thus the results in this chapter indicate that certain ecological variables do in fact affect the expression and exhibition of play behaviour, especially in terms of metabolism and home range size. It is odd that there was no relationship found between BMR and total play; the p-value falls short of significance, perhaps due to small sample sizes, or because only social play is energetically expensive.

Metabolism may certainly pose a constraint on the exhibition of play behaviour. The time and energy devoted to play is typically reported at less than 10% of a species' daily budget (Bekoff & Byers 1992). Bekoff and Byers (1992) argue that it might be more intuitive to describe time and energy devoted to play in terms of the amount exhibited relative to the daily *active* time budget, rather than include time spent resting. The examples they offer include Bekoff & Wells' (1986) study of coyotes (*Canis latrans*) whereby play accounts for 1% of the daily time budget, but 2% of the daily *active* time budget; and Miller & Byers' (1991) study of pronghorn fawns, that devote 1.9% of the day playing, which translates to 8.4% of their active daily active time budget. Martin (1984b) has also shown that kittens devote between 4 and 9% of their time and energy budgets in play. BMR not only varies with diet, also varies considerably with climate, with species in more tropical zones typically having lower BMR than species in colder climates (McNab 1989). This of course, is connected to diet and food availability, but in any case, future studies of play should aim to include latitude of species' populations as a dependent variable.

Although the brain is somewhat robust in terms of sensitivity to nutritional deficiencies (Guesry 1998), marked malnutrition during critical periods in development may adversely affect brain and retinal development, especially in terms of skill acquisition (Gordon 1997). It is argued that providing the developing infant receives sufficient psychomotor stimulation, the brain should develop normally (Guesry 1998). Could it then be argued that play acts as a buffer against certain aspects of malnutrition, particularly early in ontogeny? Play may certainly provide a sufficient stimulus for psychomotor development, and arguably could protect the process of myelination from the deleterious effects of malnutrition. Myelin is a fatty insulating sheath that covers nerve fibres (e.g. Bear et al. 2001). It is especially associated with brain conductivity, and thus myelination is considered to be one key indicator of intellectual performance (Miller 1994). Myelin synthesis is sensitive to nutritional effects, and severe malnutrition may lead to fewer fibres becoming myelinated (Gordon 1997). "More intelligent" brains are argued to be more energy efficient (Parks et al. 1988). Haier et al.

(1988) showed that individuals considered to be highly intelligent, performing well in a variety of neuropsychological tasks, also had thickly myelinated axons, which use less glucose, in comparison with individuals who performed less well, with thinly myelinated axons, requiring a high glucose consumption. Diamond (1988) found that rats raised in an enriched environment, which has been shown to improve maze-learning abilities, also had lower glucose utilisation in certain neural regions. Thus, thicker myelin is associated with faster reaction times and skill acuity, and importantly, its developmental trajectory appears to correspond with the honing of certain skills and stages of developmental advancement (Miller 1994). Additionally, myelination is considered to be one marker for, and explanation of, improved intelligence through juvenility and into adulthood (Miller 1994). It may be the case that species in large groups require play behaviour, and that this can be better facilitated by encouraging psychomotor development through play at crucial periods of neural development, thereby honing the CNS (see Fairbanks 2000). This may have a dual purpose of combating environmental variance, specifically fluctuations in food availability, in order to produce more efficient brains. Chapter 7 will consider the rôle of the brain to play in more detail, however, there is considerable overlap in the effects of neurological, socio-ecological, metabolic, and life-historical variables.

6.6.4 Captive and wild studies

The results here suggest that captivity is likely to have an effect on the rate at which species engage in different play categories. In regression of total play on group size for all studies, total play is positively and significantly correlated with group size. When split by captive and wild, however, we see that although captive studies reveal a positive relationship, it is not a significant one. Wild studies do not appear to make up the shortfall in this significance, showing almost no association between group size and total play time budgets in primates. Similarly, in the complete sample, we see no association between solitary locomotor play and group size; yet split by captive and wild studies, both samples are positive and significant. This discrepancy may be due to sampling effects. There are too few observations of wild object play to split wild studies from captive studies, however, here the trend is less surprising: the entire sample shows a negative but non-significant correlation between object play and group size, whereas there is a positive although non-significant relationship between object play and group size in captive studies. Captive studies may offer the best way to assess object play and its patterns, as so few of these are reported in the wild. Finally, social play in the entire sample shows a positive and significant correlation with group size. When split by captive and wild studies, we see that captive studies show the same trend, whereas wild studies, although positive, are non-significant. This suggests that the data from captive studies are driving the result. Further work is needed to establish whether the stronger correlation for captive than wild populations is a real effect or a sampling effect.

As the complete database sample takes data from wild and from captive studies, I suggest that this measure offers a reasonable way in which to assess the potential, as well as the actual play time budget investment among species. What these results do indicate however, is the need to distinguish between captive and wild studies, especially in the study of behavioural categories such as play, that are so sensitive to environmental and social factors (e.g. Bernstein 1972; Erwin & Deni 1979; Maple 1979; Fagen 1981; Smith 1984; Brown 1988; Jensen 2001; Bloomsmith 1989). It is often useful to split these categories in order to assess behavioural differences. It is always likely that more complex, or indeed novel behaviours will be both witnessed and recorded from animals housed in captivity, whereas wild observations are fewer in number and in study duration for most species. I believe that pooling captive and wild data, as well as using phylogenetic information, can provide a rounded understanding of species behaviour, provided the effects of both are borne in mind.

6.6.5 Number of play behaviours

The results here show that group size explains some of the variance in the number of distinct play behaviours recorded in a species group. Amongst primates the result is not significant, but for catarrhines alone, the result is significant. These results suggest that among Old World anthropoids, evolutionary increases in group size are correlated with increases in behavioural play repertoires. It is likely that there simply is not the same variance in group size in the platyrrhines in the database, as for the catarrhines, especially as many of the platyrrhine species in the sample are callitrichids (thus living in habitually monogamous pair bonds rather than large social groups).

6.7 Summary

Play behaviour, like other behavioural categories, appears to be affected by socio-ecological variables. The results in this chapter demonstrate the importance of group size to the expression of play behaviour in primates and where analyses were possible, in carnivores. In primates, clique size and network sizes best predict play time budgets. In carnivores there is a similar correlation between social play and population group size, and the trend holds for mean group size, although the result is not significant in this case. It is likely that "social" groups, meaning those groups within which individuals have stable, differentiated relationships, best predict the expression of social play behaviour. This may be due to the increased reliance on social relationships in larger groups. Captivity appears to increase certain play behaviours in terms of time devoted to it; this is likely to be as socio-ecological factors can be better controlled, thus limiting the time required for foraging and predator avoidance, as in their wild counterparts.

The amount of time spent playing represents a trade-off between costs and benefits. Energy expenditure is one such cost. Despite previous work, diet alone does not appear to be a key factor in the evolution of play time budgets. The correlation between play and home range size may be explained by the fact that species with larger home ranges typically form larger social groups. Further work is needed to assess the rôles of energy constraints and socio-cognitive benefits in the evolution of play time budgets.

Chapter 7:

Play and the Brain

7.1 Introduction

Despite a recent rise in interest as to the brain's rôle in play behaviour, relatively little is understood regarding relationships between the brain and play in mammals (Siviy 1998). Most studies that deal with play and neurobiology are concerned with rats (Vanderschuren et al. 1997), although comparative research is starting to focus on other mammalian species and orders (e.g. Byers 1999; Iwaniuk et al. 2001). Given the heterogeneity of both play as a behaviour, and of the brain as an organ, it is likely that different parts of the brain are involved in different aspects of play behaviour; thus a component-specific approach is required. By studying neural components that may be involved in mediating the various facets of play behaviour, it is hoped that a greater recognition of play and brain interactions will be achieved. This might be especially useful in attempting to understand evolutionary patterns and processes in brain-behaviour development.

7.2 Regions of the brain

The neuronal components of each region of the brain are selectively connected to form organised patterns (Eccles 1977), thus each part of the brain has been selected to perform different but overlapping tasks. Part of the key to understanding brain-behaviour relationships is in looking closely at the part that each brain region plays in specific behaviours, and how these are connected to make up distributed neural systems. Size comparison of different brain components across different species can assist the understanding of brain function capacity (Stephan et al. 1988). Below is an overview of the functions of various brain parts for which extensive comparative volumetric data exists. Figure 7.1 is a diagram of the lateral view of a macaque brain; a diagram of the human brain will be used to demark further brain components in this chapter.

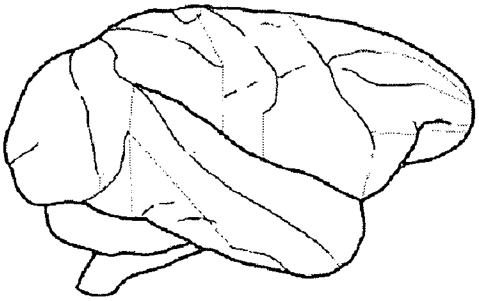


Fig. 7.1 Lateral view of the macaque cerebral cortex

7.2.1 Forebrain

The forebrain comprises various structures that function in the perception, awareness, cognition, and voluntary actions, through sensory-motor neuron interconnections of the brain stem and spinal cord (Bear et al. 2001). Evidence from the play literature suggests that forebrain structures are likely to be important to play behaviour (Burghardt 2001). The structures of the forebrain are detailed below.

7.2.1.1 Neocortex

Possibly the most important forebrain structure is the cerebral cortex (or cerebral *neo*cortex), which is thought to be the most expanded part of the brain in human evolution (Deacon 1997). The neocortex encloses the entire midbrain region in humans, and comprises between 50-80% of the brain's volume in primates, and 75% of the brain's neurons (Russell 1988), and is present only in mammals (Bear et al. 2001). Indeed, most differences between extant primate species have been brought about by neocortical evolution (Passingham 1973; Dunbar 1992). Although the size of the neocortex has expanded in mammals over evolutionary time, its basic structure has not (Jerison 1973). It appears that large areas of the cortex are not associated with a single modality, but integrate information from various senses in order to create a coherent understanding of the external environment. These are called association areas (Russell 1988). Recent comparative studies of the neocortex have found correlations with group and network sizes in mammalian taxa, such as primates (Dunbar 1992, 1995; Kudo & Dunbar 2001), and in particular haplorhines (Barton 1993, 1996), as well as carnivores and selected insectivores (Dunbar & Bever 1998) and dolphins (Marino et al. 2000). These studies particularly refer to the way in which large brained species such as primates process social information and other cognitive aspects of group living, or "social intelligence" (e.g. Dunbar 1992), and aspects of behavioural ecology (e.g. Barton 1996). Dunbar & Bever (1998) have demonstrated that primates and carnivores share a comparable pattern of neocortical evolution, and thus they state the similarity between the orders in terms of social cognition: in essence, the larger the neocortex, the larger the group, and the greater the capacity for social intelligence.

Lewis (2000) applied Dunbar's theory to the evolution of social play behaviour in primates. If the neocortex is a measure of social cognition, then perhaps it can be meaningfully applied to evolutionary elaborations in socially complex aspects of primate play behaviour. Even having controlled for the confounding effects of group size, the study demonstrated a positive and significant relationship between social play and neocortex ratio in non-human primates. This relationship might be best explained in terms of the extent to which social complexity is vital to a successful bout of social play; if an individual is to ensure the success (in terms of length) of its play with a partner, it is necessary to react to play-specific cues in a suitable manner (Fagen 1981; Lewis 2000). Failure to do so risks the termination of play, either through aggression or abandonment. To a behaviour such as social play, where the flipping of rôles is commonplace, appropriate processing of social information is crucial, and this may require increased cognitive skills (Lewis 2000). Alternatively, or additionally, it may be that species with elaborate social skills, and large brains, need to develop these skills through play.

7.2.1.2 Limbic system

The limbic system is a group of structures situated just beneath the corpus callosum (that joins the two hemispheres of the brain) (Carter 1999), and comprises structures that are widely considered to be vital to the experience of emotion and motivation (Russell 1988), such as the olfactory system, brain stem, hippocampus, amygdala, hypothalamus, anterior nuclei of the thalamus, septum, and the cingulate cortex (Isaacson 1982; Joseph 1999; Burghardt 2001). These structures project to the neocortex, and are concerned with both the "primitive" functions of response, as well as the more "advanced" functions of cognition and emotion – thus demonstrating both mosaic and correlated evolutionary change (Barton & Aggleton 2000). Traditionally, the limbic system was believed to be the evolutionarily oldest part of the mammalian brain (Carter 1999), and subsequently it was believed that the functions of the limbic system must also be primitive in comparison with more advanced systems such as the neocortex (Barton & Aggleton 2000). Recent research suggests that this is not necessarily the case, and that over evolutionary time, limbic components have changed together with the neocortex (Barton & Aggleton 2000; Barton & Harvey 2000). Similarly, the traditional view was that the limbic system was the neural system for emotions. Generally, modern neuroscientists no longer view the limbic system as existing as a coherent entity. This is due to the fact that structures once believed to be absolutely intrinsic to the expression of emotion, such as the hippocampus, are currently viewed as having different functions, such as memory formation (Bear et al. 2000). Similarly, the concept of a "system" implies that all the various structures are working together (Barton & Aggleton 2000); we now understand that such structures have both evolved, and function in different ways, thus making the classification of a limbic "system" *per se* somewhat trickier to define. "Limbic system" remains a commonly-used term, but these issues should be borne in mind.

In a recent review of the extensive neurological literature on (primarily) rodent play fighting, Burghardt (2001) hypothesised that play derives from instinctive behaviour patterns and associated affective states; thus the basal ganglia and limbic system may be important to the generation, mediation, and expression of play behaviour. The first study supporting this conclusion using modern comparative methods documented that the size of the primate amygdala predicts the amount of sexual, but not non-sexual, play in adult primates (Pellis & Iwaniuk 2002). Unfortunately, there has not been sufficient comparative documentation of juvenile play in primates to extend this analysis, and even the existing studies are based on ranking the prevalence of play in a three category system (0, 1, and 2).

7.2.1.3 Olfactory bulb

The olfactory bulb differentiates from the telencephalon during development, and receives neural information from the olfactory receptor neurons, which is vital to olfaction (Bear et al. 2001) and gustation (Russell 1988).

7.2.1.4 Hippocampus

The hippocampus is fundamental in the formation of long-term conscious memory (recognition memory) (Woolf 1998; Carter 1999), perceptual learning (Manns & Squire 2001), and the regulation of stress responses (Bear et al. 2001; Nestler et al. 2002). Crucially, the hippocampus is vital to the formation of spatial memory (Chiba et al. 2002; Yamada et al. 2002), such as recognising and responding to landmarks in pigeons (Gagliardo et al. 2002), object-recognition in rats (Garcia-Moreno et al. 2002), and maze-learning and long-term spatial memory (Kesner 2000; He et al. 2002; Ramos 2002). The hippocampus also appears to be critical in the retention of information concerning new faces and facial expressions (Crane & Milner 2002). It is possible that the hippocampus is also involved in the expression and experience of emotions, as damage to this area results in hyperemotional expression, such as impulsive crying or hysterical laughter, and hyperactivity and stereotypical behaviour in some animals (Bauman & Kemper 1994). Early evidence for the rôle of the hippocampus to emotions was found in rabies victims; characterised by hydrophobia and other exaggerated emotional responses of fear and anxiety, the rabies virus damages the hippocampus (Bear et al. 2001). However, current thinking tends to restrict the hippocampus as playing a lead rôle in emotions, and its rôle in declarative memory is considered key (Bear et al. 2001).

7.2.1.5 Amygdala

The amygdala is located within the temporal lobe and situated anteriorly to the hippocampus (Bear et al. 2001). It is a part of that brain that becomes sexually-differentiated by gonadal hormones during the perinatal stages of development, along with the hypothalamus (Hines & Shipley 1984); such differentiation ultimately leads to sex-differences in behaviour, namely sexual orientation, aggression, and also play behaviour (Collaer & Hines 1995), further suggesting that such behaviours from a "continuum", as sex and aggression remain key elements of play-directed behaviour. The amygdala appears to be concerned with recognising and generating emotion (Bear et al. 2001), which might include basic emotional responses, such as fear, anger, anxiety, and hunger (Davis 1992) – emotive states that ultimately reduce play behaviour (Panksepp 1998) - as well as more complex aspects of emotion, such as love or shame (Bear et al. 2001). Indeed, Pellis & Iwaniuk's (2002) findings that the amygdala may be important to sexual play in adult primates further suggest its potential importance to the study of play evolution.

Until recently, the amygdala was conventionally thought of as the brain's "alarm system", having evolved to produce and execute survival mechanisms of fight, flight, and appeasement (Carter 1999). Traditionally, the amygdala is seen as the site of control for "negative" emotions and vigilance reactions, but this view is beginning to change. Recent evidence suggests that the control of more positive emotions, as well as negative ones, is also within the remit of amygdala function (Hamman et al. 2002). It has also been suggested by Kahn et al. (2002), that the amygdala plays a rôle in decision-making processes that are governed by a potential negative outcome. Recent research suggests that the amygdala has evolved with both visual and olfactory connections. It may therefore play a vital rôle in socio-cognitive, and socio-sexual processing, with an emphasis on vision or olfaction, depending on the ecology of the species (Barton & Aggleton 2000).

Additionally, the amygdala responds to facial and vocal expressions, and appears to play some rôle in unconscious memory (Carter 1999). This may be important to play in reading play faces and species-specific "play-chuckles", as well as in recognising conspecifics as potential play-partners. It has been shown that the amygdala may have evolved for emotional responses of an individual to an "emotional" face, such as an anxious, or tearful face; faces that impart social information (Ohman 2002). Interestingly, the amygdala is relatively mature by birth in contrast with the cortex, to which it is connected. This goes some way towards explaining the imbalance of the juvenile brain; the immature cortex cannot override the powerful urges of the fully active amygdala (Bear et al. 2001).

Damage to the amygdala in humans is associated with reduced articulation of emotional responses, and an inability to recognise facial expressions, and respond to fear and anger (Adolphs et al. 1994). In animals, such damage is expressed through an apparent loss of fear (Bear et al. 2001). Similarly, damage to both the amygdala and the caudate-putamen nuclei have been shown to reduce the performance of play behaviour in rats (Panksepp 1998). In addition, although the amygdala is not believed to be a primary locus for memory, it does appear to be strongly implicated in emotional memory, or rather, the emotional content of memory (Bear et al. 2001). Current thinking appears to suggest that the amygdala is important in regulating and expressing the emotional states of an individual through behaviour, but moreover that it enables an individual to cognitively assess the emotional content of complex perceptual cues, such as facial expression and body language (Gallagher & Chiba 1996).

7.2.1.6 Complexus centro-medialis & Complexus cortico-basolateralis

The amygdala is divided into two regions, the cortico-, or centro-medial, and the cortico-basolateral complexes. The former is considered to be a part of the olfactory system, the latter with organising self-protective behaviour - the basic responses such as fight-flight mechanisms (Bear et al. 2001). In addition, it has recently been demonstrated in rats that the basolateral nucleus is vital in associative learning between sensory information and behavioural outputs, especially regarding appetite (Toyomitsu et al. 2002). The cortico-basolateral complex receives sensory input from the inferior temporal lobe, and its output is directed towards the hypothalamus (Bear et al. 2001).

7.2.1.7 Septum

The septum appears to play an important rôle in the regulation of emotions, most specifically in the production of fear and also in the reduction of anxiety, or relief (Yadin et al. 1993). Similarly, studies on rats have shown that high levels of oestrogen in the septum can contribute to the facilitation and execution of maternal behaviour (Sheehan & Numan 2002). The septum may also play a part in sexual and copulatory behaviour (Panzica et al. 2001), and damage to this region in humans may result in male priapism (permanent erection) or conversely in impotence (Carter 1999).

7.2.1.8 Triangular septal nucleus

This nucleus is part of the limbic system and is vital in the control of response inhibition (Bear et al. 2001). It has been shown that septally-damaged animals cannot exhibit behaviourally appropriate responses (Menard & Treit 1996), and thus the septal area of the brain (septum and its nuclei) may prove important to play behaviour in exhibiting appropriate reactions: one of the hallmarks of successful play behaviour (Fagen 1981). In addition, the septal nuclei in general may also be important for regulating fluid ingestion (Bear et al. 2001).

7.2.1.9 Diencephalon

The diencephalon lies between the telencephalon and optic vesicles (Bear et al. 2001). The diencephalon differentiates into two further structures: the thalamus and the hypothalamus (Bear et al. 2001). Whilst temporal lobe structures such as the amygdala and the hippocampus are implicated in the formation of recognition memory, outside of the temporal lobe, it is the diencephalon that is associated with memory. Indeed, damage to the human diencephalon may result in amnesia (Bear et al. 2001).

7.2.1.10 Thalamus

The thalamus is key in relaying information from one area of the cortex to another, and also sensory information to the cortex, interacting with the reticular formation and the limbic system (Russell 1988; Bear et al. 2001). The anterior and dorsomedial nuclei of the thalamus are involved in the processing of recognition memory (Bear et al. 2001). Recently, the thalamus has also been implicated alongside the amygdala as a neural centre for "moral" behaviours and emotions in humans (Moll et al. 2002). It has also been demonstrated in rats that thalamic structures are key to the expression of rough-and-tumble (R&T) play (Panksepp 1998).

7.2.1.11 Lateral Geniculate Nucleus (LGN)

The lateral geniculate body is made of two nuclei located within the thalamus, and is generally abbreviated to the initials LGN. Most of the primate visual system is well-developed by birth, however, the LGN increases in volume by approximately 17% (in macaques) between birth and 4 weeks of age; the percent volume increase differs between species depending on maturational variables (Kaas & Huerta 1988). The LGN is an important part of the brain as it receives input from both eyes and integrates the information permitting binocular vision; as such, it is often referred to as the "gateway to the visual cortex" and is thus important in perceiving visual information (Bear et al. 2001). Damage to the LGN critically affects visual behaviour (Kaas &

Huerta 1988). Social cognition may rely very heavily on visual acuity, especially in primates, which are heavily reliant on vision (Barton 1998). Similarly, as thalamic nuclei are increasingly considered to be involved in the articulation of social skills (Armstrong et al. 1987; Dunbar 1992), including rough-and-tumble play (Panksepp 1998), it might be expected that neural components such as the LGN may be important to social aspects of play behaviour.

7.2.1.12 Hypothalamus

The hypothalamus is a tiny yet vital part of the brain (Russell 1988) that is a collection of nuclei controlling and maintaining bodily functions such as homeostasis (Isaacson 1982). The basic structure and function of the hypothalamus has changed little over the course of its evolution, and performs many primitive or basic bodily functions, such as the fight-or-flight response (Bear et al. 2001). It is the part of the brain that is vital in generating and regulating the visceral (autonomic) nervous system, controlling blood-flow, breathing, hunger and appetite, thirst, temperature, sleep, sexual behaviour and emotions (Russell 1988). It may also be an important component in regulating and expressing aggression (Bear et al. 2001), and moreover is a part of the brain that becomes sexually differentiated during development, specifically giving rise to sex-differences in aggressive, sexual, and play behaviour (Collaer & Hines 1995). The mammilliary bodies in the hypothalamus are involved in the processing of recognition memory (Bear et al. 2001). The hypothalamus is important as it can change the neural activity in regions of the forebrain such as other limbic structures and the neocortex, and also in the midbrain and hindbrain, such as the brain stem and spinal cord (Isaacson 1982). Such alterations provide a rôle for the hypothalamus in learning, memory, motivation, and performance, and crucially the lateral hypothalamus may be enable the experience and understanding of pleasure (Isaacson 1982); this may prove to be an important factor in the experience of play behaviour (see Fagen 1992).

7.2.1.13 Epithalamus

The epithalamus is part of the diencephalon, above the thalamus, that comprises the habenular nuclei, the stria media, and the pineal body (Concha & Wilson 2001). This part of the brain appears to play a vital rôle in maintaining the body clock, and producing melatonin, a hormone that regulates sleep and wakefulness. The epithalamus may also regulate menstrual cycles in females, as melatonin controls the balance of oestrogen in the body (Mikkelsen et al. 2001).

7.2.1.14 Habenular nuclei

The habenular nuclei are part of the epithalamus in mammals, and are believed to function in facilitating interactions between the limbic forebrain and the midbrain (Sutherland 1982). This structure has therefore been hypothesised to be important to olfactory responses, sleep patterning, food and water intake, and arguably may even facilitate certain elements of some social behaviours such as mating and feeding (Sandyk 1991). The habenular nuclei might also play a rôle in avoiding stressful situations, and avoidance learning (Concha & Wilson 2001).

7.2.1.15 Corpus pineale (pineal body)

The corpus pineale is a minute part of the brain situated between the corpus callosum and the third ventricle, and is also a part of the epithalamus (Bear et al. 2001). Its function in mammals is to secrete the hormone melatonin, which regulates body temperature and photoperiodism, or how an animal responds to changes in the length of daily and annual periods of light (Brown 1994). Disruptions to the balance of melatonin levels can result in sleeplessness, negatively affect sexual maturation (Webb & Puigdomingo 1995), and even induce depression, stress, and some forms of cancer (Bartsch 1989).

7.2.1.16 Basal ganglia

The basal ganglia are often referred to as the primitive "reptilian brain" (e.g. Panksepp 1998), and comprise a group of nuclei, including the caudate nucleus, putamen, globus pallidus, and subthalamus, that are responsible for unconscious and automatic motor acts, attention, and consciousness (Carter 1999; Bear et al. 2001). If dopamine becomes restricted in this area, it can lead to motor disorders, which in humans might include Parkinson's disease, attention deficit disorder, depression, and schizophrenia (Carter 1999). Caudate-putamen impairment has been shown to reduce play behaviour in rodents (Panksepp 1998), and thus further comparative study of these structures with play may prove useful to our understanding of how the basal ganglia perform in the expression of play behaviour in other mammals.

7.2.1.17 Subthalamus and subthalamic nucleus

The subthalamus is situated laterally between the thalamus and the hypothalamus, and is also part of the basal ganglia. It is believed to play a critical rôle in regulating movements performed by the skeletal muscles (Bear et al. 2001). Most of the subthalamus comprises of the grey-matter structure of the subthalamic nucleus. Damage to the subthalamus and the surrounding area may contribute towards Parkinson's disease and Huntington's disease in humans (Moretti et al. 2001).

7.2.1.18 Pallidum

Part of the basal ganglia, the pallidum is comprised of the globus pallidus and the ventral pallidum. The pallidum, along with the other nuclei of the basal ganglia, is key in motor control and movement (Wannier et al. 2002), as well as forming part of the secondary olfactory region along with the thalamus, hypothalamus, hippocampus, and striatum (Weisman et al. 2001). In addition, in a rodent model, it has recently been hypothesised that the pallidum may also function in the promotion of context recognition of social behaviours, assisting the assessment of social stimuli, and even regulating and maintaining social relationships and pair-bonding (Young 2002).

7.2.1.19 Striatum

The striatum comprises two nuclei that also form the basal ganglia: the putamen and the caudate nucleus, and these control automatic movement (Carter 1999; Bear et al. 2001) as well as skilled motor control (Laforce & Doyon 2001). The putamen is connected to both the pre-motor and motor cortices, and the caudate nucleus is connected to the orbital cortex, believed to be vital in planning action (Carter 1999). In this vein, the striatum is critical in procedural memory and may be instrumental in forming and executing behavioural habits (Jog et al. 1999; Bear et al. 2001). In humans, over-activity in the putamen can result in Tourettic tics, and over-activity in the caudate nucleus may result in compulsive-obsessive and other stereotypic disorders (Carter 1999).

7.2.1.20 Piriform lobe

The piriform lobe is a pear-shaped structure that is important in detecting and processing odour information (Valverde 1965). In humans, it may play a rôle in emotional memory, due to certain smells triggering "associative memories" (Barkai & Hasselmo 1997).

7.2.1.21 Corpus subfornicale

The corpus subfornicale, or subfornical organ, has extensive connections to the hypothalamus and is key in maintaining homeostasis of blood pressure and bodily fluids through fluid and sodium intake (Simon 2000; Starbuck & Fitts 2001).

7.2.1.22 Corpus subcommissurale

Although found in all vertebrates, the function of the corpus subcommissurale, or the subcommissural organ, is currently not fully understood. It is however involved in the development of the brain during the embryonic stage, and is indeed the first secretory brain structure to differentiate (Rodriguez et al. 2001). It is believed that the subcommissural organ plays a rôle in cerebrospinal fluid (CSF) circulation (Perez-Figares et al. 2001), which ensures the healthy functioning of the brain (Bear et al. 2001).

7.2.1.23 Capsula interna (internal capsule)

The capsula interna joins the cortex to the brain stem via the thalamus, and is continuous with the cortical white matter (Bear et al. 2001). The capsula interna appears to be important in evaluating motor ability (Morecraft et al. 2002) or the sensory guidance of movement (Glickstein 1998); indeed, axon-loss to this area of the brain, typically following a stroke, is associated with severe motor-impairment and paralysis (Shelton & Reading 2001).

7.2.2 Midbrain (Mesencephalon)

The midbrain or mesencephalon contains structures that act as transmitters of neural information between the midbrain, forebrain, and spinal cord, and contains neurons that factor in sensory information and motor-control (Bear et al. 2001). Axons of cells within the midbrain penetrate the CNS, and function to control and regulate moods (such as pleasure), pain, and consciousness (Bear et al. 2001).

7.2.2.1 Inferior colliculus

The inferior colliculus is vital in transmitting neural and sensory information to and from the ear, via the thalamus (Bear et al. 2001). Both the superior colliculus, and the inferior colliculus, are part of the tegmentum, which comprises the red nucleus and the substantia nigra (black substance), concerned with the control of voluntary movement (Bear et al. 2001). A recent study focusing on the activation of *c-fos* genes during rough-and-tumble play in rats suggests that the inferior colliculus may indeed be specifically accessed during play behaviour, and may aid the reaction to vocal cues, given that it receives information from auditory pathways (Gordon et al. 2002). The authors advise caution in assigning such a relationship, due to the possibility of the gene activation being due to other sounds during play behaviour, and further studies should be able to determine to what extent there is a relationship.

7.2.2.2 Optic tract

The optic tract extends between the optic chiasm to the brain stem and is comprised of retinal ganglion cell axons. Two vital targets of the optic tract are the superior colliculus, and the LGN (Bear et al. 2001).

7.2.3 Hindbrain

During development, the hindbrain differentiates into three major structures: the cerebellum, the pons, and the medulla oblongata. The structures of the hindbrain are vital in the passing of information to and from the spinal cord and the forebrain, and act to process both sensory information, and regulate voluntary movement and the autonomic nervous system (Bear et al. 2001).

7.2.3.1 Cerebellum

The cerebellum is situated posteriorly to the cerebrum (Eccles 1977), and has extensive connections both to the neocortex and spinal cord (Bear et al. 2001). The cerebellum is a vital centre for motor co-ordination and integration of information to produce smooth and accurate movement (Russell 1988). The cerebellum also maintains posture and balance (Ackerman 1992), but it seems that the cerebellum may be much more than a mere motor-control centre. It also acts as a "tracking system" in all vertebrates, not only controlling and co-ordinating the bodily movements of the individual, but also tracking those made by others in the environment (Paulin 1993). This has implications for the study of play, as it may be necessary for the individual to follow trajectories of moving objects and individuals in play, as well as in the context of more serious behaviour patterns, notably hunting and foraging; the cerebellum may well facilitate this ability. The late postnatal maturation of the cerebellum and its control of skilled motor movements (Ackerman 1992) suggest a sensitive period in animal development; it might be specifically during this time that the motor patterns of play behaviour in young animals influence brain and muscular development. The traditional view that the cerebellum acts only in the control of movement has recently been disputed in the literature with increasing evidence that the cerebellum contributes to cognitive functions as well (Akshoomoff & Courchesne 1992; Habas 2001); it seems that the long-standing opinion that motor development begins and ends relatively early in ontogeny, whereas cognitive development is initiated relatively later, is now challenged with some evidence that the two are very much more closely interrelated and occur during the same time window (Diamond 2000).

Byers & Walker (1995) looked at the relationship between play behaviour and the cerebellum very closely; they concluded that cerebellar synaptogenesis was one of the permanent and true effects of all play. They showed that in mice (locomotor play), cats (social play), and rats (locomotor and social play), it appears that play may be timed to actively modify or terminate synapse formation in the cerebellum, and in this view characterises a sensitive period in mammalian development. Cerebellar synaptogenesis is one effect that seems permanently affected by postnatal behaviour in mammals, and the modification of these structures results in enhanced motor-performance skills. Play might be an important mechanism as in some species the timing of play and such cerebellar changes are linked (Byers & Walker 1995).

7.2.3.2 Pons

The pons is often referred to as the brain's "switchboard", connecting the cerebellum to the cerebral cortex. It is estimated that 90% of axons passing through the midbrain synapse on the neurons in the pons (Bear et al. 2001). The trigeminal motor nucleus situated within the pons is believed to be vital to the control of vocalisation, forming a network between the amygdala and spinal cord to control sound, facial position, and respiratory movements required to emit controlled vocalisations (Jurgens 2002) as well as startle responses (Pissiota 2002).

7.2.3.3 Medulla oblongata

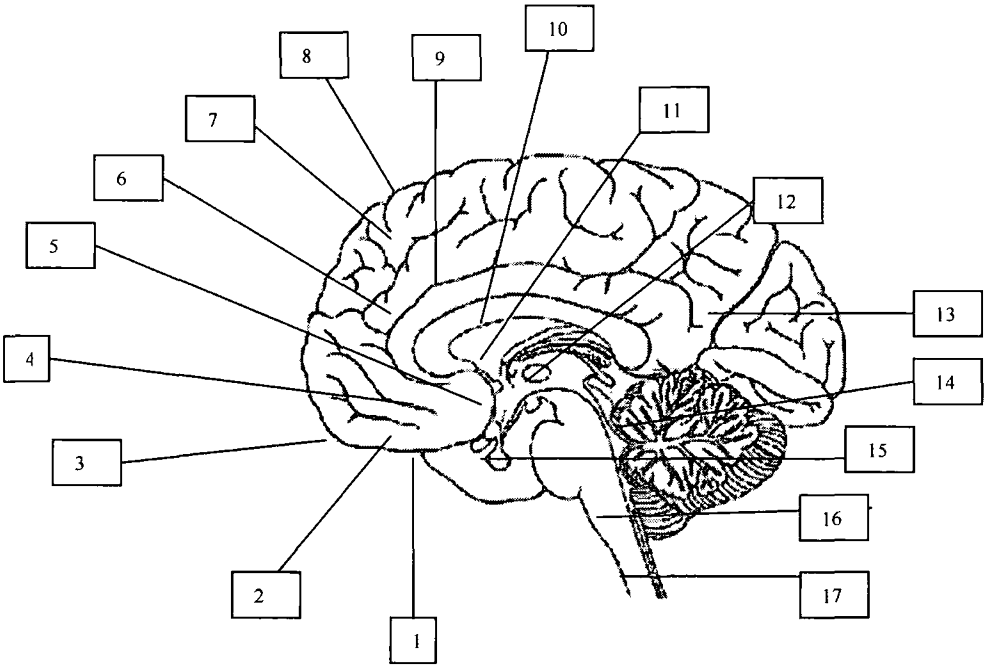
The medulla oblongata (medulla) is key to various sensory and motor functions, including auditory information, touch, smell, and taste. Its neurons relay information from the spinal cord to the thalamus (Bear et al. 2001). The medulla may be especially important to the regulation of the sleep-wake cycle (Gottesmann 1999), sexual reflexes (Holmes et al. 2002), and in the control of involuntary mechanisms of the CNS, such as hiccupping (Musumeci et al. 2000).

7.2.3.4 Vestibular complex and vestibular nuclei

The vestibular nuclei are situated inside the medulla, and are instrumental in receiving input from the vestibular complex of the inner ear. This is a vital area for detecting head motion and maintaining balance (Bear et al. 2001).

7.2.3.5 Visual cortex

The visual cortex is a critical part of the brain, especially to primates (including humans), as primates rely so heavily on sight. In fact, amongst diurnal primates, the visual cortex comprises up to 50% of the variance in neocortex size (Barton 1996). The visual system of primates undergoes much of its development prenatally, and hence is considerably more developed at birth in comparison with most other mammals (Kaas & Huerta 1988). The primary visual cortex is often referred to interchangeably as Brodmann's area 17, V1, and striate cortex (Bear et al. 2001). This cortex is formed of six layers of cells, axons, and pathways, enabling visual function and perception. The visual cortex projects to many other areas of the neocortex, especially in primates.



1 = hippocampus
2 = amygdala
3 = olfactory bulb
4 = hypothalamus
5 = mesencepahlon
6 = corpus callosum
7 = telencephalon
8 = neocortex
9 = cingulate gyrus
10 = striatum
11 = thalamus
12 = pineal body
13 = visual cortex
14 = cerebellum
15 = pons
16 = medulla oblongata
17 = brain stem (leading to spinal cord).

Fig. 7.2 Diagram of the human brain and its major components

7.3 Methods

Adult brain weights (g) for primates were taken from Barton (1999), and for carnivores from Deaner et al. (in press). Pinniped brain and body size data were taken from Bininda-Emonds (2000). The data for fundamental adult brain parts for primates were taken from Stephan et al. (1981), and pons data are from Matano et al. (1985). Cerebellar data for carnivores are taken from Putnam (1927). The data on each category of play behaviour (total play, social play, solitary locomotor play and object play) and dichotomous variables were collected from the primate and carnivore behaviour literature, as detailed in Chapter 2. I used the method of independent contrasts (Felsenstein 1985; Harvey & Pagel 1991) with the primate phylogeny based on Purvis (1995), and the carnivore phylogeny from Bininda-Emonds et al. (1999). The analyses were conducted using the CAIC computer programme (Purvis & Rambaut 1995), using the CRUNCH option for continuous variables, and the BRUNCH option for dichotomous variables. Statistical analyses of the output from CAIC were carried out using StatView version 4.0. Regressions were set through the origin (Purvis & Rambaut 1995). As brain size is subject to the effects of allometry, it is necessary that a relative measure be used in analysis. Body size correlates strongly with brain size, with larger species typically having larger brains; but there is much variation in brain size for species of the same body size. For this reason, studies of brain size must remove body size from the analysis (e.g. Jerison 1973; Northcutt 1985). Here, the confounding effect of body size has been removed by regression for *all* results. For the purposes of these analyses, the data have been log-transformed, rendering them suitable for standard regressions (Freckleton 2000; Purvis & Rambaut 1995).

Additionally, as body and brain size are correlated, Table 7.27 at the end of the results section takes the brain components for which there were significant correlations with one or more of each play category, and controls for the confounding effect of both body size and the rest of the brain, through removal by partial correlation. The "rest of the brain" variable has been calculated by summing the significant brain components (i.e. the parts that are correlated with play in this chapter) for which there are full species matches (i.e. no missing brain data), and subtracting this total from the total brain volume as provided by Stephan et al. (1981).

Thus, the sum of the medulla, mesencephalon, cerebellum, septum, striatum, neocortex, and hippocampus for each species in the database was taken. This total, S, was then subtracted from the measurement for total brain, B.

$$B - S = R$$

Where R is the rest of the brain.

Multiple regression analyses of each play category (dependent variable Y) on adult body mass, rest of brain, and the brain component that showed a significant relationship in the independent contrasts analyses in this chapter (3 independent variables X) were conducted.

7.4 Hypotheses

The following hypotheses are presented for play in primates and carnivores with regard to constituent parts of the brain. The null hypothesis, H_0, states that there will be no association between play behaviour and the neural component in question. Below, alternative hypotheses, H_a, are presented.

1. The amount of time spent in play should correlate with relative brain size; and more specifically, social play behaviours should correlate with neocortical expansion.

If aspects of play behaviour are cognitively demanding, or contribute to the facilitation of learning in large-brained species (e.g. Fagen 1981; Lewis 2000), then it is expected that the amount of play behaviour should correlate positively and significantly with relative brain size in primates and carnivores. In particular, the play categories that are associated with higher cognitive capacities, such as object and social play, should show this trend more significantly than with solitary locomotor play, which is deemed less cognitively demanding (Poole 1985). Moreover, areas of the brain that are especially associated with the processing of social information should also be positively correlated with social play. Given that the neocortex is key in mammalian brain evolution (Jerison 1973), and that primates and carnivores are widely considered to be the most playful of these mammals (e.g. Fagen 1981; Bekoff et al. 1984; Bekoff & Byers 1998), and further that the neocortex functions in the representation of social intelligence (Dunbar 1992, 1995), it is predicted that neocortical expansion will reflect similar elaborations in primate and carnivore social play behaviours.

Brain size is a variable that may affect play behaviours that are argued to be associated with increased intelligence, such as object manipulation and socially complex aspects of play. In terms of the dichotomous variables detailed here, it is expected that there will be an evolutionary correlation with interspecific play, as it may be argued that in order to engage in play behaviour that is appropriate (e.g. reading signals sufficiently) with a different species requires a high level of cognitive ability. It is also expected that increased brain size accompanies increases in the propensity of a species to engage in polyadic play. This is because keeping track of several players in the surrounding environment requires that appropriate actions and reactions are directed to more than one conspecific simultaneously. This is likely to represent a heavy parallel processing load.

2. Play may correlate with limbic structures and the basal ganglia.

Burghardt (2001) suggests that play may stem from instinctive behavioural patterns, and thus calls for a closer analysis of play with limbic structures and basal ganglia. Such structures are believed to function in the foundation and representation of emotions, and the existing literature suggests that damage to certain limbic areas may lead to a cessation of play behaviour (Panksepp 1998). Additionally, structures such as the amygdala and hypothalamus are prenatally affected by gonadal hormones, leading to their rôle in mediating sex-differential behaviour, of which play is one such behaviour (Hines 1982; Collaer & Hines 1995). Given the importance of thalamic structures to the expression of rough-and-tumble play, and the rôle that the amygdala, and also the hippocampus, play in terms of reading facial expressions (Gallagher & Chiba 1996), it is predicted here that *social* forms of play behaviour may be better represented by limbic structures than other forms of play behaviour.

In terms of the basal ganglia, it is predicted that components related to motor control may be key to the expression of play behaviour. For example, the subthalamus regulates skeletal muscle movements (Bear et al. 2001), and play is known to permanently affect skeletal muscle fibre during postnatal development (Byers & Walker 1995). Similarly, the pallidum is involved with motor control and context recognition of social behaviour (Bear et al. 2001), thus it might be hypothesised that this too contributes to aspects of social play behaviour. In addition, the striatum, which is comprised of the caudate-putamen nuclei, is implicated alongside the cerebellum in planning action and procedural memory (Russell 1988), as well as with some aspects of cognition (Laforce & Doyon 2001), which might ensure the smoothness of motor movements and cognitive competency in mammalian play behaviour.

3. Social and object play should correlate with cerebellum size.

Given the rôle of the cerebellum to motor control and accuracy (Ackerman 1992), procedural memory (Carter 1999), the ability to follow path trajectory (Paulin 1993), and arguably, cognition (Habas 2001), together with its own neuro-developmental trajectory (Byers & Walker 1995; Diamond 2000), it is expected that the cerebellum will play a crucial part in the expression and development of social and object play behaviour.

In the same vein, it is predicted that vestibular components of the brain, those that are vital in maintaining balance and motor acuity (Bear et al. 2001), are also crucial to the onset, development, and expression of motor control, including those of play behaviour.

4. Play should correlate with visual components of the brain in primates.

As there are no data available for analyses on the visual complexes of carnivores, the predictions here are limited to primates. Primates are visually specialised, and vision plays a critical rôle in social interactions in anthropoids. Thus it is predicted that play is most likely to be associated with visual expansion (in the visual cortex and LGN). In strepsirhines however, the olfactory system is critical to social interaction and social play may be important to the development of scent-marking behaviour in ring-tailed lemurs (*Lemur catta*) (Palagi et al. 2002). The same premise may also apply to some carnivores, although data for both strepsirhine and carnivore olfactory brain components for those species in the play database are lacking.

5. Play will be uncorrelated with homeostatic functions governed by the corpus subfornicale and the triangular septal nucleus.

Homeostatic functions, and hence the relative size of the structures mediating them are likely to be conserved, but there is no reason to link such fundamental physiological maintenance with play behaviour.

6. The number of behaviours observed in a species' play repertoire will be correlated with group size and relative brain size of that species.

The number of distinct play behaviours recorded in a species' repertoire may be an important indicator of other factors regarding a species' behavioural capacity. It is possible that increased numbers of behaviours stem from novel stimuli or are indicative of behavioural innovation. It is likely that larger groups offer a greater propensity to exhibit and discover new behaviours, which may in turn lead to the eventual display of more play behaviours. Alternatively, a high number of distinct play behaviours may be an indicator of cognitive abilities. In order to see which factor is most important to the evolutionary elaboration of play behaviours, the relationship is tested with both group size and relative brain size.

7. Relative brain size will predict a species' average play bout length.

If it is the case that juvenile animals are playful in order to hone the neuro-muscular system prior to adulthood (Byers & Walker 1995; Fairbanks 2000), then it might be argued that the longer an individual devotes to the pursuit of play, the more honing is required of that species during the period of plasticity. Thus, average play bout length may offer a suitable indicator of complexity. For this reason the relationship is tested against relative brain size.

7.5 Data

Data are tabulated in the Appendix. Dichotomous variables are detailed in Table 2.2 (Chapter 2). Brain structure data are taken from Stephan et al. (1981), with pons data from Matano et al. (1985), and cerebellar data for carnivores from Putnam (1927). Additional data are taken from Deaner et al. (in press).

7.6 Results

The following regressions of brain component and play type contrasts control for the effect of body size through residual regression analyses. Graphs detail regressions of all play categories and relative adult brain size for primates and carnivores; thereafter in brain component analyses, graphs are only presented for significant results. It should be noted that where sufficient data are available, results for both primates and carnivores are analysed and presented; however, due to a lack of play data, many carnivore analyses are apparently "missing". A summary of the results is presented in Table 7.27 at the end of this section.

Before analyses are presented, Figure 7.3 details a simple regression (i.e. non-contrasted) comparison of brain weight against brain volume in primates. Brain weight data are taken from Barton (1999), and brain volume data are taken from Stephan et al. (1981) (F (1, 21) = 340.07, co-efficient = 1.07, p = <0.0001, $r^2 = 0.94$).

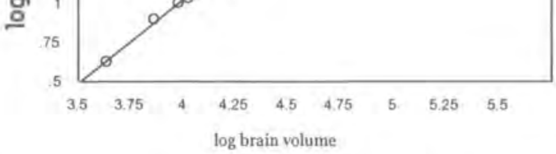


Fig. 7.3 Comparison of brain weight and brain volume in primates

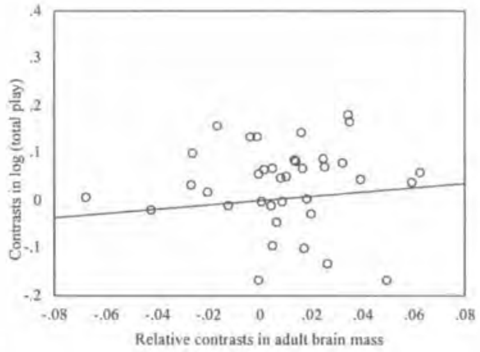
7.6.1 Primate brain size

Table 7.1 shows regression analyses of each play category on brain size in primates. Relative adult brain size shows no significant correlation with any of the play categories in primates (Figures 7.4-7.7). One outlier has been removed as specified by the CAIC programme for regressions of total play and object play.

Table 7.1 Regression analyses of play category on brain size in primates

Play type	DF	F-value	p-value	co-efficient	r^2
Total	1, 36	0.59	0.45	0.43	0.002
Solitary	1, 18	0.004	0.95	0.11	2.38
Object	1, 13	0.51	0.49	1.12	0.04
Social	1, 22	1.56	0.22	1.17	0.07

Table 7.2 shows regression analyses of each play category on the size of the relative brain in primates; that is, brain controlling for relative neocortex size. Figures 7.8-7.11 illustrate the correlations. Relative brain size is positively and significantly correlated with both object play and social play in primates.



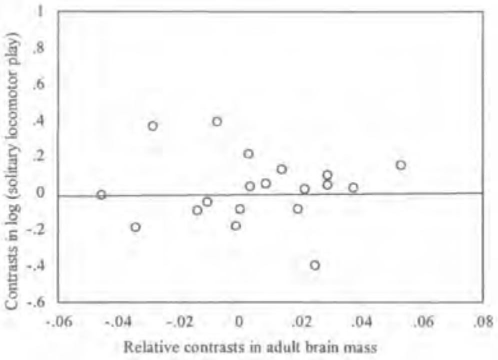


Fig. 7.4 Regression plot of log (total play) on residual log (adult brain) in primates

Fig. 7.5 Regression plot of log (solitary locomotor play) against residual log (adult brain) in primates

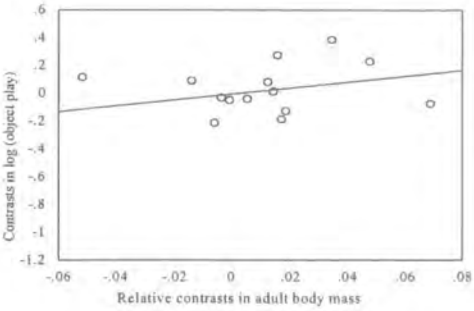


Fig. 7.6 Regression plot of log (object play) on residual log (adult brain) in primates

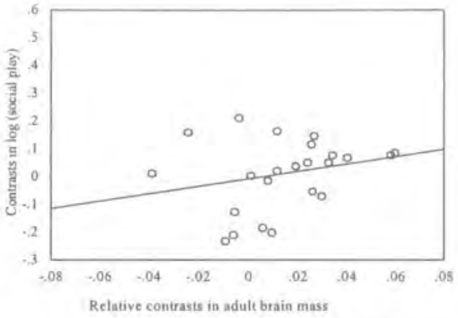


Fig. 7.7 Regression plot of log (social play) on residual log (adult brain) in primates

Table 7.2 Regression analyses of play category on brain size-neocortex size in primates

Play type	DF	F-value	p-value	co-efficient	r^2
Total	1, 14	1.78	0.20	0.46	0.11
Solitary	1, 5	0.12	0.74	0.19	0.02
Object	**1, 3**	**30.97**	**0.01**	**1.03**	**0.91**
Social	**1, 7**	**16.03**	**0.005**	**0.66**	**0.70**

7.6.2 Carnivore brain size

Table 7.3 shows regression analyses of each play category on brain size in carnivores. Relative adult brain size is not significant with total play in carnivores (Figure 7.12). One outlier has been removed as specified in the CAIC programme; the trend of the graph is largely unaffected. Relative adult brain size is positively and significantly correlated with solitary locomotor play in carnivores (Figure 7.13), although Bonferroni correction renders this non-significant, and additionally the sample size is too small to be conclusive. Relative adult brain size is positively, but not significantly correlated with object play in carnivores (Figure 7.14). Relative adult brain size is positively and significantly correlated with social play in carnivores (Figure 7.15).

Table 7.3 Regression analyses of play category on brain size in carnivores

Play type	DF	F-value	p-value	co-efficient	r^2
Total	1, 11	0.01	0.91	-0.11	0.001
Solitary	**1, 2**	**17.83**	**0.05**	**9.13**	**0.89**
Object	1, 4	2.62	0.18	6.27	0.33
Social	**1, 7**	**11.37**	**0.01**	**2.58**	**0.62**

Bonferroni = 0.013, solitary n.s.

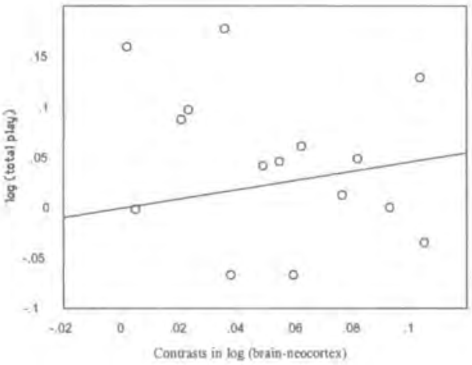


Fig. 7.8 Regression plot of log (brain-neocortex) on log (total play) in primates

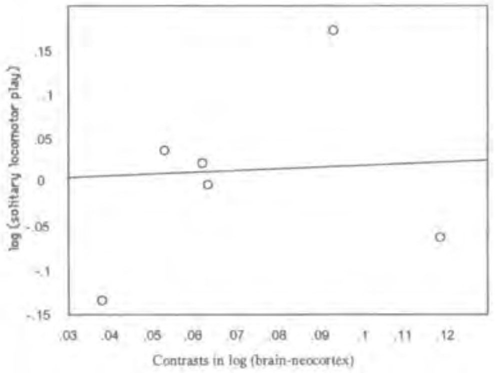


Fig. 7.9 Regression plot of log (brain-neocortex) on log (solitary locomotor play) in primates

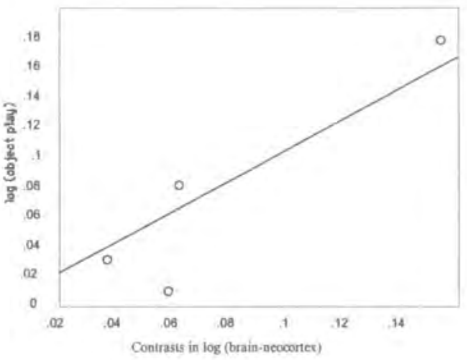


Fig. 7.10 Regression plot of log (brain-neocortex) on log (object play) in primates

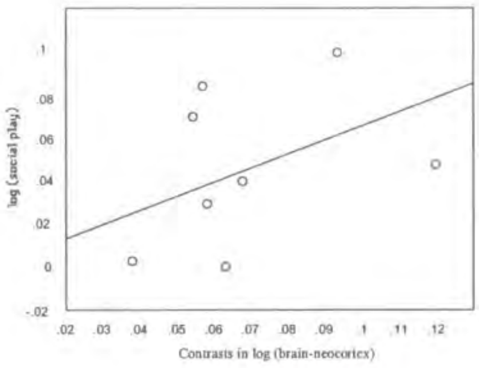


Fig. 7.11 Regression plot of log (brain-neocortex) log (social play) in primates

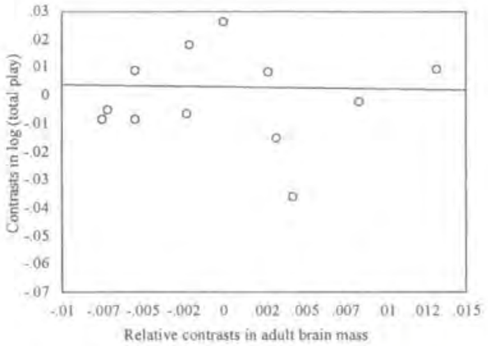


Fig. 7.12 Regression plot of log (total play) on residual log (adult brain) in carnivores

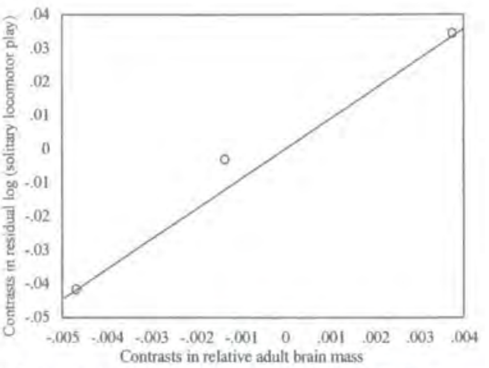


Fig. 7.13 Regression plot of log (solitary locomotor play) on residual log (adult brain) in carnivores

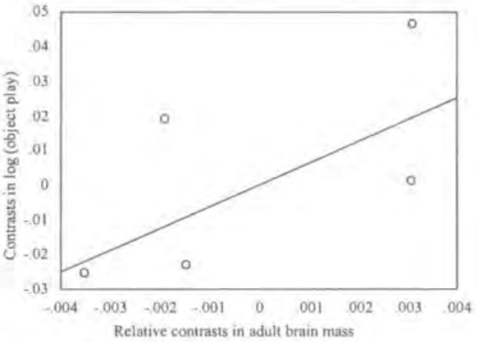


Fig. 7.14 Regression plot of log (object play) on residual log (adult brain) in carnivores

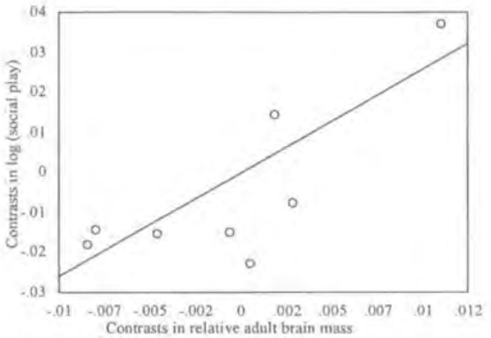


Fig. 7.15 Regression plot of log (social play) on residual log (adult brain) in carnivores

7.6.2 Brain parts

The following results detail contrasts analyses of each category of play and brain components. The brain component data are from Stephan et al. (1981) and Matano et al. (1985).

7.6.2.1 Telencephalon

Table 7.4 shows the results of regression analyses for each play category on telencephalon size in primates. Telencephalon size is not significantly correlated with either solitary locomotor or object play. Telencephalon size is however positively and significantly correlated with total play and social play (Figures 7.16 and 7.17).

Table 7.4 Regression analyses of play category on telencephalon size in primates

Play type	DF	F-value	p-value	co-efficient	r^2
Total	**1, 14**	**4.83**	**0.04**	**1.94**	**0.26**
Solitary	1, 5	0.16	0.70	-0.72	0.03
Object	1, 3	0.60	0.49	-1.72	0.17
Social	**1, 12**	**4.75**	**0.05**	**1.56**	**0.28**

Bonferroni = 0.013, n.s.

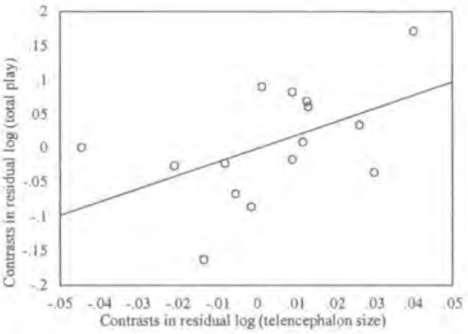


Fig. 7.16 Regression plot of residual log (total play) on residual log (telencephalon) in primates

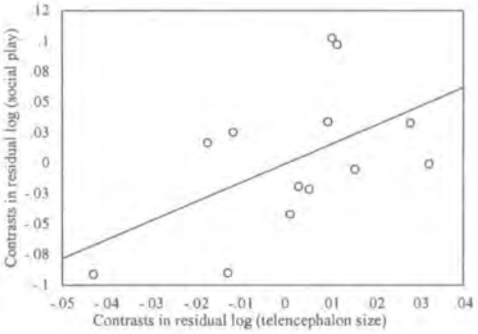


Fig. 7.17 Regression plot of residual log (social play) on residual log (telencephalon) in primates

7.6.2.2 Medulla oblongata

Table 7.5 shows the results of regression analyses for each play category on the medulla oblongata in primates. Medulla oblongata is not significantly correlated with total, solitary, or object play; medulla oblongata size is however positively and significantly correlated with social play (Figure 7.18).

Table 7.5 Regression analyses of play category on medulla oblongata size in primates

Play type	DF	F-value	p-value	co-efficient	r^2
Total	1, 14	2.43	0.14	1.77	0.15
Solitary	1, 5	1.24	0.31	-3.65	0.20
Object	1, 3	0.48	0.54	-3.65	0.14
Social	**1, 12**	**5.82**	**0.01**	**1.94**	**0.36**

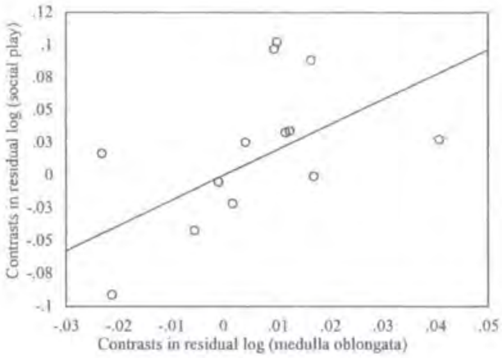


Fig. 7.18 Regression plot of residual log (social play) on residual log (medulla oblongata) in primates

7.6.2.3 Cerebellum

Table 7.6 shows the results of regression analyses for each play category on cerebellum size in primates. Cerebellum size is positively but not significantly correlated with total play. Cerebellum size is negatively and not significantly correlated with solitary locomotor play. Cerebellum size is positively correlated with object play, and although falling just short of significance, I have included the corresponding graph (Figure 7.19) to show the trend of this result as I believe the number of contrasts for object play (n = 4) may have an effect. Cerebellum size is however, positively and significantly correlated with social play (Figure 7.20).

Table 7.6 Regression analyses of play category on cerebellum size in primates

Play type	**DF**	**F-value**	**p-value**	**co-efficient**	**r^2**
Total	1, 14	3.81	0.07	1.99	0.21
Solitary	1, 5	2.31	0.19	-2.93	0.32
Object	1, 3	5.65	0.09	5.82	0.65
Social	**1, 13**	**8.19**	**0.01**	**2.52**	**0.38**

Regression of cerebellum size on total play in carnivores was non-significant. Unfortunately, there are too few observations of solitary locomotor, object and social play to permit a statistical result.

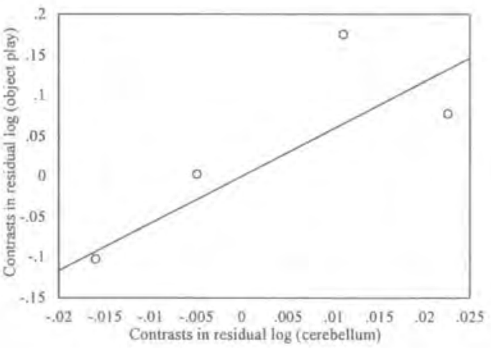


Fig. 7.19 Regression plot of residual log (object play) on residual log (cerebellum) in primates

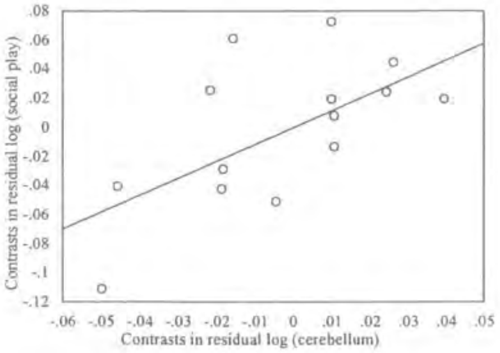


Fig. 7.20 Regression plot of residual log (social play) on residual log (cerebellum) in primates

7.6.2.4 Septum

Table 7.7 shows the results of regression analyses for each play category on septum size in primates. Septum size is not significantly correlated with total, solitary locomotor, or social play; but is negatively and significantly correlated with object play (Figure 7.21).

Table 7.7 Regression analyses of play category on septum size in primates

Play type	DF	F-value	p-value	co-efficient	r^2
Total	1, 14	0.84	0.37	-1.05	0.06
Solitary	1, 5	2.75	0.16	-4.22	0.36
Object	**1, 3**	**97.01**	**0.001**	**-7.96**	**0.97**
Social	1, 12	2.41	0.15	-1.31	0.17

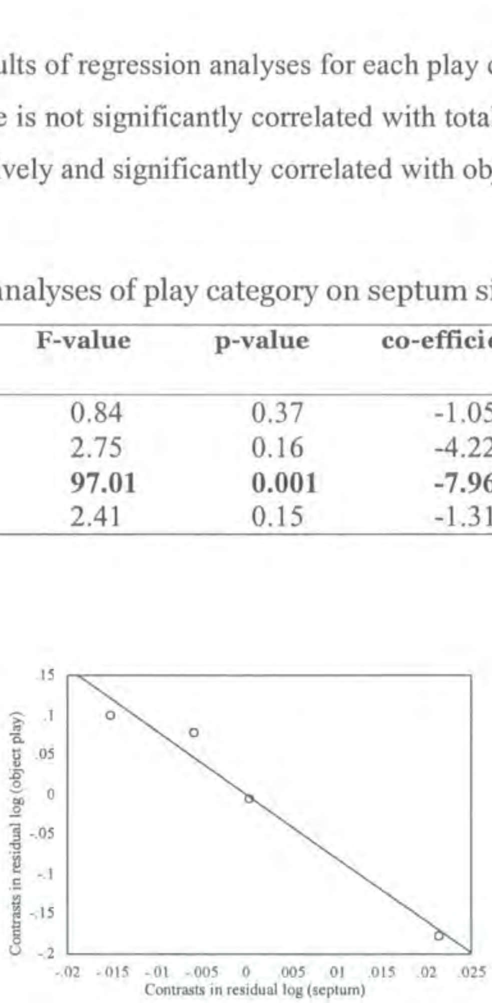


Fig. 7.21 Regression plot of residual log (object play) on residual log (septum size) in primates

7.6.2.5 Striatum

Table 7.8 shows the results of regression analyses for each play category on striatum size in primates. Striatum size is not significantly associated with solitary locomotor or object play; it is however, positively and significantly correlated with total play (although this is non-significant after Bonferroni correction) and social play (Figures 7.22 and 7.23), thus according with its rôle in motor systems.

Table 7.8 Regression analyses of play category on striatum size in primates

Play type	DF	F-value	p-value	co-efficient	r^2
Total	**1, 14**	**4.86**	**0.04**	**1.94**	**0.26**
Solitary	1, 5	1.04	0.35	-1.68	0.17
Object	1, 3	3.79	0.14	-3.55	0.56
Social	**1, 12**	**4.93**	**0.01**	**1.43**	**0.39**

Bonferroni = 0.013, total n.s.

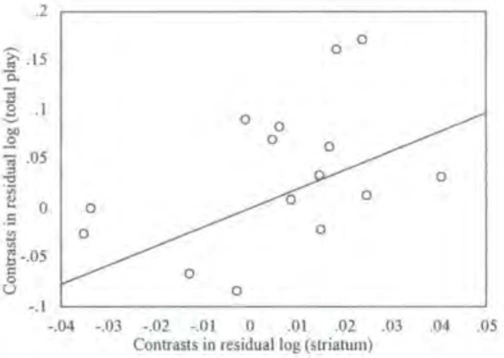


Fig. 7.22 Regression plot of residual log (total play) on residual log (striatum size) in primates

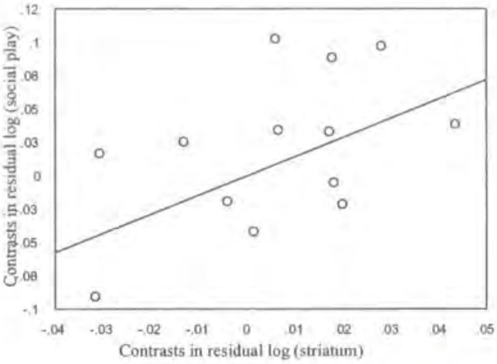


Fig. 7.23 Regression plot of residual log (social play) on residual log (striatum size) in primates

7.6.2.6 Hippocampus

Table 7.9 shows the results of regression analyses for each play category on hippocampus size in primates. Hippocampus size is not positively correlated with total play or social play; it is however, negatively and significantly correlated with solitary locomotor and object play (Figures 7.24 and 7.25).

Table 7.9 Regression analyses of play category on hippocampus size in primates

Play type	DF	F-value	p-value	co-efficient	r^2
Total	1, 14	1.00	0.33	0.93	0.07
Solitary	**1, 5**	**15.51**	**0.01**	**-3.11**	**0.76**
Object	**1, 3**	**52.15**	**0.005**	**-7.83**	**0.95**
Social	1, 12	0.02	0.90	0.09	0.001

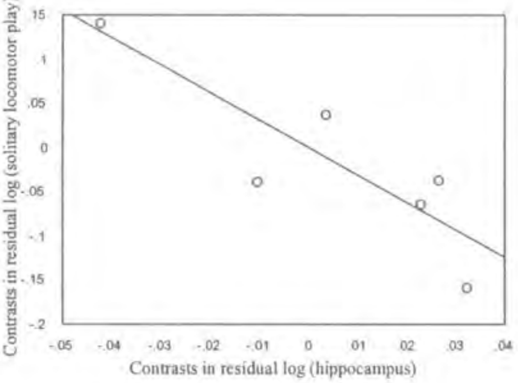


Fig. 7.24 Regression plot of residual log (solitary locomotor play) on residual log (hippocampus size) in primates

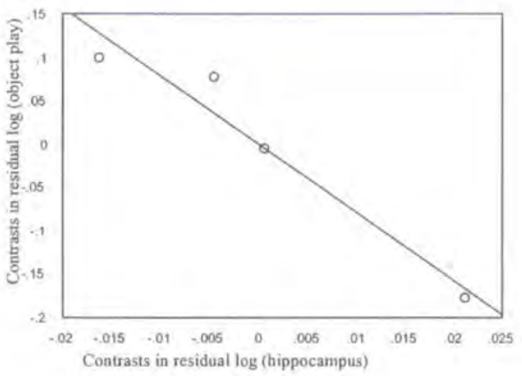


Fig. 7.25 Regression plot of residual log (object play) on residual log (hippocampus size) in primates

7.6.2.7 Schizocortex

Table 7.10 shows the results of regression analyses for each play category on schizocortex size in primates. Schizocortex size is not significantly associated with total, object, or social play, but is however, negatively and significantly correlated with solitary locomotor (Figure 7.26). This is perhaps not surprising given that the schizocortex (comprising the entorhinal cortex and subiculum) are part of the hippocampal formation (see section 7.6.2.6 above).

Table 7.10 Regression analyses of play category on schizocortex size in primates

Play type	DF	F-value	p-value	co-efficient	r^2
Total	1, 14	1.53	0.24	1.39	0.10
Solitary	**1, 5**	**17.59**	**0.008**	**-3.76**	**0.78**
Object	1, 3	2.64	0.20	-9.13	0.47
Social	1, 12	0.01	0.92	-0.08	0.001

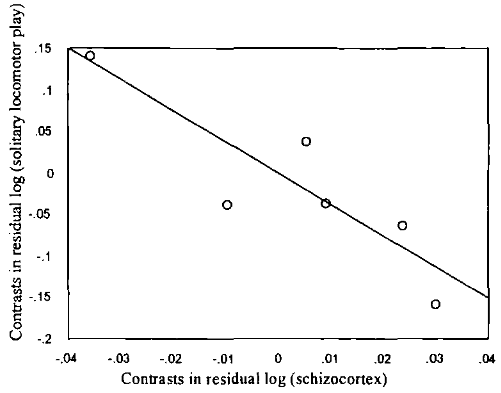


Fig. 7.26 Regression plot of residual log (solitary locomotor play) on residual log (schizocortex size) in primates

7.6.2.8 Neocortex

Table 7.11 shows the results of regression analyses for each play category on neocortex size in primates. Neocortex size is not significantly correlated with total play, solitary locomotor play or object play; it is however, positively and significantly correlated with social play (Figure 7.27).

Table 7.11 Regression analyses of play category on neocortex size in primates

Play type	**DF**	**F-value**	**p-value**	**co-efficient**	**r^2**
Total	1, 15	0.07	0.79	0.13	0.005
Solitary	1, 5	0.001	0.97	0.05	2.90
Object	1, 3	1.37	0.33	-1.50	0.31
Social	**1, 12**	**9.77**	**0.008**	**0.91**	**0.45**

Table 7.12 shows the results of regression analyses for each play category on neocortex size in carnivores. Neocortex size is not significantly correlated with total play. There were too few observations of solitary locomotor and object play to permit a statistical result. Neocortex size is however positively and significantly correlated with social play (Figure 7.28).

Table 7.12 Regression analyses of play category on neocortex size in carnivores

Play type	DF	F-value	p-value	co-efficient	r^2
Total	1, 5	1.10	0.34	-0.98	0.20
Solitary+	-	-	-	-	-
Object+	-	-	-	-	-
Social	**1, 3**	**42.24**	**0.007**	**1.73**	**0.93**

+ Too few observations

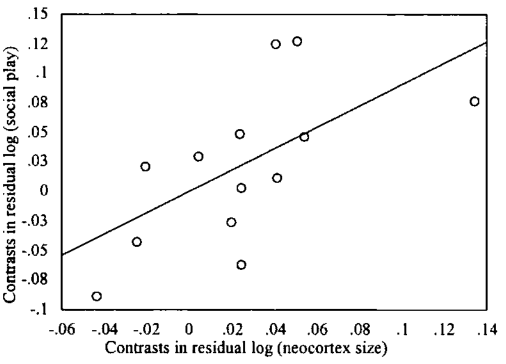


Fig. 7.27 Regression plot of log (social play) on play) on log (neocortex size) in primates

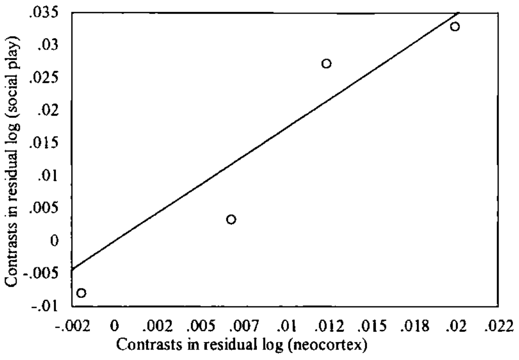


Fig. 7.28 Regression plot of log (social log (neocortex size) in carnivores

7.6.2.9 Thalamus

Table 7.13 shows the results of regression analyses for each play category on thalamus size in primates. Thalamus size is not significantly correlated with total play. There were too few observations of solitary locomotor and object play to permit a statistical result. Thalamus size is however, positively and significantly correlated with social play (Figure 7.29).

Table 7.13 Regression analyses of play category on thalamus size in primates

Play type	DF	F-value	p-value	co-efficient	r^2
Total	1, 6	0.26	0.63	0.26	0.04
Solitary+	-	-	-	-	-
Object+	-	-	-	-	-
Social	**1, 6**	**6.00**	**0.01**	**1.27**	**0.50**

+ Too few observations

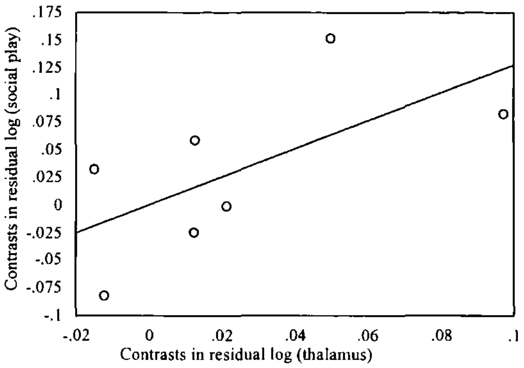


Fig. 7.29 Regression plot of log (social play) on log (thalamus) in primates

7.6.2.10 Hypothalamus

Table 7.14 shows the results of regression analyses for each play category on hypothalamus size in primates. Hypothalamus size shows no significant relationship with total play. There were too few observations of solitary locomotor and object play to permit a statistical result. Hypothalamus size is however positively and significantly correlated with social play (Figure 7.30).

Table 7.14 Regression analyses of play category on hypothalamus size in primates

Play type	**DF**	**F-value**	**p-value**	**co-efficient**	**r²**
Total	1, 6	0.42	0.54	0.44	0.07
Solitary+	-	-	-	-	-
Object+	-	-	-	-	-
Social	**1, 6**	**11.61**	**0.01**	**1.87**	**0.66**

+ Too few observations

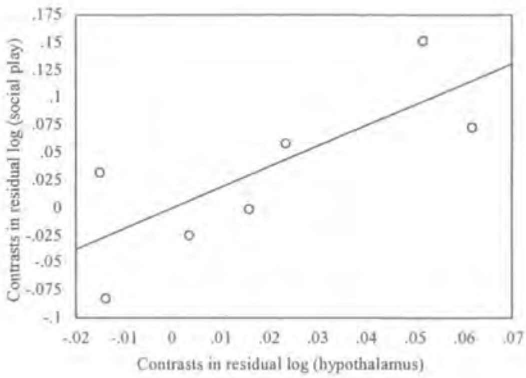


Fig. 7.30 Regression plot of log (social play) on log (hypothalamus) in primates

7.6.2.11 Optic tract

Table 7.15 shows the results of regression analyses for each play category on optic tract size in primates. Optic tract size shows no significant correlation with total play; it is however, positively and significantly correlated with social play (Figure 7.31). There were too few observations of solitary locomotor and object play to permit a statistical result.

Table 7.15 Regression analyses of play category on optic tract size in primates

Play type	DF	F-value	p-value	co-efficient	r^2
Total	1, 6	0.70	0.44	0.39	0.10
Solitary+	-	-	-	-	-
Object+	-	-	-	-	-
Social	**1, 6**	**14.20**	**0.009**	**1.49**	**0.71**

+ Too few observations

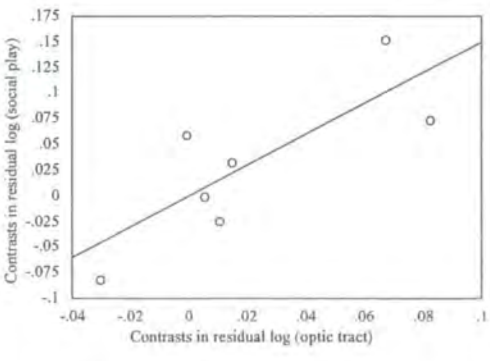


Fig. 7.31 Regression plot of log (social play) on log (optic tract) in primates

7.6.2.12 Visual cortex

Table 7.16 shows the results of regression analyses for each play category on visual cortex size in primates. Visual cortex size is not significantly associated with total or object play. It is however, positively and significantly correlated solitary locomotor play (although non-significant after Bonferroni correction) and social play (Figures 7.32 and 7.33).

Table 7.16 Regression analyses of play category on visual cortex size in primates

Play type	**DF**	**F-value**	**p-value**	**co-efficient**	**r^2**
Total	1, 12	1.64	0.22	0.62	0.12
Solitary	**1, 4**	**8.69**	**0.04**	**1.33**	**0.69**
Object	1, 3	0.42	0.56	-1.19	0.12
Social	**1, 10**	**15.91**	**0.003**	**1.24**	**0.61**

Bonferroni = 0.013, solitary n.s.

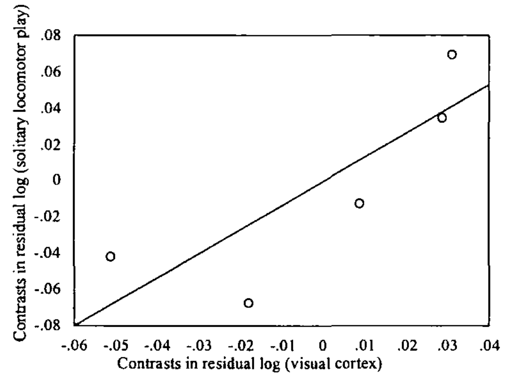


Fig. 7.32 Regression plot of log (solitary locomotor play) on log (visual cortex) in primates

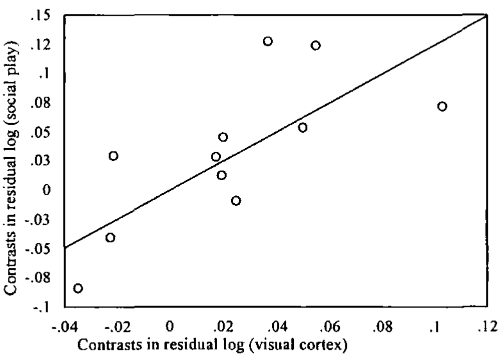


Fig. 7.33 Regression plot of log (social play) on log (visual cortex) in primates

7.6.2.13 Lateral geniculate nucleus (LGN)

Table 7.17 shows the results of regression analyses for each play category on Lateral geniculate nucleus (LGN) size in primates. LGN size is positively and significantly correlated with total play (although non-significant after Bonferroni correction) and social play (Figures 7.34 and 7.35). LGN size is not significantly correlated with solitary locomotor or object play.

Table 7.17 Regression analyses of play category on lateral geniculate nucleus (LGN) size in primates

Play type	**DF**	**F-value**	**p-value**	**co-efficient**	**r^2**
Total	**1, 13**	**5.44**	**0.03**	**1.02**	**0.30**
Solitary	1, 5	0.08	0.78	-0.56	0.02
Object	1, 3	1.27	0.34	-2.44	0.30
Social	**1, 11**	**9.92**	**0.009**	**1.31**	**0.47**

Bonferroni = 0.013, total n.s.

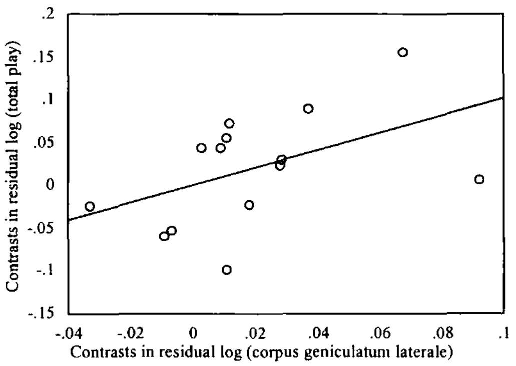


Fig. 7.34 Regression plot of log (total play) on log (lateral geniculate nucleus [LGN]) in primates

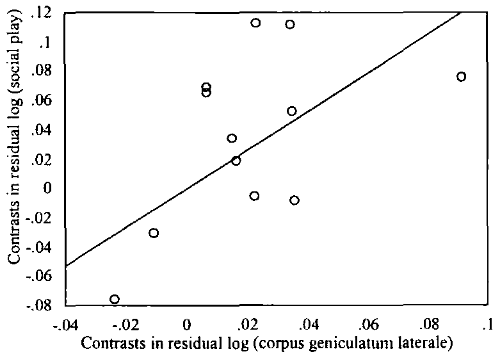


Fig. 7.35 Regression plot of log (social play) on log (lateral geniculate nucleus [LGN]) in primates

7.6.2.14Amygdala

Table 7.18 below shows the results of regression analyses for each play category on amygdala size in primates. Amygdala size is not significantly associated with total or solitary locomotor play; it is however, positively and significantly correlated with social play (Figure 7.36). There were too few observations of object play to permit a statistical result.

Table 7.18 Regression analyses of play category on amygdala size in primates

Play type	DF	F-value	p-value	co-efficient	r^2
Total	1, 9	0.08	0.79	-0.22	0.008
Solitary	1, 3	1.89	0.26	-5.93	0.39
Object+	-	-	-	-	-
Social	**1, 7**	**15.64**	**0.005**	**1.442**	**0.69**

+Too few observations

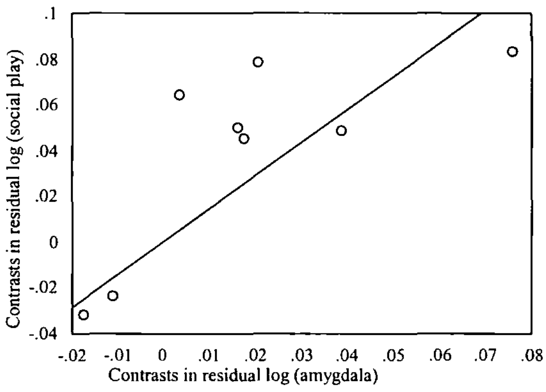


Fig. 7.36 Regression plot of log (social play) on log (amygdala) in primates

7.6.2.15 Complexus centromedialis

Table 7.19 below, shows the results of regression analyses for each play category on complexus centromedialis size in primates. Complexus centromedialis is not significantly associated with total or solitary locomotor play; it is however, positively and significantly correlated with social play (Figure 7.37). There were too few observations of object play to permit a statistical result.

Table 7.19 Regression analyses of play category on complexus centromedialis size in primates

Play type	DF	F-value	p-value	co-efficient	r^2
Total	1, 9	0.14	0.72	-0.27	0.02
Solitary	1, 3	0.14	0.74	-1.88	0.04
Object +	-	-	-	-	-
Social	**1, 7**	**13.36**	**0.008**	**1.28**	**0.66**

+Too few observations

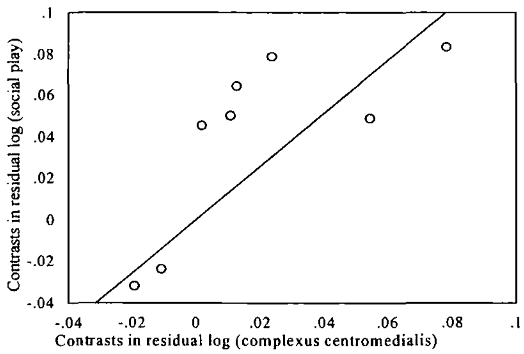


Fig. 7.37 Regression plot of log (social play) on log (complexus centromedialis) in primates

7.6.2.16 Nucleus amygdalae basalis, pars magnocellularis

Table 7.20 shows the results of regression analyses for each play category on nucleus amygdalae basalis, pars magnocellularis size in primates. Nucleus amygdalae basalis, pars magnocellularis is positively and significantly correlated with social play (Figure 7.38); this result however is rendered non-significant following Bonferroni correction. There is no significant association with total, solitary locomotor, or object play.

Table 7.20 Regression analyses of play category on nucleus amygdalae basalis, pars magnocellularis size in primates

Play type r^2	**DF**	**F-value**	**p-value**	**co-efficient**	
Total	1, 9	0.007	0.94	0.06	0.001
Solitary	1, 3	2.64	0.20	-2.51	0.47
Object	1, 3	1.44	0.35	-1.26	0.42
Social	**1, 7**	**7.44**	**0.02**	**1.04**	**0.52**

Bonferroni = 0.013, n.s.

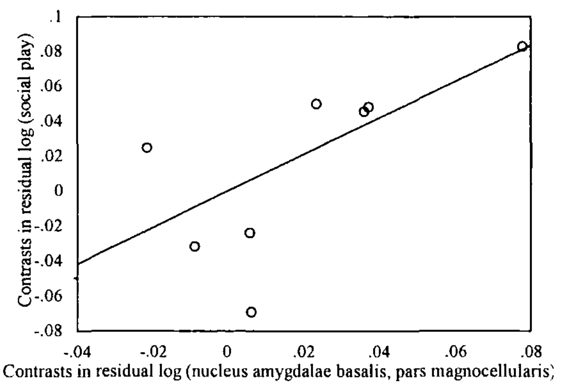


Fig. 7.38 Regression plot of residual log (social play) onresidual log (nucleus amygdalae basalis, pars magno-cellularis) in primates

7.6.2.17 Complexus vestibularis

Table 7.21 shows the results of regression analyses for each play category on complexus vestibularis size in primates. Complexus vestibularis is not significantly associated with total play; it is however positively and significantly correlated with social play (Figure 7.39). There were too few observations of both solitary locomotor play and object play to permit a statistical result.

Table 7.21 Regression analyses of play category on complexus vestibularis size in primates

Play type	**DF**	**F-value**	**p-value**	**co-efficient**	**r^2**
Total	1, 6	0.38	0.56	0.47	0.06
Solitary +	-	-	-	-	-
Object+	-	-	-	-	-
Social	**1, 6**	**7.54**	**0.01**	**1.84**	**0.56**

+ Too few observations

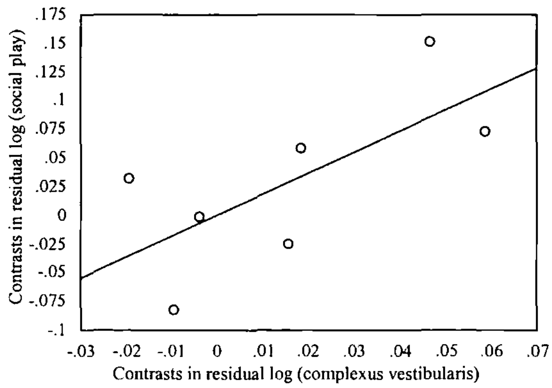


Fig. 7.39 Regression plot of log (social play) on residual log (complexus vestibularis) in primates

7.6.2.18 Nucleus vestibularis superior

Table 7.22 shows the results of regression analyses for each play category on nucleus vestibularis superior size in primates. Nucleus vestibularis superior is positively and significantly correlated with total play (Figure 7.40), although this result is non-significant when controlled for Bonferroni procedure. There is no correction with social play. There were too few observations of both solitary locomotor play and object play to permit a statistical result.

Table 7.22 Regression analyses of play category on nucleus vestibularis superior size in primates

Play type	**DF**	**F-value**	**p-value**	**co-efficient**	**r^2**
Total	**1, 6**	**6.33**	**0.04**	**1.09**	**0.51**
Solitary +	-	-	-	-	-
Object+	-	-	-	-	-
Social	1, 6	1.46	0.27	0.79	0.20

+ Too few observations; Bonferroni = 0.013, n.s.

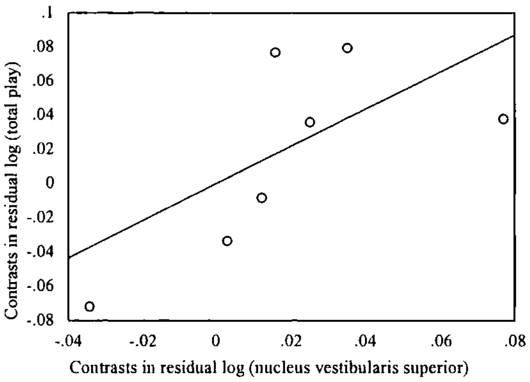


Fig. 7.40 Regression plot of log (total play) on residual log (nucleus vestibularis superior) in primates

7.6.2.19 Nucleus vestibularis medialis

Table 7.23 shows the results of regression analyses for each play category on nucleus vestibularis medialis size in primates. Nucleus vestibularis medialis is not significantly correlated with total play; it is however positively and significantly correlated with social (Figure 7.41). There were too few observations of both solitary locomotor play and object play to permit a statistical result.

Table 7.23 Regression analyses of play category on nucleus vestibularis medialis size in primates

Play type	**DF**	**F-value**	**p-value**	**co-efficient**	**r^2**
Total	1, 6	0.18	0.69	0.32	0.03
Solitary+	-	-	-	-	-
Object+	-	-	-	-	-
Social	**1, 6**	**11.86**	**0.01**	**1.98**	**0.66**

+ Too few observations

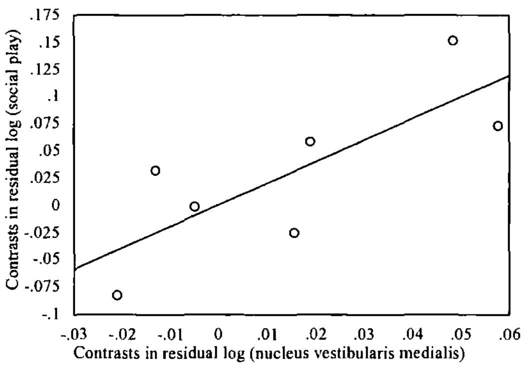


Fig. 7.41 Regression plot of residual log (social play) on residual log (nucleus vestibularis medialis)

7.6.2.20 Nucleus vestibularis descendens

Table 7.24 shows the results of regression analyses for each play category on nucleus vestibularis descendens size in primates. Nucleus vestibularis descendens is not significantly correlated with total play; it is however, positively and significantly correlated with social play (Figure 7.42). There were too few observations of both solitary locomotor play and object play to permit a statistical result.

Table 7.24 Regression analyses of play category on nucleus vestibularis descendens size in primates

Play type	**DF**	**F-value**	**p-value**	**co-efficient**	**r^2**
Total	1, 6	0.26	0.63	0.29	0.04
Solitary +	-	-	-	-	-
Object+	-	-	-	-	-
Social	**1, 6**	**16.45**	**0.006**	**1.70**	**0.73**

+ Too few observations

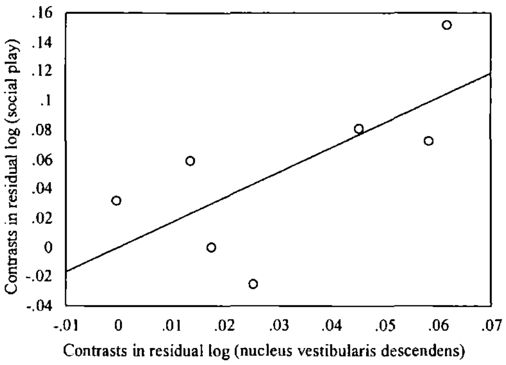


Fig. 7.42 Regression plot of residual log (social play) on residual log (nucleus vestibularis descendens) in primates

7.6.2.21 Corpus subfornicale

Table 7.25 shows the results of regression analyses for each play category on corpus subfornicale size in primates. Regression of total play on corpus subfornicale shows a negative and significant relationship (Figure 7.43). After Bonferroni correction however, this result is rendered non-significant. Regressions of all other types of play on corpus subfornicale show no significant association.

Table 7.25 Regression analyses of play category on corpus subfornicale size in primates

Play type	**DF**	**F-value**	**p-value**	**co-efficient**	**r^2**
Total	**1, 12**	**4.81**	**0.05**	**-0.69**	**0.29**
Solitary	1, 4	0.33	0.60	-0.53	0.75
Object	1, 3	1.38	0.32	-2.12	0.32
Social	1, 11	0.41	0.54	-0.23	0.04

Bonferroni = 0.013, n.s.

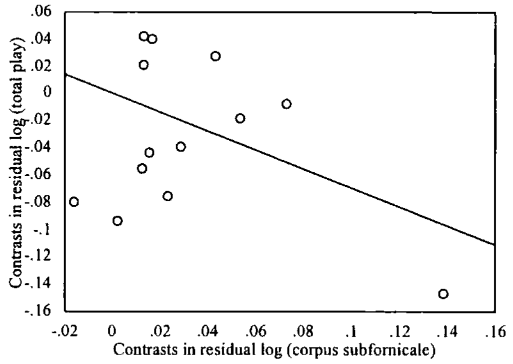


Fig. 7.43 Regression plot of residual log (total play) on residual log (corpus subfornicale) in primates

7.6.2.22 Pons

Table 7.26 shows the results of regression analyses for each play category on pons size in primates. Total, solitary locomotor, and object play show no significant association with pons. Social play however, is positively and significantly correlated with relative pons size in primates (Figure 7.44).

Table 7.26 Regression analyses of play category on pons size in primates

Play type	**DF**	**F-value**	**p-value**	**co-efficient**	**r^2**
Total	1, 8	0.75	0.41	0.47	0.09
Solitary	1, 3	0.15	0.72	-0.63	0.05
Object	1, 3	0.11	0.77	-0.65	0.05
Social	**1, 5**	**9.09**	**0.01**	**0.66**	**0.65**

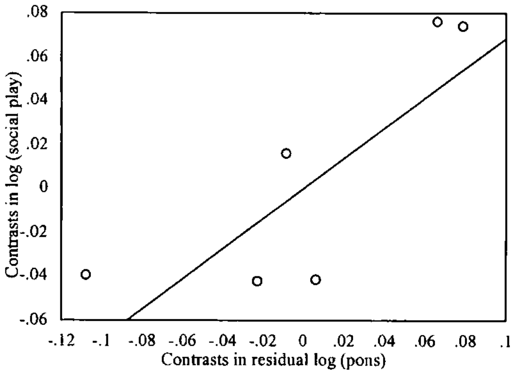


Fig. 7.44 Regression plot of log (social play) on residual log (pons) in primates

The following brain components did not show a significant correlation when regressed against any play category: mesencephalon, diencephalon, olfactory bulb, piriform lobe, epithalamus, subthalamus, pallidum, nucleus subthalamicus, capsula interna, nucleus tractus olfactorii lateralis, complexus basolateralis, nucleus vestibularis lateralis, nucleus septalis triangularis, nucleus habenularis medialis, corpus pinneale, and corpus subcommisurale.

Table 7.27 Summary of results of brain components with each play category in primates and carnivores

Brain part	Play category: significant correlation?							
	Total		Solitary locomotor		Object		Social	
Whole brain	✗		✗		✗		✗	
		✗		✓+		✗		✓+
Whole brain-neocortex	✗		✗		✓+		✓+	
Forebrain:								
Neocortex		✗		✗		✗		✓+
		✗		-		-		✓+
Limbic system:								
Olfactory bulb	✗		✗		✗		✗	
Hippocampus:	✗		✓-		✓-		✗	
Schizocortex		✗		✓-		✗		✗
Amygdala:		✗		✗		-		✓+
Complexus centromedialis		✗		✗		-		✓+
Complexus cortico-basolateralis	✗		✗		✗		✗	
Nucleus tractus olfactorii lateralis		✗		✗		-		✗
Nucleus amygdalae basalis, pars magnocellularis	✗		✗		✗		✓+	
Septum:		✗		✗		✓-		✗
Triangular septal nucleus		✗		✗		✗		✗
Diencephalon:	✗		✗		✗		✗	
Thalamus		✗		-		-		✓+
Corpus geniculate laterale (LGN)	✓		✗		✗		✓+	
Hypothalamus	✗		-		-		✓+	
Epithalamus		✗		-		-		✗
Habenular nuclei		✗		✗		✗		✗

Brain part	Play category: significant correlation?			
	Total	Solitary locomotor	Object	Social
Corpus pineale	×	×	×	×
Telencephalon	✓+	×	×	✓+
Basal ganglia:				
Subthalamus	×	-	-	×
Subthalamic nuclei	×	-	-	×
Pallidum	×	-	-	×
Striatum	✓+	×	×	✓+
Piriform lobe	×	×	×	×
Corpus subfornicale	✓-	×	×	×
Corpus subcommissurale	×	×	×	×
Capsula interna	×	-	-	×
Midbrain (mesencephalon):	×	×	×	×
Optic tract	×	-	-	✓+
Hindbrain				
Cerebellum	×	×	×	✓+
	×	-	-	-
Pons	×	×	×	✓+
Medulla oblongata	×	×	×	✓+
Vestibular complex	×	-	-	✓+
Vestibular nuclei:				
Nucleus vestibularis superior	✓+	-	-	×
Nucleus vestibularis lateralis	×	-	-	×
Nucleus vestibularis medialis	×	-	-	✓+
Nucleus vestibularis descendens	×	-	-	✓+
Visual cortex	×	✓+	×	✓+

✓ = significant, × = not significant, + = positive correlation, - = negative correlation/no data;
Black = primates, Red = carnivores.

7.6.2.23 Rest of Brain analyses

As detailed in the Methods section, it is necessary to control for the rest of the brain in conducting brain component analyses, and to further assess the significant results detailed in the above sections. The following analyses in Table 7.28 details multiple regression analyses of each play category (dependent variable Y) on adult body mass, rest of brain, and the brain component that showed a significant relationship in the independent contrasts analyses in this chapter (3 independent variables X).

Table 7.28 Summary of multiple regression analyses of each play category on body mass, rest of brain, and each significant brain component for play in primates

Play category	Brain component	Standard co-efficient	t-value	p-value	r^2
Total	Medulla	0.272	0.66	0.52	0.32
Solitary		0.29	0.41	0.69	0.20
Object		1.07	1.45	0.29	0.91
Social		**1.08**	**2.87**	**0.01**	**0.58**
Total	Cerebellum	-0.05	-0.11	0.92	0.30
Solitary		0.18	0.29	0.78	0.19
Object		0.87	1.15	0.36	0.89
Social		**1.30**	**3.25**	**0.01**	**0.67**
Total	Septum	-0.28	-0.86	0.41	0.34
Solitary		-0.86	-0.73	0.50	0.25
Object		2.00	1.69	0.23	0.92
Social		0.54	1.67	0.12	0.43
Total	Striatum	0.18	0.36	0.72	0.31
Solitary		-0.23	-0.35	0.74	0.20
Object		1.15	2.35	0.14	0.95
Social		**1.58**	**3.85**	**0.003**	**0.87**
Total	Hippocampus	0.13	0.39	0.71	0.31
Solitary		**-0.75**	**-3.20**	**0.02**	**0.73**
Object		1.54	1.12	0.38	0.89
Social		0.22	0.57	0.58	0.31
Total	Schizocortex	**1.16**	**0.02**	**0.04**	**0.30**
Solitary		**-0.95**	**-3.06**	**0.02**	**0.71**
Object		4.03	1.17	0.36	0.89
Social		0.13	0.27	0.79	0.30
Total	Neocortex	0.42	0.84	0.41	0.34
Solitary		0.61	0.72	0.50	0.25
Object		1.02	1.16	0.34	0.89
Social		**1.29**	**3.26**	**0.009**	**0.71**

Play category	Brain component	Standard co-efficient	t-value	p-value	r^2
Total	Thalamus	-0.13	-0.24	0.82	0.44
Solitary+		-	-	-	-
Object+		-	-	-	-
Social		**1.75**	**3.61**	**0.03**	**0.91**
Total	Hypothalamus	0.20	0.52	0.63	0.35
Solitary+		-	-	-	-
Object+		-	-	-	-
Social		**1.48**	**4.23**	**0.01**	**0.89**
Total	Optic tract	0.18	0.51	0.64	0.46
Solitary+		-	-	-	-
Object+		-	-	-	-
Social		**1.41**	**4.67**	**0.009**	**0.92**
Total	Visual cortex	0.18	0.39	0.70	0.35
Solitary		0.47	1.03	0.36	0.73
Object		0.62	0.83	0.49	0.86
Social		**1.27**	**3.01**	**0.01**	**0.68**
Total	LGN	-0.42	-0.07	0.94	0.35
Solitary		0.66	1.46	0.22	0.78
Object		0.88	1.23	0.34	0.89
Social		**1.68**	**3.15**	**0.01**	**0.67**
Total	Amygdala	-0.81	-0.23	0.72	0.25
Solitary		0.20	0.57	0.45	0.41
Object+		-	-	-	-
Social		**1.60**	**3.97**	**0.004**	**0.82**
Total	Complexus centro-medialis	-0.74	-0.18	0.58	0.31
Solitary		-0.73	-0.20	0.61	0.31
Object+		-	-	-	-
Social		**1.18**	**2.94**	**0.009**	**0.71**
Total	Nucleus amygdalae basalis, pars magnocellularis	0.03	0.14	0.79	0.20
Solitary		0.56	0.89	0.32	0.51
Object+		-	-	-	-
Social		0.92	1.08	0.19	0.69
Total	Vestibular complex	0.38	0.86	0.43	0.51
Solitary+		-	-	-	-
Object+		-	-	-	-
Social		**2.28**	**8.47**	**0.01**	**0.99**
Total	Nucleus vestibularis medialis	0.36	0.59	0.58	0.47
Solitary+		-	-	-	-
Object+		-	-	-	-
Social		1.49	1.21	0.29	0.61
Total	Nucleus vestibularis descendens	0.22	0.53	0.62	0.46
Solitary+		-	-	-	-
Object+		-	-	-	-
Social		1.03	1.37	0.24	0.64

Play category	**Brain component**	**Standard co-efficient**	**t-value**	**p-value**	**r^2**
Total	Corpus subfornicale	-0.43	-1.80	0.10	0.49
Solitary		-0.12	-0.39	0.71	0.67
Object		0.18	0.38	0.74	0.83
Social		0.16	0.54	0.60	0.31
Total	Pons	0.47	0.94	0.38	0.44
Solitary		-0.05	-0.07	0.95	0.14
Object		1.31	1.32	0.41	0.93
Social		**1.27**	**4.93**	**0.002**	**0.89**

+ Too few observations

These results show that a range of brain structures correlate positively with play independently of variation in the rest of the brain, including the neocortex, cerebellum, visual system, vestibular system, striatum, and pons. These brain regions are all connected to visuo-motor co-ordination, as well as to socio-cognitive processes. These results show a general pattern of an increased strength in the correlation between the significant play category from the previous analyses, and the brain component, controlling for body mass and rest of brain. This is especially true of the results for social play. The above multiple regression analyses typically increase the value of r^2, even if the p-values are reduced in significance. This suggests that the relationship between significant play categories and significant brain components is statistically robust.

7.6.3 Brain size

The following analyses continue to focus upon the number of behaviours in a species' repertoire, but with relative brain size as the independent variable. Research effort is controlled for by regressing the play variable against the total number of months of study (as reported in the literature); a residual is taken from this line.

7.6.3.1 Primates

Regression analyses of number of play behaviours observed in a species' repertoire (controlled for research effort in months) on relative brain size (controlled for body size) in primates show a positive and significant correlation (F (1, 24) = 16.89, p = 0.0004, co-efficient = 3.46, $r^2 = 0.44$) (Figure 7.45).

7.6.3.2 Platyrrhines

Regression analyses of number of play behaviours observed in a species' repertoire (controlled for research effort in months) on relative brain size (controlled for body size) in platyrrhines show a positive and significant correlation (F (1, 3) = 10.72, p = 0.04, co-efficient = 3.17, $r^2 = 0.78$) (Figure 7.46).

7.6.3.3 Catarrhines

Regression analyses of number of play behaviours observed in a species' repertoire (controlled for research effort in months) on relative brain size (controlled for body size) in catarrhines show a positive and significant correlation (F (1, 18) = 12.78, p = 0.002, co-efficient = 3.48, $r^2 = 0.42$) (Figure 7.47).

7.6.3.4 Bout length

Independent contrasts analyses aim to focus on the evolutionary relationship of play category and bout length, by using a species mean for bout length in seconds. Figure 7.48 shows partial regression analyses for bout length. Average bout length is positively and significantly correlated with adult brain weight in primates (F (1, 7) = 7.26, p = 0.03, co-efficient = 280.76, $r^2 = 0.51$). One outlier has been removed from this analysis as specified by the CAIC programme.

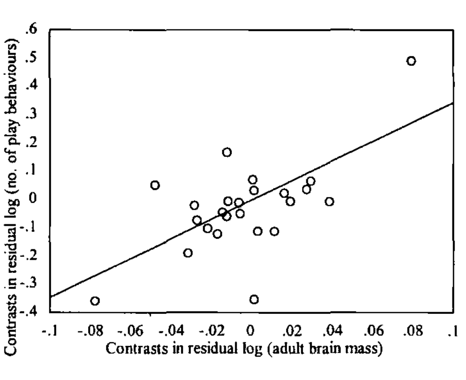


Fig. 7.45 Partial correlation of relative brain size on no. of behaviours in the repertoire of primates

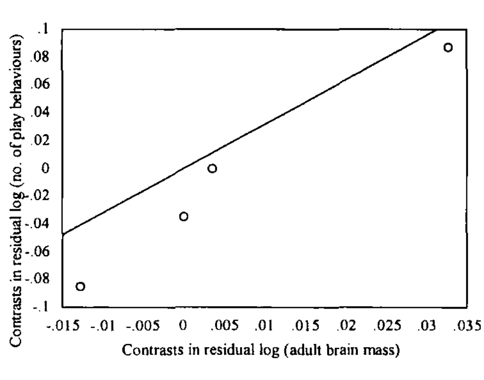


Fig. 7.46 Partial correlation of relative brain size on no. of behaviours in the repertoire of platyrrhines

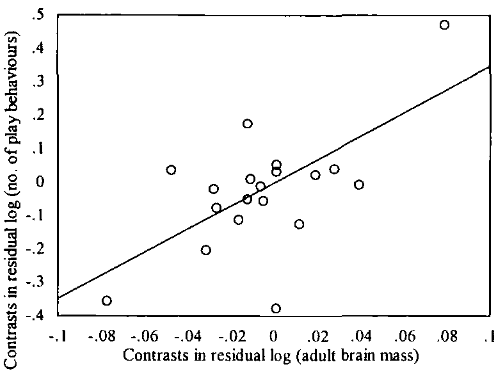


Fig. 7.47 Partial correlation of relative brain size on no. of behaviours in the repertoire of catarrhines

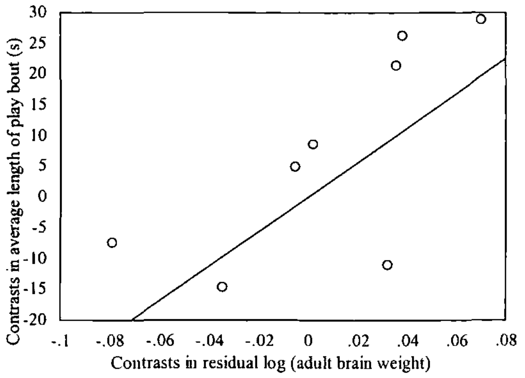


Fig. 7.48 Partial correlation of brain size, body size and average playbout length (s) in primates

7.6.4 Dichotomous variables

Table 7.29 shows the using one-sample t-tests detailing the evolutionary changes in relative brain size relative to the transitions in the above dichotomous variables in primates.

Table 7.29 Results of relative log brain size and dichotomous play variables in primates

Variable	Mean	DF	*t*	*p*	Significance?
Adult play	-0.006	13	-0.378	0.71	N.S.
Adult male play	-0.02	11	-0.94	0.38	N.S.
Adult-adult play	0.007	16	0.50	0.62	N.S.
Sex play	-0.001	17	-0.06	0.95	N.S.
SSD	-0.03	15	-1.96	0.07	N.S.
SSP	-0.004	11	-0.17	0.87	N.S.
SAD	-0.002	12	-0.10	0.92	N.S.
SAP	0.014	8	0.62	0.55	N.S.
Sibling	0.03	4	0.84	0.45	N.S.
Relatedness	-0.06	5	-2.22	0.07	N.S.
Dominance	0.02	3	0.35	0.75	N.S.
Vocalisation	-0.005	10	-2.14	0.83	N.S.
Polyadic	0.042	8	1.93	0.09	N.S.
Interspecific	0.02	3	0.35	0.75	N.S.
Place	-0.03	5	-1.02	0.35	N.S.

There were too few observations of dyadic play to permit a result.

7.7 Discussion

The results in this chapter show that there were significant correlations between certain play categories and certain brain areas, namely the neocortex, cerebellum, striatum, vestibular system, amygdala, hypothalamus, and visual areas. The following sections discuss these relationships in more detail.

7.7.1 Brain size and play

Although we might expect brain expansion to reflect cognitive elaborations in play behaviour, these results show no significant evolutionary correlation between whole brain size and play behaviour in primates. These results support those of Iwaniuk et al. (2001) who found no correlation between adult primate play and overall brain size. Here, the results suggest that in juvenile *and* adult primates, the trend holds for relative brain size also. In carnivores however, these results show a conflicting trend from the results for primates, in that both solitary play (although non-significant after Bonferroni correction) and social play are positively correlated with brain size, supporting the claim that larger-brained species may also be among the most playful. Moreover, although not statistically significant in this case, object play shows a strong tendency towards correlation with brain size in carnivores also. In carnivores, it may be that group size accounts for this trend, that is, group-living carnivores may have a larger overall brain size (perhaps through neocortical expansion, Dunbar & Bever 1998) to cope with the demands of social living. This in turn not only provides a greater opportunity to engage in social play behaviours, but also suggests that social play is beneficial to such species in terms of honing brain development to cope with the rigours of group life. Primates are habitually more social in terms of group size and social complexity than are carnivores, the vast majority of which are solitary (Bekoff et al. 1984), and thus for primates it might be even more necessary to concentrate on the evolutionary relationships between play and specific neural components, rather than with the relative size of the entire brain.

7.7.2 Neocortex and play

One of the most noticeable patterns in the results presented in this chapter is the prominence of social play over other forms of play in the co-evolution of play and brain structures. I suggest that this provides some support to the hypothesis that social play represents a distinct category of behaviour (Panksepp 1998), and that social play may be an especially cognitive aspect to play behaviour. The results here indicate a positive and significant evolutionary relationship between neocortex size and social play behaviour in primates. This result supports previous findings based on an independent dataset (Lewis 2000) that social play, but not total, solitary locomotor, or object play, show an evolutionary correlation with neocortex size. The results here reveal the same relationship for carnivores – the larger the relative neocortex size, the more social play behaviour is exhibited. For both primates and carnivores, these relationships hold true when the confounding effects of body size are removed, thus the results presented in this section support the hypothesis that neocortex size can predict the frequency of social play in primates and carnivores. Additionally, these results support the theory that primates and carnivores share a similar pattern of neocortical evolution (Dunbar & Bever 1998). The neocortex comprises most of the volume of the telencephalon in mammals, thus forebrain, and especially telencephalic (and neocortical) evolution, is a factor that drives behavioural evolution in mammals, and thus it may be expected that species with larger telencephalons (and therefore neocortices) exhibit not only more, but more complex, play behaviour (Burghardt 2001). In birds, for example, forebrain size can be used to predict innovative patterns of feeding behaviour (Lefebvre et al. 1997); it would be interesting to see if feeding innovations can predict object play, for example (Burghardt 2001).

The significant correlation between social play and neocortex size is an interesting finding in that primates and carnivores are especially playful mammalian orders, and both contain species that are highly social. Indeed, insofar as carnivores are concerned, it is most likely to be the more easily-observable diurnal and social species that have been recorded engaging in playful episodes (Bekoff et al. 1984). Given the propensity of species with large neocortices to be social species, and those both requiring and exhibiting evidence of social intelligence to maintain this sociality (Dunbar 1992), it seems likely that neocortical expansion over evolutionary time reflects social play behaviour, and further that social play occurs at higher rates in species with relatively more socio-cognitive processing power. Social play can only been successful if there is an awareness of rôle-appropriateness (Fagen 1981). In some primate and carnivore species where the level of social play behaviour can become especially complex, the continued accuracy of reading behavioural cues is rendered all the more important. I suggest that the species that are especially skilled in social interactions, such as chimpanzees (*Pan troglodytes*), are also the species that are especially skilled in social play, and it is no coincidence that these are also the species with the largest relative neocortex size (relative to body size). These playful interactions, especially those during the juvenile period, occur in order to assist in the formation of social relationships, but crucially enable the developing brain to be perfected in readiness for adult life. Thus social play may represent the development of an adult socio-cognitive system. The finding that a socially complex behaviour such as social play, correlates strongly with the size of the largest socio-cognitive structure of the brain, further supports this hypothesis.

7.7.3 Limbic system and play

As mentioned in the previous sections of this chapter, there is some evidence to suggest that structures of the limbic system might be important to play behaviour (Burghardt 2001). The results presented here suggest that this is the case and that much can be learned from studying these components in relation to neural co-evolution with play. These results are concerned only with primates from Stephan et al.'s (1981) database, as there are no comparable data for carnivores.

7.7.4 Amygdala

The positive and significant result in the correlation of social play and the amygdala indicates that over the course of primate evolution, there has been some degree of co-evolution between expansions in both the size of the amygdala, and in social play behaviour. This relationship does not hold for any other type of play. Other studies, mainly concerning the evolution of rat play-fighting, suggest that the importance of the amygdala in the emotional regulation of behaviour seems to be an important aspect in the expression of social play behaviour, in terms of assessment, affiliation and in social bonding (Pellis & Pellis 1998;

Burghardt 2001). As the amygdala is also important in the expression of aggression (Davis 1992), it might also be the case that the amygdala regulates the aggressive elements of play-fighting; in carnivores and primates this might be especially important, as one of the key elements is that of the play-bite (Symons 1978). Playful attack and defence are the basis of play-fighting (Aldis 1975), and this is also the play behaviour that demonstrates the greatest degree of sex- and age-differences, with younger males being far rougher in their play than older individuals and like-aged females (e.g. Biben 1986; Brown 1988). With the gonadal hormone influence on the amygdala contributing to sex-differences in aggression, sexual orientation, and play (e.g. Hines 1982), and the "confusion" between play-fighting and aggression, and gradual cessation of play towards the period when the individual reaches sexual maturity (Pellis & Pellis 1988, 1998), it seems likely that the amygdala is connected to the representation of social play behaviour. Pellis & Pellis (1998) suggest that the need for affiliation in social play may be dependent on both the amygdala and the cingulate cortex, and thus limbic structures may require further study in relation to play; my results contribute to the confirmation of this hypothesis for primates. Thus, the amygdala in particular seems to play a key rôle in the task of assessing play-partners and eliciting appropriate responses during social play behaviour (Burghardt 2001).

7.7.5 Hypothalamus

Parallel with the amygdala, the results here indicate a similar trend for the hypothalamus and social play behaviour in primates. This is interesting as like the amygdala, the hypothalamus is also a target for perinatal androgens resulting in sexually differentiated behaviours, including play (Hines & Shipley 1984). It is also important in the regulation of sexual and aggressive behaviours, as well as in the experience of emotions (Russell 1988), thus play-fighting and sexual elements of social play behaviour may also have a point of localisation in the hypothalamus. Similarly, both the amygdala and the lateral hypothalamus are deemed to be important neural "pleasure regions" that generate the understanding of enjoyable experiences (Isaacson 1982); it might be the case that play behaviour, as a "fun" behaviour (Fagen 1992), is incorporated in such experiences controlled by this part of the brain. It might be, however, that the ancient evolutionary origins of hypothalamic elaboration, has played a key part in the evolution of play behaviour. For example, one of the most basic emotional behavioural responses in animals is that of the fight-flight mechanism (Bear et al. 2001). It has been shown, specifically in ungulates, that some forms of behaviour mimic both flight response, and interspecific aggression (Byers 1984). As the hypothalamus is one part of the brain that regulates this response, there is an argument for the co-evolution of hypothalamic structures with play behaviour. Unfortunately, there are insufficient data here to test for a relationship between play that might usually reveal elements of fight-flight (i.e. locomotor play), but I predict that given sufficient data, such a relationship will emerge.

7.7.6 Thalamus

Results here show that the thalamus is positively and significantly correlated with social play behaviour in primates. As the thalamus contains the LGN, it might be argued that this result is supportive of the rôle of vision to social play interactions. However, the thalamus contains relays to for all cortical-sub-cortical traffic, not just vision. The thalamus, and especially its anterior nuclei, appears to be involved in recognition memory and emotion (Bear et al. 2001), and thus it is perhaps social play, rather than other forms of play, that is especially relevant. Social play may require emotional memory to augment its behavioural complexity, such as is witnessed in some primates and carnivores. Moreover, the context recognition of behaviour, and the recognition memory of other players and past interactions, may enhance play bouts and play complexity. Additionally, it has been shown that damage to the thalamic nuclei drastically reduces the performance of R&T (social-aggressive) play episodes in rats, and thus it has been hypothesised that the thalamus is important in the generation and mediation of social play (Panksepp 1998); thus my result here supports this hypothesis.

7.7.7 Hippocampal Formation (including schizocortex)

Given the apparent social rôle of the hippocampus to the regulation of emotions, learning, and conscious memory, not least its regulation of stress responses and recognition of new faces (Woolf 1998; Bear et al. 2001; Nestler 2002; Crane &

Milner 2002), it was predicted that the hippocampus would show a strong positive co-evolutionary relationship with social play behaviour. The results however, indicate a very different trend. There are strong negative correlations with the hippocampus and both solitary locomotor play and object play behaviour, and no significant correlations with either total play or social play. These results suggest that evolutionarily, increases in hippocampus size are correlated with decreases in the propensity for non-social forms of behaviour. The possible reasons for this are unclear, however, perhaps increases in relative hippocampus size have been at the cost of increases in neural components that control motor and reasoning tasks, such as that are more closely associated with solitary locomotor and object play responses, than emotive regions that may mediate social play more readily. Alternatively, the reverse may be true as both the hippocampus and solitary locomotor play are relatively ancient components in evolutionary terms (Byers 1984; Bear et al. 2001).

7.7.8 Septum

The septum is concerned with some basic emotional responses; those such as fear and relief, maternal instincts, and copulation (Yadin et al. 1993; Panzica et al. 2001; Sheehan & Numan 2002). With such elements arguably being present in some forms of play behaviour, it might be expected that the septum will show a positive elaborations with play through evolution. The results suggest however, that like the results for hippocampal-play evolution, this is not the case. Evolutionary relationships between object play and the septum are significantly, yet strongly negatively, correlated, suggesting that over the course of primate evolution, increases in septum size map onto decreases in the exhibition of object play behaviour. The triangular septal nucleus, which is a part of the septum, is believed to function in the regulation of appropriate behavioural responses (Menard & Treit 1996), and thus is also expected to be vital to the expression of play behaviour. These results present no such finding, as there are no significant correlations between this nucleus and primate play. Speculations for these results arguably suggest that increases in more "cognitive" regions of the brain are greater than limbic structures, thus render the locus of "cognitive" areas of play, such as object play, to regions such as the neocortex, for example. It might be the case that behavioural responses are more greatly mediated by other neural areas, or that the septum functions in the "serious" expression of serious behavioural responses, rather than play, which by definition appears functionless or non-serious (e.g. Martin & Caro 1985).

7.7.9 Olfactory complex

It was predicted that in primates, an order with a reliance on vision, that brain structures involved with olfaction were unlikely to be strongly associated with the expression of play behaviour. The results presented in this section confirm this hypothesis, with both the olfactory bulb, and the piriform lobe showing no evolutionary association with any play type. This relationship holds primarily for haplorhine primates, given their representation in the data used here; future results might show a different trend across strepsirhine primates and carnivores, as they show a greater adaptation for olfaction, and exhibit the presence of a nasal rhinarium for scent marking and detection (Fleagle 1988).

7.7.10 Basal ganglia and play

The basal ganglia, or striatopallidal complex (Butler & Hodos 1996), have been implicated as important structures in the expression of play behaviour (Burghardt 2001). The results here too indicate the potential importance of these structures to the evolution of play behaviour in primates. Indeed, the basal ganglia appear to be vital in both motor and cognitive functions (Jog et al. 1999), suggesting that both motor and cognitive functions have ancient co-evolutionary relationships, or that this is a slight adaptation from the ancestral form (Katz & Harris-Warrick 1999; Burghardt 2001). Again, as the available data derive from Stephan et al. (1981), the following discussion deals only with primates.

7.7.11 Striatum

The results here show positive and significant correlations between both total and social play and the striatum, indicating that striatum expansion has evolved with social, but not non-social, forms of play. The rôle of the striatum to social play is especially augmented as it is connected to the neocortex and the cerebellum in terms of function and cortical projections, thus suggesting the importance of both motor co-ordination and socio-cognitive processes to social play. This result supports previous studies that claim that damage to the caudate-putamen area can significantly reduce play in rats (Panksepp 1998); given that the striatum is comprised of the caudate nucleus and the putamen, this is an important finding, especially given the rôle of the striatum in motor control and motor learning (Jog et al. 1999). Indeed, the evolution of social play and the striatum ties in very closely with the co-evolution of social play and the cerebellum. It has been demonstrated in humans that damage to the striatum, and the cerebellum, results in both motor and cognitive impairment, albeit it in differing ways (Laforce & Doyon 2001). As the striatum is involved with visual systems and the planning of motor movements and procedural memory (Jog et al. 1999) it seems likely that this too will affect the expression of play, where reliance on vision and the innate understanding of motor actions is vital. Crucially, the striatal neurons project on neocortical circuits (Jog et al. 1999; Burghardt 2001), thus the striatum may be implicated in social behaviours also (see section on neocortex). My results here certainly indicate the likelihood of such an evolutionary trend.

7.7.12 Subthalamus & subthalamic nucleus

Given the rôle that the subthalamus plays in skeletal muscle motor actions (Bear et al. 2001), it was predicted that there would be a positive evolutionary relationship with play, as the performance of play behaviour during the juvenile period is known to permanently affect the modification of skeletal muscle fibre (Byers & Walker 1995). These results, however, although showing a positive relationship, fall short of statistical significance for social play, and show no significant association for total play. Unfortunately, there are too few data to conduct the analyses on solitary locomotor play or object play. I predict that given sufficient data for solitary locomotor play, a significant relationship will emerge, as it is likely that the energetic motor displays seen in locomotor play will contribute most greatly to the honing of skeletal muscle during the juvenile phase; a development that may in part be facilitated by subthalamic structures.

7.7.13 Pallidum

There is a non-significant correlation between pallidum size and social play in primates, although there is a positive trend (p = <0.1). The non-significance of this result is perhaps surprising, as, along with the subthalamic regions, the pallidum is an important region of the basal ganglia in terms of motor control (Wannier et al. 2002). More importantly, however, its rôle in social assessment and pair-bonding (Young 2002) suggest its potential as a key neural region in the expression of social play, where the context recognition of social behaviours is critical to its success.

7.7.14 Diencephalon

The results here show no correlation between play behaviour and the diencephalon in primates. As the diencephalon is heterogeneous, (e.g. containing the epithalamus), more attention should be paid to individual parts, including the thalamus.

7.7.15 Epithalamus

The results show no association between the epithalamus and play behaviour. Similarly, the habenular nucleus and the pineal body, parts that comprise the epithalamus, also do not show an association with play behaviour. This region of the brain is concerned with the body clock and with melatonin secretion, and thus supports the hypothesis that neural regions that function in somatic homeostasis are unlikely to show significant evolutionary elaborations with play behaviour.

7.7.16 Visual areas and play

The results here indicate that the visual areas of the brain are key to the play of primates, with the visual cortex being positively and significantly correlated with both solitary locomotor and social play, and the LGN and optic tract being positively and significantly correlated with social play. The hypotheses predicted that visual components of the brain would be important in the expression of primate play due to primates' reliance on vision. Indeed, Barton (1996) suggested that social complexity is reliant on the visual system, and therefore may contribute significantly to socio-cognitive interactions. Play is in many ways a very visual behaviour; social play relies on appropriate reactions to movement and intention, which are best served by sight; locomotor-rotational play may best achieved through the visual perception of the surrounding habitat and landscape; and object play relies on visual perception of items in the environment (e.g. Bekoff & Byers 1981). With a reduced reliance on olfaction, primates' dominant sensory ability is that of sight, and thus vision, and visual areas of the brain will be vital to primate survival and expression of behaviours, including play. However, as Chapter 6 has shown, the degree to which a species is frugivorous does not accurately predict play frequency. Thus, insofar as play is concerned, visual areas appear key to play, but this does not appear to be directly correlated with socio-ecological systems. Indeed, this may be another product or byproduct of the different selection pressures on the neocortex over evolutionary time (Barton 1996). Reliance on visual senses may also allow for better motor control, and social interactions, hence the importance of vision to the evolutionary elaborations of play; such neural regions might also account for trends in primate play complexity and overall frequency (see Barton 1998, 1999).

7.7.17 Medulla and play

The results here indicate that the medulla is positively and significantly correlated with social play, but not non-social forms of play, in primates. One explanation for this relationship is its control of sexual reflexes (Holmes et al. 2002); perhaps these also control forms of affiliative bonds that are expressed through play. A further point of interest and explanation is that the medulla has been shown to be extremely active during periods of vocalisation; this has been specifically demonstrated in domestic cats, where mews can be elicited by stimulation of the pons and medulla (Peters & Wozencraft 1989), and also in squirrel monkeys (*Saimiri sciureus*) (Luthe et al. 2000). Interestingly, squirrel monkeys are one of the few primate species to emit play-specific vocalisations, considered to demonstrate motivation to engage in social play behaviours (Biben & Symmes

1986). Play vocalisations are present in some New World primate species (e.g. cotton-top tamarins, *Saguinus oedipus*) (Goedeking & Immelmann 1986), and have also recently been shown to accompany social play behaviour in Barbary macaques (*Macaca sylvanus*) (Kipper & Todt 2002); similarly, "laughter" occurs in the play of chimpanzees and baboons (Marler & Tenaza 1977; Masataka & Kohda 1988). It might be the case that the medulla contributes to the emission of play-specific vocalisations, which would correlate with the expression of social play. Many fissiped carnivores incorporate vocalisations into their play behaviour, possibly to demonstrate motivation to engage in play (Bekoff 1974, 1975; Peters & Wozencraft 1989). The typical silence of primates during play has been explained in terms of predator avoidance (Biben & Symmes 1986), however, the data analysed here include that for species that are known to be atypically vocal in play. Additionally, the medulla is connected to motor control areas, such as the cortico-spinal tract and the cerebellum (Bear et al. 2001). It may be that these connections influence the performance of movement, including play.

7.7.18 Vestibular complex and play

The vestibular system is a part of the medulla, and the results indicate its importance to the expression of play behaviour in primates. The vestibular complex is positively and significantly correlated with social play; the superior vestibular nucleus is positively and significantly correlated with total play, and both the medial and descendens vestibular nuclei are positively correlated with social play. The lateral vestibular nucleus however, does not show any association with primate play. In all of these analyses, there were too few observations of solitary locomotor and object play to permit a statistical result. However, given the importance of the vestibular complex and its nuclei to maintaining balance and motor control (Bear et al. 2001), we might expect there to be a relationship between locomotor-rotational play and perhaps object play, given sufficient data. It seems clear that the vestibular system is vital in maintaining equilibrium, and this is indeed crucial to the expression of physical behaviours such as play, thus evolutionarily, selection for a well-developed vestibular system, may directly or indirectly promote the expression of play.

7.7.19 Cerebellum and play

The positive and significant relationship between social play and the cerebellum in primates is an interesting one. Unfortunately, there are insufficient data to conduct comparable analyses on carnivores, although the lack of an association for total play and cerebellum size in carnivores is comparable with that of primates. To my knowledge, this is the first comparative phylogenetic study to show a relationship between cerebellum size and social play behaviour in non-human primates. Comparative analyses here indicate that the cerebellum is still positively and significantly correlated with social play in non-human primates, even after the confounding effects of body size have been removed.

Explanations for this relationship may be that the learning and execution of playful behaviour in social groups may require that both cognitive and motor responses be highly developed. If actions and responses during a social play bout are to be interpreted and reacted to appropriately, we would expect a high level of cognitive awareness, and it is for this reason that social play is deemed to be cognitively demanding (Lewis 2000; Špinka et al. 2001). Social play in particular requires control if it is to be "successful" (Špinka et al. 2001); that is, control and understanding of the context in which the social play bout occurs, physical control of the body in exhibiting social play-specific behaviour, and often self-control in terms of "self-handicapping" with a smaller or weaker player (Pereira & Preisser 1998). The primate cerebellum seems to be integral to this type of behaviour (Thach 1996).

The cerebellum should be interesting to proponents of play behaviour as it enables practice of movement, adjusting the action for increased precision and accuracy (Thach 1996). It also plays an anticipatory rôle in the execution of movement (Blakemore et al. 1999); this of course is relevant to all movement, not only play, where predicting movement of all involved players is key. So, cerebellar circuits are trained by sensory-motor feedback, including those movements exhibited during social play, whilst play itself is performed in part to practice, develop, modify, and maintain skills (e.g. Byers & Walker 1995). This modification and development may improve performance, and in this vein may even serve to train neural networks during early brain development (e.g. Byers 1999; Fairbanks 2000). I propose that social play may be especially important for honing the functions of the cerebellum.

`It has been shown in other mammalian species that the development of all play behaviours map very closely onto the post-natal development and growth of the cerebellum (Byers & Walker 1995), and this very time-specific period marks a sensitive period in mammalian development. These sensitive periods typically mark the juvenile period, during which most play behaviour tends to occur (Fagen 1981; Joffe 1997). Indeed, it is expected that play will be more prevalent in species with extended postnatal development (Pellis & Iwaniuk 2000a). Each type of play has a distinctive timing and trajectory, the pattern of which is essential to our understanding of play function (Fairbanks 2000). Unfortunately, there is a lack of extensive data on both the time-specific development of play types, and of the cerebellum in primates. Although my results here do not show a statistically significant result for a cerebellar relationship to object play in primates, the result indicates a positive trend; it may be that the small number of contrasts (n = 4) contributes to its failure to reach significance. I predict that given further data, a similar trend for object play will emerge.

7.7.20 Number of play behaviours

Across primates, the contrasts analyses show that evolutionary increases in brain size are correlated with increases in play behaviours to the play repertoire in primates. This relationship is borne out in both platyrrhines and in catarrhines, suggesting the homogeneity of the relationship. The causation of this could arguably follow one of two trends. Firstly, that a large group size gives rise to larger brains, and also greater amounts of play behaviour, thus play correlates with both brain size and with group size. Or secondly, that a large group size requires a bigger brain, which in turn gives rise to greater amounts of play. In the latter scenario, play would still correlate with both brain size and group size (see Figure 7.49).

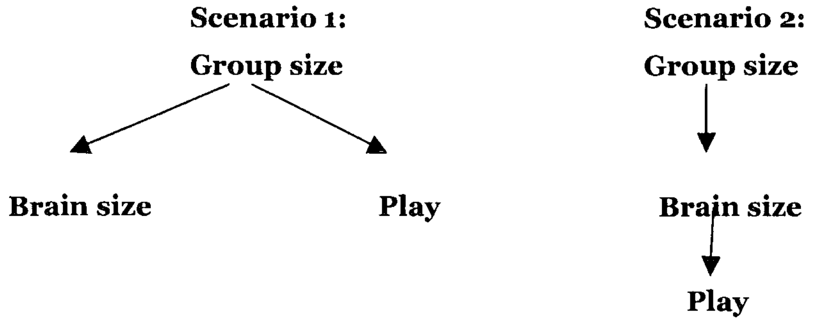


Fig. 7.49 Hypothesised causations of play frequency

A greater diversity and practice of play behaviours arguably suggests behavioural complexity and thus species with a larger relative brain may indeed be those to require and exhibit more elaborate play with variations in sequence. This might also explain some of the variance in the previous comparisons of play behaviours and group size (see Dunbar 1995).

7.7.21 Bout length

It would be preferable to conduct intra-specific analyses on bout length data in order to test for external variables such as diet or habitat that may alter the empirical expression of play behaviour in primates, although sample sizes are too small. Results of relative brain size on play bout length across primates suggest that over evolutionary time, increases in play time have been correlated with increases in brain size. It seems reasonable to suppose that species with relatively larger brains require greater extended periods of play during which to permanently affect the CNS during the juvenile period when the brain is at its most plastic (Byers & Walker 1995). Individuals that devote a lot of their daily time budget to play may risk injury or predation more so than individuals that play less, and thus there is the suggestion that play at this risky period also offers dividends. Play bout length might be a more useful measure of social play complexity, or indeed the extent to which play may be beneficial, than is the overall time budget.

7.8 Summary

The results in this chapter indicate that some brain structures are likely to have played a rôle in the evolution of play, whilst others have not. The regions of note are those of the neocortex, cerebellum, vestibular system, visual system, amygdala and hypothalamus. Interestingly, relative whole brain size does not predict play frequency in either primates or carnivores, thus providing a basis for focus on specific neural components. Social play is the type that appears to be best predicted by relative brain component size. I suggest that this is due to the fact that social play requires the social complexity afforded by larger socially-complex groups. In turn, play, during the period of developmental plasticity, and beyond, enables honing of the key neural structures, which facilitates and maintains physical and social bonding within the group; the "*social glue*" that Fagen suggested (1981). Thus play has been selected to benefit body, brain, and social environment. Thus social and cognitive species will be those that are the most playful. The neural anatomy key to play's evolution comprises cognitive centres, such as the neocortex, motor centres, such as the cerebellum, visual systems, that link into both cognitive and motor elements, and emotional recognition and regulation as controlled by the amygdala and hypothalamus. These elements are likely to be have shared patterns of evolutionary change, and developmentally permit the occurrence of play, the timing of which is likely to influence synapse termination and brain maturation (Byers & Walker 1995). The "primed" homing of these structures not only permit behaviours such as social play, and to facilitate its "success", but this success contributes to the fine-tuning of the brain, which is likely to contribute significantly to enhanced socio-cognitive abilities throughout adulthood.

Chapter 8: Conclusions & Further Study

8.1 Introduction

This thesis has focused on a comparative analysis of play behaviour in primates and carnivores, assessing play from various perspectives including phylogenetic patterns, life-history, socio-ecology, neurological components, and intra-specific analyses. Play is a behavioural category that has been frequently overlooked in the field of ethology, due to difficulties in defining and quantifying play. Indeed, one of the major difficulties in conducting a comparative analysis of play is in collating sufficient species replicates to enable statistically valid analyses within and between species. The following sections summarise the key results from each of the preceding chapters and attempt to draw conclusions regarding the relationship between play and the variables discussed throughout this thesis.

8.2 Phylogenetic patterns

The MacClade-generated trees detailed in Chapter 3 offer insights into character state changes in play over evolutionary time. We see that play categories in both primates and carnivores are rather distinct, suggesting that different categories of play possess their own evolutionary trajectories. Indeed, it has been argued in the literature that social play in particular may be further distinct from other forms of play, and is suggestive of an innate play instinct (Panksepp 1998). Social play appears to offer the individual numerous benefits, not least in shaping and perfecting the brain and body, but also in facilitating and maintaining social bonds and learning capacity (e.g. Fairbanks 2000). Additionally, social play is argued to be a vital way in which to assess partner fitness (both physiologically and sexually) in those species where potential mates play (Panksepp 1998; Pellis & Iwaniuk 1999a). That play, and social play in particular, are conserved in mammalian lineages, further suggest its importance in development and social relationships.

8.2.1 Primate play evolution

The phylogenetic reconstructions, perhaps surprisingly reveal, that social play was not only likely to have been present at the divergence of primates from other mammals, but also that dyadic play is the most widespread throughout the clade (rather than solitary or polyadic play). A two-partner play scenario is suggestive of one of two theories: that play originated between adults and their offspring; or that play originated as a means of assessing mates.

The phylogenetic reconstructions reveal social play as the most evolutionarily ancient of play behaviours. It is likely that playful forms of behaviour originated at a low level in mammals; we see that there has been a selection for higher frequencies of play in highly social and manipulative species (e.g. *Cebus apella*). Social play in its most ancient form may have arisen due to the need to assess socio-sexual relationships. Indeed, Pellis & Iwaniuk (1999a) argue that adult-adult social play should be more prevalent in solitary nocturnal species as a means for assessing potential mates when levels of male-female association are low. My results indicate that the ancestral low-level of play has been retained in extant strepsirhines: a sub-order that comprises largely solitary and nocturnal primates. Additionally, my results further indicate that sexual play has been a prominent form of adult play throughout evolution: a finding in support of Pellis & Iwaniuk's findings. My results also indicate however, that adult play is most likely to have originated between adults and their infant offspring, which tends to suggest that play may have been more likely to have originated as a means for parents to assist the neuro-muscular development of their progeny. This adds some weight to the controversial hypothesis that infant play offers one means by which parents can assess the biological fitness potential of their offspring (Chiszar 1985).

One crucial factor to be borne in mind regarding possible conclusions as to the evolutionary path of social play is that we use data from extant species in order to determine these ancient character states. Social play is by far the most widely reported of all play behaviours, thus social play is better represented in the literature for many species, than are other forms of play. Social play may indeed represent the ancestral condition, given the variety of functions argued to classify this behaviour. However, conclusions to this effect are accompanied by the caveat that social play remains the most easily-observed of play behaviours, possibly, the most widespread, and certainly the most widely-reported.

The phylogenetic reconstructions reveal that the most playful clades comprise Old World monkeys (especially the macaques and baboons), and apes. With the exception of gibbons, these families live in large groups. Given that group living requires advanced social skills, it seems likely that species in large groups will be more playful (especially in a social sense) than species in much smaller groups. One notable exception to this concerns Old World colobines. Colobus monkeys typically live in extremely large groups (e.g. Clutton-Brock 1975; Smuts et al. 1987); their play frequencies however, are rather low. Colobines subsist on a largely folivorous diet, and spend much of their daily time budget resting in order to digest their food (Dunbar 1988). Indeed, diet is one factor argued to significantly affect the performance of play (Burghardt 1988). However, in spite of this hypothesis, the results in Chapter 6 indicate no general association between diet and play time budgets. Thus colobus monkeys provide something of an enigma in primate play time budgets.

8.2.2 Carnivore play evolution

Carnivores, as assessed in the phylogenetic reconstructions, appear to be an especially playful order. Total play (i.e. all categories) persists at high levels in fissipeds throughout the clade. Pinnipeds however, have been selected for a reduction in play frequency relative to their fissiped counterparts. It is shown that pinnipeds and polar bears exhibit high levels of solitary locomotor play. This may be to counteract the effects of cold climates and to develop hunting and predator avoidance skills in aquatic environments (solitary locomotor play in these species comprises fleeing and twisting behaviour). Object play appears more commonly in carnivores (especially canids, felids, and ursids) relative to primates. This is likely to be practice for direct hunting ability. Typical behaviours include pouncing at and batting inanimate objects. Although some carnivores are not exclusive meat eaters, all carnivores exhibit carnassial dentition (Bekoff et al. 1984). This suggests that behaviourally, carnivores may possess an innate and "typical" carnivorous behavioural tendency towards this behaviour. Social play permeates the carnivore clade at high frequencies, which supports the hypothesis that social play occurs in order to facilitate the integration and social success of the individual within the group. Domestic cats exhibit an unusually high level of play behaviour, presumably due to the selective breeding for neotenous traits (Hemmer 1990). Canids appear relatively less playful than casual knowledge predicts, especially given their social structure and typical group size. However, at the node where canids and felids diverge, we see a selection for higher play frequencies in the canid clade, with far lower frequencies in the felid clade. Although some felids will live in large prides, these are often broken down into smaller hunting packs, or more usually, solitary hunting. Canids conversely, tend to live and hunt in large packs, with co-operative hunting, and a monogamous breeding pair. Thus canid social systems remain co-operative in that non-breeders contribute to the raising and provisioning of pups (Kleiman & Eisenberg 1973; Bekoff 1974; Moehlman 1986).

8.3 Intra-specific variation

The analyses of intra-specific play proved difficult, given the lack of suitable data available from the literature. This, I concede, is the case for several analyses within this thesis. However, the paucity of data is especially prominent in Chapter 4, and it remains difficult to draw any real conclusions. What this chapter does point out however, is the importance of controlling for variables that differ between populations of the same species. Using means is a useful way to derive general trends in data, especially at the genus, family or order level. At a species level however, it becomes clear that there are often significant differences between local populations, and in the resources available to them. Further still, many of these differences are not fully understood, due to what actually gets published in the literature. As I stated in Chapter 2 however, "You can only work with what you've got".

Existing literature concerning play behaviour frequently cites factors that reduce or affect play. These typically include housing and group composition. Analyses of play and sex-differences, age-class, and actual group size (as opposed to a species mean) remain inconclusive. We would expect to see higher play rates in groups with more juvenile males, and with a large group size. Patterns however, are unclear, and do not appear to reflect previous studies, or intuition. I propose that this is largely due to insufficient sample sizes, rather than any external factor. Alternatively, these results can be used to encourage further studies of play within species in order to determine the range of differences of the same species living under different conditions. Understanding these differences in behaviour in line with differences in local ecology, housing (if captive), and group size and composition, may enable us to both conserve wild species and enrich the lives of captive species in a welfare sense (Veasey et al. 1996). I conclude that not only sample sizes, but also extensive differences between populations render analyses of intra-specific play impracticable with the data currently available. This is especially true of play behaviour, given its natural fluctuations and sensitivity to external factors. Alternatively, it may be that each species is selected to exhibit play behaviour according to its *typical* group size and environment, and thus little or no correlation will be found across conspecific populations.

8.4 Life-history

Life-history variables are correlated with each other (e.g. Harvey & Clutton-Brock 1985). We tend to see trends for large-bodied females giving birth to large litters of small-bodied altricial neonates after a relatively short gestation period, that rapidly reach adulthood; or smaller-bodied females giving birth to larger neonates in smaller litters after longer gestation periods, and requiring longer periods of parental care to reach adulthood (Sacher & Staffeldt 1974; Bekoff et al. 1984; Partridge & Harvey (1988; Ross & Jones 1999). The neonates of any given species can therefore be placed on an altricial-precocial continuum. Chapter 5 focused on how these inter-related life-history variables affect play.

8.4.1 Precociality selects for increased play behaviour

The key conclusion to be drawn from these analyses is that play is more prominent in species that give birth to relatively more precocial offspring than do species that give birth to relatively more altricial offspring. In primates, we see that longer gestation periods, higher birth weights, lower litter sizes, and longer lactation periods, are all positively and significantly correlated with increased play frequency. Such is the typical primate condition. In carnivores, there is a general trend towards the typical mammalian condition, comprising females that give birth to more altricial multi-neonate litters, as opposed to the usual single births of primates. However, the same trend emerges in carnivores, in that species with a long gestation period, lower litter size, later age at independence, and sexual maturity (age at first conception), are also those that play more frequently. Additionally, carnivore species taking longer to reach adulthood engage in more object play: behaviour believed to function in hunting skills required in adulthood (Biben 1979; Biben 1982; Hall 1998).

Species that are relatively more precocial are born with more significantly developed brains, in comparison with the relatively more helpless altricial species that develop their brains more postnatally (Bennett & Harvey 1985). Hence, precocial species are far more independent at birth. In primates however, there is a degree of "behavioural altriciality" as infants remain dependent upon their mothers for nutrition and protection (Nicholson 1987; Wolff 1997). Given that play is shown to be more prominent in relatively more precocial species, an insight into the possible function of play can be proposed. Play is argued to be an innate behaviour; infants and juveniles appear to strive to engage in playful behaviour, suggesting its importance in development (Panksepp 1998). Precocial species, being born with relatively less brain development to achieve postnatally, are under significant neurological pressure to hone in their brains as quickly as possible, in order to benefit from external factors. These species are also more physiologically and neurologically capable of engaging in motor activities relatively soon into infancy. If it is the case that play behaviour serves to enrich and refine neuro-muscular systems prior to adulthood (Byers & Walker 1995; Fairbanks

2000; Burghardt 2001) then play has a relatively small time window during which to be effective (Dolhinow 1999). Indeed, sensitive and critical periods of development are well-documented (e.g. Scott 1962; Wynder 1998; Diamond 2000). It is vital for any animal to engage in behaviour that benefits its fitness, and also to maximise these benefits by engaging in them at appropriate stages. Altricial juveniles play intensively for a short period of time due to their rapid development. Precocial species conversely play over a longer period of time resulting in higher average play time budgets in comparison with their altricial counterparts. Therefore, estimates of peak time spent playing are important to the play literature as different patterns in play are likely to exist depending on the degree to which a species is altricial or precocial. I therefore suggest that play is a crucial developmental marker, which needs to be performed before the end of major neuro-muscular development prior to adulthood; precocial species therefore are able, and equally require, that play be performed as soon as possible postnatally.

8.4.2 Parental investment and play

Additionally, precocial species are likely to have the early experience of adult-infant play. This is in some way supported by the phylogenetic reconstructions of Chapter 3 in that adult play persists throughout the clade, suggesting that adults may seek to engage their neonates in play in order to assist the neurological development of their young. Precocial infant mammals are typically born into small litters, and in primates, with the notable exception of callitrichid twins, this means being born as a single neonate (e.g. Smuts et al. 1987). It seems likely that primate mothers invest considerable time not only protecting and nursing their single offspring, but also encouraging it to develop its neuro-muscular system. Thus, by playing with their offspring, primate parents may be ensuring the best possible start in life for their infants. If play can encourage an individual to develop fully within key developmental periods, and become independent, then parental investment in this way contributes to the propagation of genes (e.g. Daly & Wilson 1983). Altricial infants born in large litters may not receive this level of individual investment, given that more infants weigh more heavily on maternal resources. Indeed, if more neonates are born to counteract normal mortality rates, then we should expect to see less parental investment in these individuals. Hence, play might not be as pressing a behaviour as that of finding reported that sibling aggression occurs prior to play. This is an unusual pattern, but in large litters where resources are scarce, early injury or death from sibling rivalry ensures that only the fittest pups survive to the next developmental stage (Drea et al. 1996).

8.5 Socio-ecology

Chapter 6 concentrated on the effects that life in social groups and ecology may have on the exhibition and evolution of play behaviour. Primates are renowned for being an especially social order, even amongst the relatively more solitary strepsirhines; whereas carnivore social life varies more widely, with many species being largely solitary, and with canids in particular being highly social. Just as different group-living existences are variable, so too is the surrounding environment, in terms of what can be exploited for food, shelter, and protection. These factors are intimately bound together.

8.5.1 Group-living

It appears that life in large groups facilitates play behaviour; a trend seen for group size in primates and population size in carnivores. Certainly, we may expect that the more individuals present within a group, the more opportunity there is to engage in play, as there are an increased number of potential partners. If the propensity to play is as innate as some neurobiologists suggest (e.g. Panksepp 1998), then we would expect to see individuals playing at every opportunity. Life in a large group however, is not simply concerned with the number of individuals. It is the social relationships between these individuals that create social group life. Dunbar (1992, 1995a) demonstrated the importance of social networks to group living, and showed that neocortex size is a predictor of group size. If group members are to keep track of their social relationships, they require a socially dedicated neurological processing power. My results in Chapter 7 support this hypothesis, showing that neocortex size is actually a good predictor of social play behaviour. Thus neocortex size, group size, and social play frequency are indicative measures of sociality (see also Lewis 2000). It might therefore be the case play necessarily, but that socially complex groups require it. One key element to social play appears to be the formation, facilitation, maintenance, and on-going assessment of social relationships within a social group. Additionally, play is likely to assist in the practice and formation of skills that are used specifically in adulthood, such as mate assessment and fighting ability (e.g. Bekoff 1978; Lee 1983; Martin & Caro 1985; Rowell & Chism 1986; Govindarajulu et al. 1993; Mendoza-Granados & Sommer 1995; Smith et al. 1998). Coupled with the hypothesis that play is vital to maximise brain development, it appears that play is actually a highly important behaviour for social group living.

Some social groups can be very large indeed, and although members of these groups are likely to maintain some affiliation with most or all group members, it is unlikely that they will form close bonds with each and every member of the group. Smaller, more closely-knitted, groups are often formed, and these may include mothers and their offspring, females and their sisters with their offspring, or all-male bands (e.g. Smuts et al. 1987; Dunbar 1988). These smaller affiliations within a larger social group are referred to as cliques, and networks, much as in the same way as we as humans might differentiate friends from a wider social circle (Kudo & Dunbar 2001). These smaller social cliques and networks are thought to underpin the essence of social group living. Indeed, my results in Chapter 6 add further weight to this hypothesis, demonstrating that both clique size, and network size predict social play frequency in primates. These smaller social units may be a factor of overall group size, but these interrelated correlations suggest that they are good indicators of sociality, and by extension that social play has been selected to assist in such affiliations.

8.5.2 Habitat

The ecology of a species is likely to have strong effects on its behaviour, and social and physiological requirements. Play has consistently been shown to be sensitive to these effects, diminishing under stressful conditions, including lack of food, insufficient shelter, and high levels of predation (e.g. Burghardt 1984; Jensen 2001). For example, Sommer & Mendoza-Granados (1995) showed that Hanuman langurs (*Semnopithecus presbytis*) are more playful in rich habitats than poorer ones. This is likely to be due to an abundance of food and resources, limiting the time required to forage, and freeing up spare time during which to engage in play. My results indicate that species occupying large home ranges also play more frequently than do those occupying smaller home ranges. This may be due to access to a wider range of food resources over a large area;

however, large habitats tend only to be occupied by species when resources are sparsely distributed, hence requiring larger areas in which to find sufficient food. Species in larger groups also tend to have relatively larger body sizes, and additionally live in large groups. These factors combined are suggestive of play being beneficial in the maintenance of social relationships over a wide area. Play is not significantly correlated with feeding groups in either primates or carnivores, thus it is likely that play occurs within smaller social cliques or networks between infants and juveniles of adults in a particular feeding group, thus maintaining social affiliation within and between different facets of the local species population.

8.5.3 Diet

Previous hypotheses in the literature point to diet being influential in the exhibition of play behaviour; indeed, it has been suggested that a high-quality diet, rich in protein (especially animal protein) facilitates play due to an increase in energetic availability and a reduction in the need for lengthy digestion of plant matter (e.g. Baldwin & Baldwin 1976; Müller-Schwarze et al. 1982; Burghardt 1988; Sommer & Mendoza-Granados 1995). My results do not support this hypothesis and show that diet does not in fact appear to be a good indicator of the evolutionary patterning of play. No play category in my sample was significantly correlated with either percentage of leaves, prey items, or fruit in the diet. Given the visual and cognitive capacities required to find and process ripe fruits and prey items (Barton 1996), it was predicted that omnivorous, carnivorous, and frugivorous species would be significantly more playful than folivorous species. The results however, failed to find a significant relationship. It may be that diet, and its subsequent effect on behaviour, such as play, is reliant upon other "hidden" factors. Despite the small sample sizes however, a positive and significant correlation was found between play and basal metabolic rate (BMR). BMR is linked not only to diet, but also to body size, which has been shown to be a key variable in predicting play behaviour, hence the need to control for body size throughout certain thus it seems likely that BMR should be an important variable in analyses of play behaviour. It should be borne in mind however, that current ethological thinking precludes play as being performed for the purposes of exercise, although this may indeed be a small byproduct of the performance of play (Byers 1998b). As BMR is often incorrectly estimated in the field, especially in tropical species, (e.g. McNab

1989), future studies regarding play and BMR should aim to include latitude as a dependent variable.

8.5.4 Growth

That growth rate is not significantly correlated with play behaviour is interesting, given that the results in Chapter 5 are highly indicative of play being connected to the degree of precociality of neonates. It is likely that small sample sizes play an effect in this analysis; explanations however, remain unclear.

8.5.5 Ecology and myelination

It is often difficult to completely separate analyses of socio-ecology from analyses of the brain. This is especially true of play behaviour where neural capacity is an apparently driving force in the exhibition of play across species. Play is shown to be prevalent among species that occupy large home range sizes. As previously mentioned, species in these habitats are faced with the likelihood of widely dispersed resources (Poole 1985). It may also be the case that such species are prone to seasonal fluctuations in food availability, which will affect their capacity to maintain nutritional equilibrium, as well as potentially altering their social behaviour. The brain is actually fairly well protected against fluctuations in nutritional deficiency, although severe malnutrition may have an adverse effect on the developing brain (Guesry 1998). This is suggested to largely affect the development of skill acquisition during sensitive periods (Gordon 1997). However, sufficient sensory-motor stimulation during this period usually ensures limitation of adverse effects on the developing brain (Guesry 1998). Play and nutrition may therefore have synergistic effects. One effect that is prominent in malnourished infants is in the thickness of the neural insulating sheath, myelin. As explained in Chapter 6, myelin aids the efficiency of brain conductivity, and skill acuity; or more simply: better brains (Parks et al. 1988; Haier et al. 1988; Miller 1994; Gordon 1997). The process of myelination appears to be especially crucial during early development: the time at which play is most prominent (Miller 1994; Byers & Walker 1995). Myelination is clearly important during development, but may also be crucial to studies of socio-ecology, if play during this sensitive period can assist myelination and contribute to the combative effects of a changing environment. Arguably, this would make it doubly important for parents to encourage play in their offspring to assist the honing of their developing CNS, especially in species that occupy large habitats and where food and resources are widely dispersed, or during periods of food scarcity. This adds further weight to the conclusion that play frequencies are higher in species living in large social groups, with large body sizes, and in large home ranges. Play therefore, is more than simply a behavioural category that helps to facilitate a cohesive social structure; play may indeed, be a critical developmental marker, promoting a stronger and more efficient neurological system (as for example, Byers & Walker 1995, Fairbanks 2000, and Burghardt 2001 suggest).

8.6 Brain

One of the most striking patterns in analyses of brain components and play behaviour, is the prominence of social play in the co-evolution of play and brain structures. This may be a reflection of the increased number of reports and observations of social play found in the literature. Alternatively, these results might further provide an insight as to the brain's rôle in social play, and further elucidate the hypothesis that social play is a behavioural category distinct from other forms of play (Panksepp 1998).

8.6.1 Neocortex size predicts social play frequency

Results in Chapter 6 demonstrated the importance of group size to the frequency of social play behaviour. Dunbar (1992) and Dunbar & Bever (1998) have demonstrated that neocortex size in primates and carnivores is a good predictor of group size. My results in Chapter 7 add to Dunbar's findings, and support the findings of Lewis (2000) by showing that neocortex size also predicts social play frequency in primates and carnivores. This further supports Dunbar & Bever's (1998) suggestion that neocortical evolution in primates and carnivores is similar. The neocortex is a vital part of the brain in terms of social complexity. Indeed, it is often argued that primates possess advanced social intelligence as a measure of their highly complex social systems (Whiten 2000), and that the neocortex mediates this social intelligence. Thus species with relatively larger neocortices should show more complex social behaviour than species with smaller ones (Social Brain Hypothesis: Brothers 1990). Social play is argued to be a potentially highly complex social behaviour, especially among social species with large neocortices, such as primates and carnivores (e.g. Bekoff 1974, 1978, 1995; Bekoff & Allen 1998; Panksepp et al. 1994; Pereira & Preisser 1998; Pellis & Iwaniuk 1999b, 2001a, 2002). Additionally, Pawlowski et al. (1998) have shown that species with relatively larger neocortices may hold an advantage in being better able to manipulate socio-sexual situations in order to gain access to mates by employing social strategies. They argue that heightened cognitive processing power enables socially complex advancement. That social play is so strongly correlated with neocortex size might provide further support for the theory that adult play at least assists in socio-sexual assessment (Iwaniuk & Pellis 2002). It seems reasonable to conclude that social play during developmental periods in such species assists the development of these social skills as well as in developing the neuro-muscular system (Fairbanks 2000; Špinka et al. 2001). Indeed, infants and juveniles exposed to socially-complex or even "Machiavellian" sequences in play, are likely to develop these skills within the remit of other adult social behaviours, thus being more able to utilise them should the need or opportunity arise to gain a social advantage.

8.6.2 Cerebellum size predicts social play

One of the key findings in Chapter 7 is that cerebellum size also provides a good predictor of social play in primates, even after removing the confounding effects of body size. This may be due to the need for accurate and complex cognitive and motor skills during social play: functions controlled by the cerebellum (Diamond 2000). This trend was not shown to be true of carnivores, although this may be due to insufficient data.

The cerebellum is a crucial part of the brain in terms of motor control (e.g. Bear et al. 2001). The traditional theory that motor control develops and ends early in ontogeny, whereas cognitive development begins and ends relatively later, has recently been challenged, with some controversy. It has been suggested that the two developmental trajectories actually share a very similar time frame of postnatal development and are thus much more closely interlinked than was previously thought (Akshoomoff & Courchesne 1992; Diamond 2000; Habas 2001). My results here may in fact offer some support to this theory, given that play behaviour actually occurs during this motor-cognitive developmental time window (Byers & Walker 1995). In fact, this evidence has been used to purport that the true function of play is to terminate synapse formation in the cerebellum, in effect "finishing off" crucial cerebellar development; additionally, this only occurs during the developmental sensitive period when synapses are terminated, and play occurs (Byers & Walker 1995). Given the evolutionary correlation between cerebellum size and social play, I suggest that this is likely. Social play requires the modification of many skills if it is to be successful. Socio-cognitive and socio-motor skills contribute strongly to successful playing. When we also consider the other vital rôles of the cerebellum, it seems intuitive that cerebellum development and size should also be vital to the expression of social play. The cerebellum is important for the practice, perfection, and accuracy of motor performance (Thach 1996), for posture and balance (Ackerman 1992), and to track the trajectory of objects in the environment (Paulin 1993). These factors are all vital to development, but I propose that given the co-evolution of social play and cerebellum size in primates, as demonstrated by the independent contrasts analyses, that these are also intrinsic to social play behaviour. Moreover, I suggest that social play actively requires motor and cognitive skills, and that these skills are strongly rooted in the cerebellum, especially given the sensitivity of cerebellar development during a critical period during which play occurs, the cerebellum has clearly been a vital brain structure in the evolution of play.

In the light of these findings, I believe it would be useful to study in greater depth the cerebellar relationship with other categories of play behaviour, not analysed here. Object play, for example, demonstrated a positive evolutionary correlation with cerebellum size, although the result fell short of significance. Given the function of the cerebellum in the development of manual skills and co-ordination, and sufficient data on object play, I predict a strong positive relationship between the cerebellum and object play behaviour to emerge. However, the data for object play behaviour in species for which there are cerebellar data are limited, and object play itself is a rarer play category in the literature (Pellis & Iwaniuk 1999).

I intend this result to offer a general starting point for future work into which categories of social play activity may be associated with cerebellar and other brain functions. This thesis concentrates on a general description of social play; future studies might aim to collect and analyse data on the timing of specific motor patterns in play categories with reference to the developing brain and nervous system, which would prove extremely important to behavioural neuroscience. This may, for example, delineate specific behavioural aspects, such as proportion of wrestling or chasing, and complexity. Such markers may prove critical to our understanding of the relationship between play and brain development.

8.6.3 Striatum, Medulla, and Vestibular complex

Supporting the evolutionary relationship between social play and the cerebellum is the finding that social play is also correlated with the striatum, medulla, and vestibular system. Akin to the cerebellum, these neural components play a rôle in motor control, motor learning, and balance. Additionally, I suggest that the medulla may be crucial to vocalisation within play, and further studies should aim to determine the differences in play and medulla size between New World and Old World monkeys, given that most instances of play vocalisations are reported only in platyrrhines (Biben & Symmes 1986; Luthe et al. 2000). Similarly, the rôle of the medulla in sexual behaviour may further add to its importance in the evolution of social play, especially if social play in adults does indeed function as a means of mate-assessment in primates, as Iwaniuk & Pellis (2002) suggest. There are also strong ties to the visual system, which is also demonstrated here to be key in the evolution of play behaviour (Jog et al. 1999) (see section 8.5.4). My findings here support previous findings that damage to the striatum (the caudate-putamen area) severely adversely affects the performance of rough-and-tumble play in rats (Panksepp 1998). These findings are suggestive of the importance of *both* motor *and* cognitive proficiency in the exhibition of social play in mammals. My findings further imply that these systems have co-evolved with social play to enhance the socio-cognitive capabilities of the species.

8.6.4 Visual areas

Adding further support to the rôle of motor and cognitive neural regions sharing a correlated evolutionary history with play, is the finding that visual areas of the brain correlate strongly with social play in primates, namely the visual cortex, the LGN, and the optic tract. The co-evolution of all these brain components with social play is suggestive of a visual system being key to socio-cognitive processes within the performance of social play behaviour. Primates are highly reliant on vision, and the visual system may provide a level of socio-cognitive competence within the lives of primates (Barton 1996). It is interesting that frugivory and diurnality failed to show significant correlations with play in Chapter 6, especially given the evidence for correlated evolution between social play and visual systems in Chapter 7. Primate vision appears to have been selected for diurnal existence, especially among haplorhines, and is likely to aid in distinguishing fruits from a leafy background and in identifying ripe fruits. The results here however, point to the conclusion that the primate visual system aids and facilitates the complex social behaviours observed within social play. Social play relies heavily on the reading of behaviour, and in responding quickly and appropriately (Špinka et al. 2001). In primates, where facial expressions can be highly indicative of an individual's emotive state, reliance on vision is an important factor. Indeed, this adds further support to the amygdala being involved in social play (see section 8.5.5), given its importance in reading social signals and responding to facial expression (Ohman 2002). I conclude that over the course of evolution, increased reliance on vision by primates has co-evolved with socio-cognitive and socio-emotive systems (Barton 1996; Burghardt 2001, in press), giving rise to enhanced social play behaviours that are both motor-driven, and cognitively-driven. This further suggests evidence for the mosaic evolution of brain structures that facilitate these interrelated behavioural patterns (Barton & Aggleton 2000; Barton & Harvey 2000).

8.6.5 Amygdala and hypothalamus

The structures of the limbic system have been suggested to play a rôle in the execution of playful behaviour, given that play is supposed to derive from instinctive behavioral patterns (Burghardt 2001). Additionally, given the rôle of the neocortex to social play, as reported in Chapter 7, and the fact that limbic structures project to the neocortex, we might expect to see some overlap in the relationship between limbic and neocortical structures and play.

I found evidence for correlated evolution between play and the amygdala and the hypothalamus in primates. These two limbic structures have previously been implicated in the expression of play. Principally, it is these two structures that become sexually-differentiated by gonadal hormones during the perinatal period; these hormonal changes give rise to sexually-differentiated behaviours, namely aggression, sexual orientation, and play behaviour (Hines 1982; Collaer & Hines 1995). Aggression and play in particular, are marked as being dominant among males (thus males are both more aggressive and typically more playful than females) (e.g. Brown 1988). That the amygdala has also recently been implicated in the performance of adult sexual play and in juvenile play-fighting is strongly indicative of an evolutionary relationship between sex, aggression, play, and the amygdala (Pellis & Pellis 1998; Burghardt 2001; Pellis & Iwaniuk 2002). My findings support this theory from an evolutionary perspective. I propose that behaviours driven by the amygdala, such as social assessment, recognising and responding to facial expression, and response-appropriateness (Ohman 2002), drive matched facets of play. Thus the instinctive socio-emotive aspects of play are those determined by the size of the amygdala in primates.

The rôle of the amygdala, coupled with that of the hypothalamus, may ensure that the instinctive underpinnings of play are further elaborated. Play behaviour is argued to represent a behavioural equivalent of "fun" (Fagen 1992; Bekoff 2001b). This can be dangerous terminology insofar as ethology is concerned, and I am reluctant to use the term. However, the hypothalamus is implicated in the experience of pleasurable emotions (Isaacson 1982). Few humans would disagree that the experience of play is one that elicits great pleasure, especially among children. Humans are primates, and although largely elaborated from our non-human primate relatives, our brains are not dissimilar. Could it then be argued, that play, for all its apparent (and yet seemingly hidden) functions, can also be fun? Indeed play as being fun may represent the proximate mechanism for ensuring play occurs. If play is pleasurable, as well as useful in terms of developing brains, bodies, and skills, then this explains why mammals appear to strive to engage in play when the opportunity arises. I therefore tentatively conclude, that brain components, such as the hypothalamus, that are believed to function in the experience of emotive states, ensure that play is performed, through it being "fun", thus also ensuring that play occurs to benefit the developing brain.

8.6.6 Brain size

Although my results in Chapter 7 found no evidence for whole brain size predicting play frequency in primates (supporting the work of Iwaniuk et al. 2001), I found strong evidence to suggest that brain size can be used to predict the number of different behaviours observed within the play repertoire of primates; this relationship holds when primates are split into platyrrhines and catarrhines. Although relatively crude, the number of different behaviours is a simple and effective way of quantifying play complexity. This result therefore, demonstrates that implied cognitive processing capacity, as determined by the relative size of the brain (removing the effect of body size), in turn can be used to predict the potential capacity of play complexity in primates. A similar finding was reported for brain size and play bout duration in primates; the larger the relative brain size, the longer the play bout. I conclude that relatively larger and therefore presumably more complex brains in primates, require that play occurs during development in order to sharpen the brain during neural and behavioural plasticity. Therefore, longer bouts of play comprising increased numbers of different motor and cognitive behaviours should ensure that the brain be honed to the best possible advantage.

Social play in particular appears to be a highly complex behaviour insofar as the brain is concerned. My results in this thesis point to the conclusion that brains that have been selected for highly developed motor and cognitive skills are also those that have been selected for increased frequencies in social play behaviour. It seems likely that parts of the brain concerned with cognitive and motor complexity, and emotive states, have co-evolved, facilitating complex social behaviours, of which social play is one such behaviour. Social play during neural development has been posited as a behavioural aid to the individual in terms of perfecting the CNS within the confines of the environment (Fairbanks 2000). I therefore conclude that social play has been selected for to enhance the development of these highly complex brain structures, to ensure that motor, cognitive, and emotive states are sufficiently "fused" during the period of neural plasticity. This must surely help an individual in achieving the best possible neural, behavioural, and social route to adulthood.

This thesis has demonstrated that although play remains an often somewhat difficult ethological topic, it is also a highly important behavioural category in terms of development and life in social groups. It is hoped that this thesis has contributed to the greater understanding of play behaviour. This thesis also attempts to point out to other workers that more needs to be achieved in identifying, quantifying, and reporting play episodes, and more widely across many more taxa, enabling a greater comparative knowledge of play and the factors that facilitate and affect it. Only then, can we arrive at a true understanding of this enigmatic behaviour, and its place in evolution and development. I believe that play remains however, a category of behaviour worthy of extensive study. And as Bekoff and Byers (1985) point out "*That unwelcome guest is here to stay, like it or not!*"

Appendices

Appendix A:	Tables of data incorporated within the analyses of this thesis
Appendix B:	Statistical tables of non-significant regression analyses from Chapter 5, 6, and 7.
Appendix C:	Additional analyses not presented within the main body of the thesis.
Appendix D:	Database for primate play behaviour categories with associated variables.
Appendix E:	Database for carnivore play behaviour categories with associated variables

Appendix A. Table 1. Group size and body weight (g) with mean % values for total play, solitary play, object play and social play in primates

Species	**Adult brain size (g) †**	**Mean group size***	**Mean body weight (g)†**	**Total play %**	**Solitary play %**	**Object play %**	**Social play %**
Allenopithecus nigroviridis	62.50	39.0	5495	2.50	-	-	-
Alouatta palliata	55.10	12.9	6577	1.56	1.04	-	0.08
Ateles geoffroyi	110.90	42.0	7568	1.00	-	-	-
Callicebus moloch	19.00	3.2	900	1.44	-	-	-
Callithrix jacchus	7.90	9.0	288	1.08	-	-	-
Cebus albifrons	82.00	25.0	2489	1.00	-	-	-
Cebus apella	71.00	15.0	2742	12.4	5.69	3.18	18.87
Cebus capucinus	79.40	18.8	3006	3.49	-	-	-
Cebus olivaceus	80.8	21.5	-	3.50	-	-	-
Cercocebus albigena	109.60	15.4	7362	-	-	-	9.0
Cercocebus atys	-	26.9	8933	8.99	-	-	-
Cercopithecus aethiops	59.80	21.4	4178	8.95	6.00	-	4.40
Cercopithecus diana	77.30	26.9	3811	5.44	5.20	1.45	4.49
Cercopithecus hamlyni	72.30	10.0	-	6.93	1.65	1.25	4.75
Cercopithecus mitis	75.00	18.6	5821	4.00	-	-	-
Cercopithecus neglectus	70.80	4.0	5559	5.09	0.03	3.15	1.86
Colobus badius	73.80	34.0	7998	2.98	-	-	2.41
Colobus guereza	82.30	6.9	9863	4.60	-	-	-
Erythrocebus patas	82.30	28.0	8690	12.58	-	-	-
Gorilla gorilla	505.90	11.0	114551	10.01	2.55	9.21	13.64
Hylobates lar	107.70	3.4	5559	13.59	0.50	-	3.68

Species	Adult brain size (g) †	Mean group size*	Mean body weight (g)†	Total play %	Solitary play %	Object play %	Social play %
Hylobates syndactylus	121.70	4.0	10839	18.76	5.00	0.40	10.67
Lemur catta	25.60	16.0	2466	3.85	4.15	0.00	1.60
Macaca arctoides	104.10	22.5	8590	8.19	5.25	-	11.15
Macaca fascicularis	69.20	24.5	4977	4.00	-	-	-
Macaca fuscata	109.10	36.3	10447	18.33	-	-	14.93
Macaca mulatta	95.10	33.0	5902	8.14	1.28	-	5.50
Macaca nemestrina	106.00	26.9	7762	5.78	-	-	-
Macaca nigra	94.90	56.8	8492	6.91	-	-	-
Macaca radiata	76.80	34.7	5000	6.19	8.43	-	18.13
Macaca silenus	85.00	18.9	5902	3.50	-	-	-
Macaca sinica	69.9	18.6	4656	-	-	-	-
Macaca sylvanus	93.20	24.0	9750	6.69	4.00	9.55	6.50
Mandrillus sphinx	159.40	251.2	16444	13.59	5.91	-	18.65
Nycticebus coucang	10.00	1.5	659	1.20	1.20	0.00	0.00
Pan troglodytes	410.30	28.0	37844	18.60	8.97	6.98	13.27
Papio anubis	165.20	50.0	17579	5.51	-	-	-
Papio cynocephalus	169.10	41.0	17140	12.5	-	-	12.5
Papio hamadryas	142.5	66.5	13996	-	-	-	-
Papio ursinus	214.4	34.7	21777	20.9	-	-	-
Pithecia spp.	38.10	2.7	1710	2.82	4.20	0.70	3.00
Pongo pygmaeus	413.30	2.0	55208	17.34	22.28	16.03	13.74
Presbytis entellus	135.2	19.1	12647	-	-	-	-
Pygathrix nemaeus	108.5	-	9550	-	-	-	-

Species	Adult brain size (g) †	Mean group size*	Mean body weight (g)†	Total play %	Solitary play %	Object play %	Social play %
Saguinus fuscicollis	9.30	6.5	395	9.84	0.20	4.08	7.57
Saguinus midas	10.50	4.7	543	4.72	4.39	0.16	3.00
Saguinus oedipus	10.00	6.0	417	1.87	-	-	-
Saimiri sciureus	24.4	34.7	752	-	-	-	-
Theropithecus gelada	131.90	10.0	15560	15.89	14.90	-	19.86

* Barton 1999 & Smuts et al. 1987; †Barton 1999 only.

Appendix A Table 2. Mean body weight (g), and female body weight (kg), with total play (%), solitary locomotor play (%), object play (%) and social play (%) values, for the carnivore species examined.

Species	Mean body * weight (g)	Female body+ weight (kg)	Mean † group size	Total play %	Solitary locomotor play%	Object play%	Social play%
Acinonyx jubatus	58 748.9	60.0	-	3.39	0.35	0.50	2.96
Ailuropoda melanoleuca	13 4586.0	96.8	1.0	22.02	-	17.2	4.81
Arctocephalus australis	103 752.8‡	52.5‡	-	6.09	-	-	-
Canis latrans	10 592.5	9.7	2.1	1.09	-	-	-
Cerdocyon thous	5 997.9	6.0	-	13.49	-	-	-
Crocuta crocuta	51 999.6	55.3	55.0	6.99	-	-	-
Felis silvestris	4 666.6	4.33	-	11.48	-	-	-
Haliochoerus grypus	193 642.2‡	182.5‡	-	1.46	-	3.54	10.10
Helogale undulata	456.0	0.27*	-	5.15	-	-	-
Lontra canadensis	8 203.5	7.80*	3.2	15.52	9.11	4.14	10.19
Mustela putorius	1 030.4	0.80*	1.0	19.45	-	-	1.46
Mustela vison	388.2	0.61*	1.0	-	-	-	3.99
Panthera leo	155 955.3	135.0	8.7	3.03	-	5.12	-
Phoca vitulina	112 460.5‡	102.35‡	-	9.04	-	-	15.52
Selenarctos thibetanus	103 752.8	77.50*	-	-	-	-	-
Speothos venaticus	7 998.3	8.00*	-	21.38	0.83	2.62	15.99
Ursus americanus	110 407.9	97.0	1.0	10.54	-	-	4.1
Ursus arctos	298 538.3	298.5	-	-	-	-	-
Thalarctos maritimus	363 915.0	320.0	-	8.99	12.56	-	3.17

* Deaner & Barton (2002) partly derived from Gittleman (1986); + Oftedal & Gittleman (1989); † Dunbar & Bever 1998; ‡ Bininda-Emonds (2000).

Appendix A. Table 3. Fundamental brain part measurements for primates from Stephan et al. 1981

Species	**Medulla oblongata (mm3)**	**Cerebellum (mm3)**	**Mesen-cephalon (mm3)**	**Dien-cephalon (mm3)**	**Telen-cephalon (mm3)**	**Olfactory bulb (mm3)**	**Piriform lobe (mm3)**
Ateles geoffroyi	1834	12438	1482	5334	79946	90.4	1625
Callicebus moloch	787	1622	530	1375	13465	19.2	454
Callithrix jacchus	318	757	295	554	5318	22.8	191
Cebus albifrons	1738	7871	1221	3996	52113	39.9	931
Cercocebus albigena	2708	10726	1770	5351	77049	121	1639
Cercopithecus mitis	1999	6758	1354	4176	56277	117	1265
Colobus badius	2007	8648	1333	3945	57885	51.3	937
Erythrocebus patas	2616	8738	1621	5423	84770	51.8	1339
Gorilla gorilla	7509	69249	4352	19370	369878	316	4871
Hylobates lar	2251	12078	1459	5716	76001	43.9	1264
Macaca mulatta	1992	8965	1380	4480	71080	84.3	1220
Nycticebus coucang	528	1310	345	1077	8495	159	510
Pan troglodytes	5817	43663	3739	15392	313493	257	2750
Papio anubis	5297	18683	2711	9280	154987	287	2111
Pithecia sp.	1009	3908	754	2285	24920	34.8	675
Saguinus midas	428	1061	332	692	7055	17.3	243
Saguinus oedipus	413	984	333	754	7052	19.1	256

Appendix A. Table 3 (continued). Fundamental brain part measurements for primates from Stephan et al. 1981

Species	Septum (mm³)	Striatum (mm³)	Schizo-cortex (mm³)	Hippo-campus (mm³)	Neocortex (mm³)	Ventricles (mm³)	Meninges (mm³)	Epi-thalamus (mm³)
Ateles geoffroyi	324	4950	732	1366	70856	1389	1824	30.5
Callicebus moloch	86.4	920	234	588	11163	279	242	-
Callithrix jacchus	49.8	372	90.0	221	4371	52.0	42.9	-
Cebus albifrons	174	3258	390	890	46429	729	864	23.7
Cercocebus albigena	294	4146	630	1485	68733	742	2041	27.9
Cercopithecus mitis	246	2733	617	1366	49933	467	1363	-
Colobus badius	288	3217	814	1671	50906	455	1016	22.3
Erythrocebus patas	330	3624	693	1591	77141	561	519	-
Gorilla gorilla	1173	14567	2729	4781	341444	3608	8659	106
Hylobates lar	302	4784	1136	2673	65800	555	395	31.2
Macaca mulatta	271	4032	639	1353	63482	834	1038	-
Nycticebus coucang	92.0	760	212	566	6192	142	169	-
Pan troglodytes	851	12246	2018	3779	291592	1899	6924	53.6
Papio anubis	559	7182	1309	3398	140142	1081	1977	65.4
Pithecia spp.	140	1918	289	834	21028	631	286	-
Saguinus midas	40.9	471	120	280	5883	251	122	-
Saguinus oedipus	60.5	453	107	262	5894	62.6	52.8	4.93

Appendix A. Table 3 (continued). Fundamental brain part measurements for primates from Stephan et al. 1981

Species	Thalamus (mm³)	Hypo-thalamus (mm³)	Sub-thalamus (mm³)	Pallidum (mm³)	Nucleus sub-thalamicus (mm³)	Capsula interna (mm³)	Optic tract (mm³)	Visual cortex (mm³)	LGN (mm³)
Ateles geoffroyi	2930	629	860	807	52.8	570	204	4738	151
Callicebus moloch	-	-	-	-	-	-	-	1502	53.2
Callithrix jacchus	-	-	-	-	-	-	-	692	25.7
Cebus albifrons	2163	418	609	567	41.7	549	207	4690	137
Cercocebus albigena	2933	681	726	674	52.4	708	308	6831	182
Cercopithecus mitis	-	-	-	-	-	-	-	5274	150
Colobus badius	2164	484	553	521	31.9	460	201	3984	128
Erythrocebus patas	-	-	-	-	-	-	-	7780	266.7
Gorilla gorilla	10547	2215	2782	2604	178	2471	671	15185	384
Hylobates lar	3226	629	777	715	61.6	693	302	-	175
Macaca mulatta	-	-	-	-	-	-	-	6586	158
Pan troglodytes	7987	1739	2078	1951	127	2510	630	14691	356
Papio anubis	4788	1076	1241	1147	94.7	1257	601	10001	-
Pithecia spp.	-	-	-	-	-	-	-	2154	72.3
Saguinus midas	-	-	-	-	-	-	-	1077	36.8
Saguinus oedipus	410	152	77.6	73.2	4.45	62.7	50.5	1003	33.0

Appendix A. Table 3 (continued). Fundamental brain part measurements for primates from Stephan et al. 1981

Species	**Amygdala (mm³)**	**Complexus centro-medialis (mm³)**	**Nucleus tractus olfactorii lateralis (mm³)**	**Complexus cortico-baso-lateralis (mm³)**	**Nucleus amygdalae basalis, pars magnocellularis (mm³)**	**Complexus vestibularis (mm³)**	**Nucleus vestibularis superior (mm³)**
Ateles geoffroyi	869	224.4	0	644.2	74.6	49.7	7.2
Callicebus moloch	-	-	-	-	-	-	-
Callithrix jacchus	113	28.3	0.195	84.6	8.6	-	-
Cebus albifrons	458.1	120.5	0	384	36	50.2	11.2
Cercocebus albigena	-	-	-	-	-	87.1	16.2
Cercopithecus mitis	704.7	210.9	0	493.2	66.4	-	-
Colobus badius	501	123.6	0	377.6	47.8	57.3	8.68
Erythrocebus patas	688.7	199.5	0	488.7	63.7	-	-
Gorilla gorilla	2754	755.1	0	1999.8	227.5	136	34.7
Hylobates lar	666.8	156	0	510.5	84.5	59.3	14.9
Macaca mulatta	-	-	-	-	-	-	-
Nycticebus coucang	189.2	67.8	2.6	121.3	11.4	-	-
Pan troglodytes	1422.3	375	0	1047.1	136.1	118	23.5
Papio anubis	-	-	-	-	-	107	14.4
Pithecia spp	365.6	91.6	0	273.5	31.7	-	-
Saguinus midas	-	-	-	-	-	-	-
Saguinus oedipus	-	-	-	-	-	18.4	2.98

Appendix A. Table 3 (continued). Fundamental brain part measurements for primates from Stephan et al. 1981

Species	**Nucleus vestibularis lateralis (mm^3)**	**Nucleus vestibularis medialis (mm^3)**	**Nucleus vestibularis descendens (mm^3)**	**Nucleus septalis triangularis (mm^3)**	**Corpus subfornicale (mm^3)**	**Nucelus habenularis medialis (mm^3)**	**Corpus pinneale (mm^3)**	**Corpus subcommissurale (mm^3)**
Ateles geoffroyi	6.81	23.8	11.9	3.18	0.443	7.29	3.10	0.608
Callicebus moloch	-	-	-	0.890	0.135	2.66	2.90	0.154
Callithrix jacchus	-	-	-	0.440	0.133	1.63	0.486	0.0789
Cebus albifrons	7.45	19.2	12.3	1.50	0.410	4.90	3.80	0.425
Cercocebus albigena	10.0	35.6	25.2	1.69	0.658	6.00	11.9	0.233
Cercopithecus mitis	-	-	-	1.96	0.432	5.38	15.3	0.258
Colobus badius	10.0	24.1	14.5	2.26	0.454	4.54	7.31	0.265
Erythrocebus patas	-	-	-	-	-	-	-	-
Gorilla gorilla	19.5	58.4	23.6	5.79	1.30	23.9	7.96	1.41
Hylobates lar	5.53	24.5	14.5	-	0.359	-	-	-
Macaca mulatta	-	-	-	2.83	0.360	7.66	12.4	0.270
Nycticebus coucang	-	-	-	1.34	0.175	2.04	1.83	0.154
Pan troglodytes	9.65	54.7	29.8	2.70	0.606	9.40	38.0	0.387
Papio anubis	10.5	48.1	33.9	1.86	0.405	12.7	51.1	0.347
Pithecia spp.	-	-	-	1.31	0.300	2.53	0.0623	0.189
Saguinus midas	-	-	-	0.559	0.0795	1.18	0.216	0.0994
Saguinus oedipus	3.63	7.25	4.49	1.08	0.167	1.55	0.392	0.0921

Appendix A. Table 4. Brain weight, body weight, neocortex volume, and cerebellum size in carnivores

Species	Brain * weight (g)	Body * weight (g)	neocortex † volume (mm^3)	cerebellum+ (g)
Acinonyx jubatus	110.9	58 748.9	-	-
Ailuropoda melanoleuca	234.4	13 4586.0	136435.7	-
Arctocephalus australis	307.6‡	103 752.8‡	-	-
Canis latrans	88.3	10 592.5	53217	5.66
Cerdocyon thous	41.8	5 997.9	-	-
Crocuta crocuta	143.5	51 999.6	106105	-
Felis silvestris	37.5	4 666.6	-	-
Haliochoerus grypus	307.6‡	193 642.2‡	-	-
Helogale undulata	-	456.0	-	-
Lontra canadensis	53.5	8 203.5	33718	2.05
Mustela putorius	8.3	1 030.4	4326	0.61
Mustela vison	8.5	388.2	4512	-
Panthera leo	223.4	155 955.3	145983	19.65
Phoca vitulina	273.5‡	112 460.5‡	-	29.51
Selenarctos thibetanus	312.6	103 752.8	-	-
Speothos venaticus	40.5	7 998.3	-	-
Ursus americanus	258.8	110 407.9	88420.25	-
Ursus arctos	338.0	298 538.3	-	35.97
Thalarctos maritimus	459.2	363 915.0	-	68.8

* Deaner & Barton (2002) partly derived from Gittleman 1986; † Dunbar & Bever 1998; +Putnam 1927; ‡ Bininda-Emonds 2000.

Appendix B

B.1 Life-History

The following tables detail the statistics for non-significant results of analyses of each play category on life-history variables in Chapter 5.

Table B.1.1. Partial correlation analyses of play category on gestation length, controlling for body size in primates

Play type	DF	F-value	p-value	co-efficient	r^2
Total	1, 32	0.88	0.36	1.43	0.03
Solitary	1, 17	1.14	0.29	-4.47	0.06
Object	1, 10	1.86	0.20	4.92	0.16
Social	1, 21	0.18	0.67	-1.21	0.67

Table B.1.2. Partial correlation analyses of play category on birth weight, controlling for female body weight in carnivores

Play type	DF	F-value	p-value	co-efficient	r^2
Total	1, 6	1.27	0.30	-0.34	0.18
Solitary+	-	-	-	-	-
Object+	-	-	-	-	-
Social	1, 2	5.82	0.13	-0.28	0.74

+ Too few observations

Table B.1.3. Partial correlation analyses of play category on litter size, controlling for body size in primates

Play type	DF	F-value	p-value	co-efficient	r^2
Total	1, 37	0.61	0.44	1.58	0.02
Solitary	1, 18	0.06	0.80	-1.18	0.004
Object	1, 11	0.01	0.92	-0.38	0.001
Social	1, 23	0.36	0.55	1.65	0.02

Table B.1.4. Partial correlation analyses of play category on age at weaning, controlling for body size in carnivores.

Play type	**DF**	**F-value**	**p-value**	**co-efficient**	**r^2**
Total	1, 7	0.16	0.70	-0.49	0.02
Solitary+	-	-	-	-	-
Object	1, 2	3.31	0.21	3.93	0.62
Social	1, 2	0.96	0.43	-0.93	0.33

+ Too few observations

Table B.1.5. Partial correlation analyses of play category on age at sexual maturation, controlling for body size in primates

Play type	**DF**	**F-value**	**p-value**	**co-efficient**	**r^2**
Total	1, 18	0.17	0.68	-0.17	0.01
Solitary	1, 10	2.44	0.15	-3.28	0.19
Object	1, 4	2.06	0.22	1.61	0.34
Social	1, 12	0.46	0.51	-0.52	0.04

Table B.1.6. Partial correlation analyses of play category on maximum lifespan, controlling for body size in carnivores.

Play type	**DF**	**F-value**	**p-value**	**co-efficient**	**r^2**
Total	1, 3	0.36	0.59	-0.48	0.11
Solitary+	-	-	-	-	-
Object+	-	-	-	-	-
Social	1, 2	09.47	0.06	-0.60	0.99

+ Too few observations

B.2 Socio-Ecology

The following tables detail the statistics for non-significant results of analyses of each play category on socio-ecological variables in Chapter 6.

Table B.2.1. Partial correlation analyses of play category on feeding group size in primates

Play type	DF	F-value	p-value	co-efficient	r^2
Total	1, 7	0.27	0.62	0.20	0.04
Solitary	1, 4	0.38	0.58	0.61	0.11
Object	1, 3	9.56	0.09	1.42	0.83
Social	1, 6	0.09	0.76	0.12	0.02

Table B.2.2. Partial correlation analyses of play category on feeding group size in carnivores

Play type	DF	F-value	p-value	co-efficient	r^2
Total	1, 5	0.27	0.63	-0.16	0.05
Solitary+	-	-	-	-	-
Object+	-	-	-	-	-
Social+	-	-	-	-	-

\+ Too few observations

Table B.2.3. Partial correlation analyses of play category on percentage of leaves in diet in primates

Play type	DF	F-value	p-value	co-efficient	r^2
Total	1, 9	0.002	0.97	-0.01	1.7
Solitary	1, 3	0.43	0.56	0.37	0.12
Object	1, 3	14.23	0.06	0.85	0.88
Social	1, 7	0.02	0.89	0.04	0.003

Table B.2.4. Partial correlation analyses of play category on percentage of prey items in diet in primates

Play type	DF	F-value	p-value	co-efficient	r^2
Total	1, 8	0.35	0.57	-0.14	0.04
Solitary	1, 3	0.31	0.63	-0.28	0.13
Object+	-	-	-	-	-
Social	1, 6	0.12	0.68	-0.11	0.03

\+Too few observations.

Table B.2.5. Partial correlation analyses of play category on percentage of fruit in diet in primates

Play type	DF	F-value	p-value	co-efficient	r^2
Total	1, 31	0.69	0.41	-0.18	0.02
Solitary	1, 16	0.78	0.39	-0.75	0.05
Object	1, 11	0.28	0.61	-0.23	0.03
Social	1, 22	1.60	0.22	-0.27	0.07

Table B.2.6. Partial correlation analyses of play category on sex ratio in primates

Play type	DF	F-value	p-value	co-efficient	r^2
Total	1, 6	0.23	0.65	0.36	0.04
Solitary+	-	-	-	-	-
Object+	-	-	-	-	-
Social	1, 4	0.06	0.82	-0.28	0.02

+ Too few observations

Table B.2.7. Partial correlation analyses of play category on growth rate in primates

Play type	DF	F-value	p-value	co-efficient	r^2
Total	1, 4	0.22	0.67	0.84	0.07
Solitary+	-	-	-	-	-
Object +	-	-	-	-	-
Social	1, 4	0.53	0.54	-1.56	0.21

+ Too few observations

B.3 Brain

The following tables detail the statistics for non-significant results of analyses of each play category on different brain components in Chapter 7.

Table B.3.1. Regression analyses of play category on cerebellum size in carnivores

Play type	DF	F-value	p-value	co-efficient	r^2
Total	1, 4	0.54	0.50		0.12
Solitary+	-	-	-	-	-
Object +	-	-	-	-	-
Social+	-	-	-	-	-

+ Too few observations

Table B.3.2. Regression analyses of play category on mesencephalon size in primates

Play type	DF	F-value	p-value	co-efficient	r^2
Total	1, 14	1.40	0.25	2.05	0.09
Solitary	1, 5	0.14	0.73	-1.11	0.03
Object	1, 3	0.33	0.61	-2.17	0.10
Social	1, 12	2.42	0.14	1.72	0.02

Table B.3.3. Regression analyses of play category on diencephalon size in primates

Play type	DF	F-value	p-value	co-efficient	r^2
Total	1, 14	1.63	0.22	1.65	0.11
Solitary	1, 5	2.03	0.21	-2.83	0.29
Object	1, 3	2.89	0.18	-4.58	0.49
Social	1, 12	0.83	0.38	0.89	0.07

Table B.3.4. Regression analyses of play category on olfactory bulb size in primates

Play type	DF	F-value	p-value	co-efficient	r^2
Total	1, 14	1.56	0.23	-0.37	0.10
Solitary	1, 5	0.38	0.57	0.60	0.07
Object	1, 3	0.83	0.43	-1.25	0.22
Social	1, 12	1.69	0.22	0.31	0.12

Table B.3.5. Regression analyses of play category on piriform lobe size in primates

Play type	DF	F-value	p-value	co-efficient	r^2
Total	1, 14	1.74	0.21	0.63	0.11
Solitary	1, 5	3.53	0.12	-5.11	0.41
Object	1, 3	0.30	0.62	-2.61	0.09
Social	1, 12	0.05	0.82	-0.22	0.005

Table B.3.6. Regression analyses of play category on epithalamus size in primates

Play type	DF	F-value	p-value	co-efficient	r^2
Total	1, 6	0.13	0.73	0.18	0.02
Solitary+	-	-	-	-	-
Object+	-	-	-	-	-
Social	1, 6	2.58	0.16	1.06	0.30

+ Too few observations

Table B.3.7. Regression analyses of play category on subthalamus size in primates

Play type	DF	F-value	p-value	co-efficient	r^2
Total	1, 6	0.05	0.82	0.10	0.009
Solitary+	-	-	-	-	-
Object+	-	-	-	-	-
Social	1, 6	4.38	0.08	0.98	0.42

+ Too few observations

Table B.3.8. Regression analyses of play category on pallidum size in primates

Play type	DF	F-value	p-value	co-efficient	r^2
Total	1, 6	0.05	0.84	0.09	0.007
Solitary+	-	-	-	-	-
Object+	-	-	-	-	-
Social	1, 6	4.31	0.08	0.99	0.42

+ Too few observations

Table B.3.9. Regression analyses of play category on nucleus subthalamicus size in primates

Play type	DF	F-value	p-value	co-efficient	r^2
Total	1, 6	0.21	0.66	0.18	0.03
Solitary+	-	-	-	-	-
Object+	-	-	-	-	-
Social	1, 6	2.65	0.15	0.89	0.31

+ Too few observations

Table B.3.10. Regression analyses of play category on capsula interna size in primates

Play type	DF	F-value	p-value	co-efficient	r^2
Total	1, 6	0.14	0.72	0.14	0.2
Solitary+	-	-	-	-	-
Object+	-	-	-	-	-
Social	1, 6	0.87	0.39	0.39	0.13

+ Too few observations

Table B.3.11. Regression analyses of play category on nucleus tractus olfactorii lateralis size in primates

Play type	DF	F-value	p-value	co-efficient	r^2
Total	1, 9	0.02	0.88	0.11	0.003
Solitary	1, 3	0.03	0.87	4.20	0.01
Object+	-	-	-	-	-
Social	1, 7	0.44	0.53	0.38	0.06

+Too few observations

Table B.3.12. Regression analyses of play category on complexus cortico-basolateralis size in primates

Play type	DF	F-value	p-value	co-efficient	r^2
Total	1, 9	0.05	0.86	-0.18	0.006
Solitary	1, 3	1.64	0.29	-4.44	0.35
Object	1, 3	0.09	0.79	0.55	0.04
Social	1, 7	4.42	0.07	1.10	0.39

Table B.3.13. Regression analyses of play category on nucleus vestibularis lateralis size in primates

Play type	DF	F-value	p-value	co-efficient	r^2
Total	1, 6	0.22	0.66	-0.34	0.04
Solitary+	-	-	-	-	-
Object+	-	-	-	-	-
Social	1, 6	0.004	0.95	0.06	0.001

+ Too few observations

Table B.3.14. Regression analyses of play category on nucleus septalis triangularis size in primates

Play type	DF	F-value	p-value	co-efficient	r^2
Total	1, 12	1.38	0.26	-0.44	0.10
Solitary	1, 4	0.002	0.97	0.03	3.93
Object	1, 3	0.22	0.67	-1.04	0.07
Social	1, 11	0.54	0.48	-0.32	0.05

Table B.3.15. Regression analyses of play category on nucleus habenularis medialis size in primates

Play type	DF	F-value	p-value	co-efficient	r^2
Total	1, 12	1.54	0.24	-0.55	0.01
Solitary	1, 4	0.16	0.71	0.37	0.04
Object	1, 3	0.007	0.94	0.24	0.002
Social	1, 11	1.22	0.29	0.53	0.10

Table B.3.16. Regression analyses of play category on corpus pinneale size in primates

Play type	DF	F-value	p-value	co-efficient	r^2
Total	1, 12	1.47	0.25	-0.18	0.11
Solitary	1, 4	0.57	0.49	0.11	0.13
Object	1, 3	0.07	0.81	-0.10	0.02
Social	1, 11	2.34	0.15	0.24	0.18

Table B.3.17. Regression analyses of play category on corpus subcommissurale size in primates

Play type	DF	F-value	p-value	co-efficient	r^2
Total	1, 12	0.23	0.64	-0.21	0.02
Solitary	1, 4	0.56	0.51	-0.43	0.12
Object	1, 3	0.24	0.66	0.67	0.08
Social	1, 11	0.04	0.86	0.09	0.003

Appendix C

Figure 1 details a mean of daily fluctuations in play activity across all primates. The results here show the sort of pattern commonly reported in the play literature for daily fluctuations in play. Dawn and dusk are frequently cited as common times for daily play peaks; in these results, the peak in the day is certainly at dusk, but the earlier peak occurs around mid-morning rather than at dawn, but with the usual cessation of play towards the middle of the day when the sun is at its hottest. Amongst primates, morning periods have been shown to be the time at which play occurs most frequently in vervet, red-tail, patas, and squirrel monkeys, and in lemurs (Fagen 1981: 304). Daily fluctuations in the play of individual species are presented in Chapter 4.

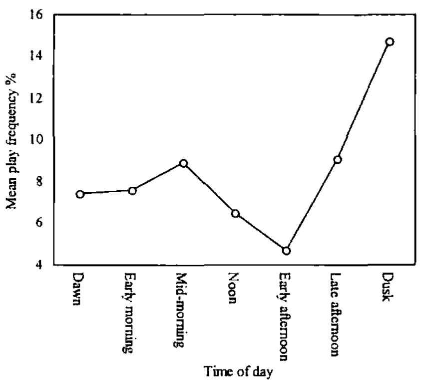


Fig. C.1 Mean daily play frequency trajectory in primates

Table C.1. Play by age group on group sizes in primates, controlling for brain and body weights.

Age & play category	DF	F-value	p-value	co-efficient	r^2
Adult play %	1,14	0.28	0.60	0.42	0.02
Subadult play%	1, 11	0.95	0.35	0.43	0.08
Juvenile play %	1, 20	0.52	0.48	-0.27	0.03
Infant play %	1, 14	7.96	0.01	0.43	0.36

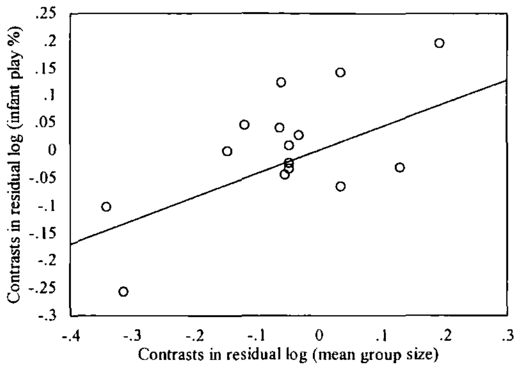


Fig.C.2 Independent contrasts partial correlation regression plot of mean group size on infant play in primates

Table C.2. Play by age group on mean group size in carnivores, controlling for brain and body weights.

Age & play category	DF	F-value	p-value	co-efficient	r²
Adult play % +	-	-	-	-	-
Subadult play% +	-	-	-	-	-
Juvenile play %	1, 3	2.89	0.18	0.27	0.49
Infant play % +	-		-	-	-

+ Too few observations

Table C.3. Independent contrasts partial correlation regression analyses of play category on sex composition in primates.

Sex (No. in group)	Play type	DF	F-value	p-value	co-efficient	r²
Male	Total	1, 26	0.02	0.88	-0.03	0.001
	Solitary	1, 17	0.25	0.62	-0.67	0.02
	Object	1, 10	3.86	0.07	1.45	0.28
	Social	1, 19	1.11	0.30	0.55	0.06
	Male	1, 16	1.72	0.21	0.30	0.10
	Female	1, 16	1.42	0.25	-0.64	0.08
Female	Total	1, 27	0.02	0.89	-0.03	0.001
	Solitary	1, 18	5.22	0.03	3.94	0.23
	Object	1, 10	9.15	0.01	3.33	0.48
	Social	1, 20	22.97	0.0001	2.05	0.54
	Male	1, 17	0.65	0.43	-0.29	0.04
	Female	1, 17	0.007	0.93	-0.05	4.34

Bonferroni = 0.004, Female solitary and object n.s.

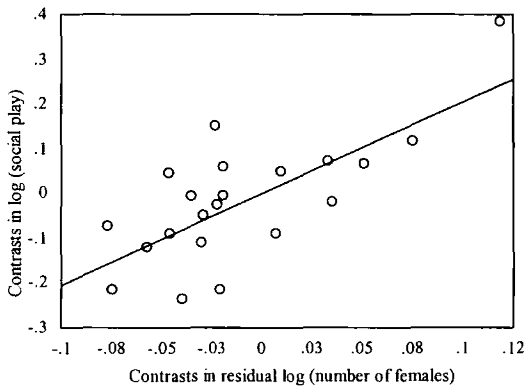


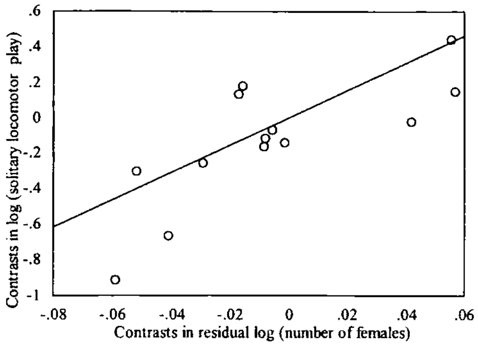
Fig. C.3 Independent contrasts partial correlation regression plot of number of females in a group on social play in primates

Table C.4. Independent contrasts regression analyses of play category on sex composition in platyrrhines.

Sex (No. in group)	Play type	DF	F-value	p-value	co-efficient	r²
Male	Total	1, 5	0.98	0.37	-1.48	0.16
	Solitary	1, 3	3.60	0.15	7.86	0.55
	Object	1, 3	15.46	0.06	-12.96	0.89
	Social	1, 3	0.14	0.73	1.83	0.04
Female	Total	1, 5	0.73	0.43	0.88	0.13
	Solitary	1, 3	2.68	0.20	-3.23	0.47
	Object	1, 3	11.37	0.07	4.94	0.85
	Social	1, 3	1.94	0.26	2.43	0.39

Table C.5. Independent contrasts regression analyses of play category on sex composition in catarrhines

Sex (No. in group)	Play type	DF	F-value	p-value	co-efficient	r²
Male	Total	1, 19	0.008	0.93	-0.02	4.18
	Solitary	1, 12	0.33	0.57	-0.88	0.03
	Object	1, 6	0.79	0.03	1.47	0.57
	Social	1, 14	0.44	0.52	0.35	0.03
	Male	1, 15	0.12	0.74	-0.12	0.008
	Female	1, 15	1.29	2.73	-0.63	0.08
Female	Total	1, 19	0.11	0.74	-0.10	0.006
	Solitary	1, 12	17.26	0.001	7.65	0.59
	Object	1, 7	0.02	0.88	-0.24	0.003
	Social	1, 14	20.68	0.0005	2.01	0.60
	Male	1, 15	1.16	0.30	-0.38	0.07
	Female	1, 15	0.005	0.95	-0.04	3.00



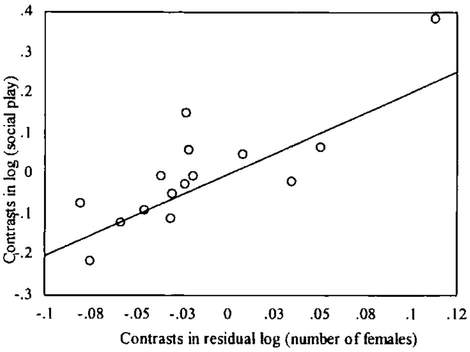


Fig. C.4 Independent contrasts partial correlation regression plot of number of females in a group on solitary play in catarrhines

Fig.c.5 Independent contrasts partial correlation regression plot of number of females in a group on social play in catarrhines

Appendix D. Table 1. Primate play database

Species	Data type	Source	Captive=0/ wild=1	No. in study group	No. observed	No. adult males	Age of adult male (yrs)	No. adult females	Age adult females (yrs)
Allenopithecus nigroviridis	Undergraduate thesis	Potter 1999	-	-	-	-	-	-	-
Alouatta caraya	Paper	Jones 1983	0	5.000	5.000	1.000	-	2.000	-
Alouatta palliata	Paper	Clarke 1990	1	28.000	11.000	3.000	-	9.000	-
Alouatta palliata	Paper	Baldwin & Baldwin 1978	1	151.000	151.000	-	-	-	-
Ateles geoffroyi	Paper	Fedigan & Baxter 1984	1	-	-	-	-	-	-
Cacajao rubicundus	Paper	Abordo et al. 1975	-	-	-	-	-	-	-
Cacajao rubicundus	Book chapter	Schapiro & Mitchell 1986	0	-	-	-	-	-	-
Callicebus moloch	Paper	Fragaszy et al. 1982	0	8.000	8.000	2.000	-	2.000	-
Callithrix geoffroyi	Undergraduate thesis	Potter 1999	-	-	-	-	-	-	-
Callithrix jacchus	Paper	Voland 1977	0	21.000	21.000	8.000	1-10	6.000	1-10
Callithrix jacchus	Paper	Stevenson & Poole 1976	0	21.000	8.000	4.000	3	4.000	2.6, 3, 3
Cebus albifrons	Paper	Bernstein 1965	0	-	-	-	-	-	-
Cebus apella	Paper	Ross & Giller 1988	0	18.000	16.000	3.000	20,6,5	6.000	9,9,7,7,6,5
Cebus apella	Paper	Terborgh 1983	1	-	-	-	-	-	-
Cebus apella	Paper	Visalberghi & Guidi 1998	0	17.000	9.000	2.000	-	6.000	-
Cebus capucinus	Paper	Fontaine 1994	-	-	-	-	-	-	-
Cebus capucinus	Paper	Fedigan 1993	-	-	-	-	-	-	-
Cebus olivaceus	Paper	Robinson 1985	1	-	-	-	-	-	-
Cercocebus atys	Paper	Bernstein 1976	-	-	-	-	-	-	-
Cercopithecus aethiops	Paper	Govindarajulu et al. 1993	1	12.000	12.000	1.000	-	4.000	
Cercopithecus aethiops	Paper	Lancaster 1971	1	55.000	55.000	7.000	-	15.000	-
Cercopithecus aethiops	Paper	Lee 1984	1	-	-	-	-	-	-
Cercopithecus aethiops	Paper	Fedigan 1972	0	17.000	17.000	1.000	-	3.000	-
Cercopithecus aethiops	Paper	Rose 1977b	1	16.000	16.000	2.000	-	2.000	-
Cercopithecus diana	Paper	Lewis 2000	0	7.000	6.000	1.000	-	1.000	-

Species	Data type	Source	Captive=0/ wild=1	No. in study group	No. observed	No. adult males	Age of adult male (yrs)	No. adult females	Age adult females (yrs)
Cercopithecus diana	Paper	Byrne et al. 1983	0	8.000	8.000	1.000	-	3.000	-
Cercopithecus diana	Undergraduate thesis	Potter 1999	-	-	-	-	-	-	-
Cercopithecus hamlyni			0	-	-	-	-	-	-
Cercopithecus hamlyni	Paper	Lewis 2000	0	7.000	7.000	1.000	-	1.000	-
Cercopithecus mitis	Paper	Lawes & Piper 1992	1	-	-	-	-	-	-
Cercopithecus neglectus	Paper	Oswald & Lockard 1980	0	10.000	10.000	1.000	-	2.000	-
Colobus badius	Book	Struhsaker 1975	-	-	-	-	-	-	-
Colobus badius	Book	Struhsaker 1975	1	-	-	-	-	-	-
Colobus badius	Paper	Marsh 1978	-	-	-	-	-	-	-
Colobus badius	Book	Struhsaker 1975	-	-	-	-	-	-	-
Colobus badius rufomitratus	Paper	Marsh 1981	1	-	-	-	-	-	-
Colobus badius tephrosecles	Paper	Clutton-Brock 1974	1	64.000	64.000	-	-	-	-
Colobus badius tephrosecles	Paper	Clutton-Brock 1974	1	58.000	58.000	-	-	-	-
Colobus badius tephrosecles	Paper	Clutton-Brock 1974	1	82.000	82.000	-	-	-	-
Colobus guereza	Paper	Horwich & Wurman 1978	0	8.000	8.000	1.000	-	2.000	-
Colobus guereza	Book	Struhsaker 1975	1	-	-	-	-	-	-
Colobus guereza	Book chapter	Oates 1977	-	-	-	-	-	-	-
Colobus guereza	PhD	Oates 1974	-	-	-	-	-	-	-
Colobus guereza	Paper	Rose 1977b	1	19.000	19.000	2.000	-	3.000	-
Erythrocebus patas	Paper	Rowell & Chism 1986	0	20.000	-	-	-	-	-
Gorilla gorilla berengei	Book chapter	Fossey 1979	1	120.000	32.000	-	-	-	-
Gorilla gorilla berengei	Paper	Yamagiwa 1992	1	6.000	6.000	4.000	21,17,11,9	0.000	-
Gorilla gorilla berengei	Book	Schaller 1965	1	-	156.000	-	-	-	-
Gorilla gorilla gorilla	Paper	Meder 1990	0	26.000	26.000	-	-	-	-
Gorilla gorilla gorilla	Paper	Hoff et al. 1981	0	7.000	6.000	1.000	12	3.000	12, 12, 16
Gorilla gorilla gorilla	Paper	Fischer & Nadler 1978	0	4.000	4.000	-	-	4.000	9-11
Hylobates lar	PhD. thesis	Bartlett 1999	1	-	-	-	-	-	-

Species	Data type	Source	Captive=0/ wild=1	No. in study group	No. observed	No. adult males	Age of adult male (yrs)	No. adult females	Age adult females (yrs)
Hylobates lar	Book chapter	Schapiro & Mitchell 1986	0	-	-	-	-	-	-
Hylobates lar	Paper	Bernstein & Schusterman 1964	0	13.000	13.000	2.000	-	2.000	-
Hylobates syndactylus	Paper 2	Orgeldinger 1996	0	3.000	2.000	1.000	-	1.000	-
Hylobates syndactylus	Paper	Lewis 2000	0	4.000	4.000	1.000	-	1.000	-
Hylobates syndactylus			0	-	-	-	-	-	-
Lemur catta			0	-	-	-	-	-	-
Lemur catta	Paper	Lewis 2000	0	9.000	9.000	0.000	-	2.000	-
Macaca arctoides	Paper	Rhine & Kronenwetter 1972	-	-	-	-	-	-	-
Macaca arctoides	Paper	O'Keefe & Lifshitz 1985	-	-	-	-	-	-	-
Macaca arctoides	Paper	Estrada & Estrada 1978	1	35.000	35.000	3.000	-	9.000	-
Macaca arctoides	Paper	Chamove 1973	0	-	-	-	-	-	-
Macaca arctoides	Paper	Bernstein 1980	0	40.000	40.000	-	-	-	-
Macaca arctoides	Review	Caine & Mitchell 1979	-	-	-	-	-	-	-
Macaca arctoides	Paper	Rhine & Kronenwetter 1972	-	-	-	-	-	-	-
Macaca arctoides	Paper	Rhine & Hendy-Neeley 1978	0	-	7.000	-	-	-	-
Macaca brunnescens	Paper 2	Kilner 2001	1	16.000	16.000	2.000	-	4.000	-
Macaca fascicularis	Review	Caine & Mitchell 1979	-	-	-	-	-	-	-
Macaca fascicularis	Paper	Sussman & Tattersall 1981	-	-	-	-	-	-	-
Macaca fuscata	Paper	Rostal & Eaton 1983	0	316.000	16.000	8.000	9-10	-	-
Macaca fuscata	Paper	Glick et al. 1986b	0	314.000	18.000	-	-	-	-
Macaca fuscata	Paper	Eaton et al. 1986	0	304.000	18.000	57.000	-	113.000	-
Macaca fuscata	Paper	Hayaki 1983	1	100.000	18.000	-	-	-	-
Macaca fuscata	Review	Caine & Mitchell 1979	-	-	-	-	-	-	-
Macaca fuscata	Paper	Imakawa 1990	1	274.000	-	42.000	5-25	82.000	5-25
Macaca fuscata	Paper	Glick et al. 1986a	0	274.000	44.000	-	-	22.000	-
Macaca fuscata	Paper	Koyama 1985	1	125.000	104.000	-	-	-	-
Macaca mulatta	Paper	Post & Baulu 1978	0	36.000	20.000	4.000	-	10.000	-
Macaca mulatta	Paper	Gard & Meier 1977	0	32.000	11.000	-	-	-	-

Species	Data type	Source	Captive=0/ wild=1	No. in study group	No. observed	No. adult males	Age of adult male (yrs)	No. adult females	Age adult females (yrs)
Macaca mulatta	Paper	Harlow & Harlow 1965	0	-	-	-	-	-	-
Macaca mulatta	Paper	Ehardt & Bernstein 1987	0	83.000	83.000	-	-	-	-
Macaca mulatta	Review	Caine & Mitchell 1979	-	-	-	-	-	-	-
Macaca mulatta	Paper	Baulu & Redmond 1980	1	32.000	16.000	3.000	4-10	11.000	6-17
Macaca mulatta	Paper	Chamove 1973	0	-	-	-	-	-	-
Macaca nemestrina	Paper	Bernstein 1970	-	-	-	-	-	-	-
Macaca nemestrina	Paper	Kirkevold et al. 1982	0	5.000	5.000	-	-	-	-
Macaca nemestrina	Review	Caine & Mitchell 1979	-	-	-	-	-	-	-
Macaca nemestrina	Paper	Bernstein 1972	0	48.000	48.000	-	-	-	-
Macaca nigra	Paper	Bernstein & Baker 1988	0	23.000	23.000	6.000	-	7.000	-
Macaca nigra	Paper	Nickelson & Lockard 1978	0	10.000	10.000	1.000	-	3.000	-
Macaca radiata	Paper	Singh & Sachdeva 1977	1	23.000	5.000	4.000	-	5.000	-
Macaca radiata	Review	Caine & Mitchell 1979	-	-	-	-	-	-	-
Macaca silenus	?	?	-	-	-	-	-	-	-
Macaca sinica	Review	Caine & Mitchell 1979	-	-	-	-	-	-	-
Macaca sylvanus	Paper	O'Leary & Fa 1993	1	27.000	27.000	-	-	-	-
Macaca sylvanus	Review	Caine & Mitchell 1979	-	-	-	-	-	-	-
Macaca sylvanus	Paper	Lahiri & Southwick 1966	-	-	-	-	-	-	-
Macaca sylvanus	Paper	Lewis 2000	0	8.000	8.000	1.000	-	3.000	-
Macaca sylvanus			0	-	-	-	-	-	-
Macaca thibetana	Paper	Zi-Yun 1993	1	-	-	-	-	-	-
Mandrillus sphinx	Undergraduate project	?	0	-	-	-	-	-	-
Mandrillus sphinx	Paper	Mellen et al. 1981	0	6.000	6.000	1.000	-	2.000	-
Nycticebus coucang	Paper	?	-	-	-	-	-	-	-
Pan paniscus	Paper	Enomoto 1990	1	-	-	-	-	-	-
Pan paniscus	Paper	Mori 1984	1	-	17.000	5.000	-	5.000	-
Pan troglodytes	Paper	Tomasello et al. 1990	0	7.000	7.000	-	-	-	-

Species	Data type	Source	Captive=0/ wild=1	No. in study group	No. observed	No. adult males	Age of adult male (yrs)	No. adult females	Age adult females (yrs)
Pan troglodytes	Book chapter	Schapiro & Mitchell 1986	0	-	-	-	-	-	-
Pan troglodytes	Paper	Bloomsmith et al. 1994	0	-	21.000	-	-	-	-
Pan troglodytes	Paper	Kraemer 1979	0	6.000	6.000	3.000	-	3.000	-
Pan troglodytes	Paper	King et al. 1980	0	7.000	7.000	1.000	26	3.000	27,24,10
Pan troglodytes			0	-	-	-	-	-	-
Pan troglodytes	Paper	Horvat & Kraemer 1981	0	23.000	10.000	-	-	5.000	-
Pan troglodytes	Paper	Bloomsmith 1989	0	-	-	11.000	-	-	-
Pan troglodytes	Paper	Tomasello et al. 1990	0	15.000	6.000	1.000	-	8.000	-
Pan troglodytes	Paper	Nishida 1983	1	34.000	-	-	-	-	-
Pan troglodytes	Paper	Merrick 1977	0	7.000	7.000	2.000	12, 10	2.000	11, 10
Pan troglodytes	Paper	Pruetz & Bloomsmith 1995	0	29.000	17.000	-	-	-	-
Pan troglodytes	Paper	Lewis 2000	0	12.000	11.000	4.000	-	4.000	-
Pan troglodytes	Paper	Mendoza-Granados & Sommer 1995	0	25.000	11.000	2.000	24, 15	9.000	34,33,31,30,21,20,13,11,11
Pan troglodytes	Paper	Hayaki 1985	1	100.000	9.000	-	-	-	-
Pan troglodytes	Paper	Kraemer et al. 1982	0	-	-	-	-	-	-
Papio	Paper	Coelho & Bramblett 1982	0	87.000	45.000	6.000	-	-	-
Papio anubis	Paper	Chalmers 1980	1	71.000	71.000	7.000	-	19.000	-
Papio anubis	Paper	Owens 1975b	1	65.000	45.000	-	-	-	-
Papio anubis	Paper	Rose 1977a	1	65.000	65.000	7.000	-	19.000	-
Papio anubis	Paper	Owens 1975a	1	65.000	45.000	-	-	-	-
Papio c. ursinus	Paper	Cheney 1978	1	30.000	30.000	-	-	-	-
Papio cynocephalus	Paper	Young & Hankins 1979	0	-	25.000	-	-	-	-
Papio cynocephalus/anubis (mixed)	Paper	Young et al. 1982	0	77.000	77.000	46.000	-	31.000	-
Papio hamadryas	Paper	Pereira & Preisser 1998	0	7.000	7.000	2.000	8, 7	3.000	7,6,5
Pithecia pithecia	?	?	-	-	-	-	-	-	-

Species	Data type	Source	Captive=0/ wild=1	No. in study group	No. observed	No. adult males	Age of adult male (yrs)	No. adult females	Age adult females (yrs)
Pithecia pithecia	Paper	Dugmore 1986	0	2.000	2.000	1.000	2	1.000	2
Pithecia pithecia	Undergraduate thesis	Potter 1999	-	-	-	-	-	-	-
Pongo pygmaeus	Paper	Zucker et al. 1978	0	4.000	2.000	1.000	19.000	2.000	20.000
Presbytis entellus	Paper	Dolhinow & Murphy 1982	0	-	19.000	-	-	-	-
Presbytis entellus	Paper	Sommer & Mendoza-Granados 1995	1	22.000	22.000	5.000	-	0.000	-
Presbytis johnii	Paper	Poirier 1969	1	212.000	212.000	27.000	-	31.000	-
Presbytis pileatus	Paper	Islam & Husain 1982	1	-	-	-	-	-	-
Pygathrix nemaeus	Paper	Kavanagh 1978	0	6.000	6.000	1.000	-	3.000	-
Saguinus fuscicollis	Paper	Vogt 1978	0	8.000	4.000	1.000	-	1.000	-
Saguinus fuscicollis	Paper	Vogt et al. 1978	0	10.000	-	1.000	-	1.000	-
Saguinus midas			0	-	-	-	-	-	-
Saguinus midas	Paper	Lewis 2000	0	8.000	8.000	1.000	-	1.000	-
Saguinus oedipus	Undergraduate thesis	Potter 1999	-	-	-	-	-	-	-
Saimiri boliviensis	Paper	Biben et al. 1989	0	13.000	13.000	1.000	-	6.000	-
Saimiri sciureus	Paper	Abordo et al. 1975	-	-	-	-	-	-	-
Saimiri sciureus	Paper	Biben & Symmes 1986	0	4.000	4.000	-	-	-	-
Saimiri sciureus	Book chapter	Schapiro & Mitchell 1986	0	-	-	-	-	-	-
Theropithecus gelada	Paper	Bernstein 1975	-	-	-	-	-	-	-

Species	No. subadult males	Age subadult males	No. subadult females	Age subadult females	No. adolescent males	age adolescent males	no. adolescent females	age adolescent females	No. juvenile males	Age juvenile males (mo)	No. juvenile females	Age juvenile females (mo)
Allenopithecus nigroviridis	-	-	-	-	-	-	-	-	-	-	-	-
Alouatta caraya	1.000	-	1.000	-	-	-	-	-	-	-	-	-
Alouatta palliata	-	-	-	-	-	-	-	-	2.000	-	3.000	-
Alouatta palliata	-	-	-	-	-	-	-	-	-	-	-	-
Ateles geoffroyi	-	-	-	-	-	-	-	-	-	-	-	-
Cacajao rubicundus	-	-	-	-	-	-	-	-	-	-	-	-
Cacajao rubicundus	-	-	-	-	-	-	-	-	-	-	-	-
Callicebus moloch	-	-	-	-	-	-	-	-	-	-	1.000	-
Callithrix geoffroyi	-	-	-	-	-	-	-	-	-	-	-	-
Callithrix jacchus	1.000	0.750	1.000	0.750	-	-	-	-	3.000	3-8	0.000	-
Callithrix jacchus	-	-	1.000	1.000	-	-	-	-	3.000	8,8,7	3.000	8,7
Cebus albifrons	-	-	-	-	-	-	-	-	-	-	-	-
Cebus apella	2.000	4.000	1.000	4.000	-	-	-	-	2.000	1,1	2.000	1
Cebus apella	-	-	-	-	-	-	-	-	-	-	-	-
Cebus apella	-	-	-	-	2.000	4.000	-	-	4.000	1,2,3	3.000	1, 2, 3
Cebus capucinus	-	-	-	-	-	-	-	-	-	-	-	-
Cebus capucinus	-	-	-	-	-	-	-	-	-	-	-	-
Cebus olivaceus	-	-	-	-	-	-	-	-	-	-	-	-
Cercocebus atys	-	-	-	-	-	-	-	-	-	-	-	-
Cercopithecus aethiops	-	-	-	-	-	-	-	-	2.000	3.5,4.6	1.000	2.5
Cercopithecus aethiops	1.000	-	3.000	-	4.000	-	3.000	-	4.000	-	4.000	-
Cercopithecus aethiops	-	-	-	-	-	-	-	-	-	-	-	-
Cercopithecus aethiops	-	-	-	-	-	-	3.000	48	7.000	36,36,36,36,12,12,12	-	-
Cercopithecus aethiops	-	-	-	-	3.000	-	2.000	-	2.000	-	2.000	-
Cercopithecus diana	1.000	-	-	-	-	-	-	-	-	-	2.000	-
Cercopithecus diana	-	-	-	-	-	-	-	-	-	-	-	-

Species	No. sub-adult males	Age sub-adult males	No. sub-adult females	Age sub-adult females	No. adol-escent males	age adol-escent males	no. adol-escent females	age adol-escent females	No. juv-enile males	Age juv-enile males (mo)	No. juv-enile females	Age juv-enile females (mo)
Cercopithecus diana	-	-	-	-	-	-	-	-	-	-	1.000	-
Cercopithecus diana	-	-	-	-	-	-	-	-	-	-	-	-
Cercopithecus hamlyni	-	-	-	-	-	-	-	-	-	-	-	-
Cercopithecus hamlyni	-	-	2.000	-	-	-	-	-	2.000	-	-	-
Cercopithecus mitis	-	-	-	-	-	-	-	-	-	-	-	-
Cercopithecus neglectus	-	-	2.000	-	-	-	-	-	4.000	-	-	-
Colobus badius	-	-	-	-	-	-	-	-	-	-	-	-
Colobus badius	-	-	-	-	-	-	-	-	-	-	-	-
Colobus badius	-	-	-	-	-	-	-	-	-	-	-	-
Colobus badius	-	-	-	-	-	-	-	-	-	-	-	-
Colobus badius rufomitratus	-	-	-	-	-	-	-	-	-	-	-	-
Colobus badius tephrosecles	-	-	-	-	-	-	-	-	-	-	-	-
Colobus badius tephrosecles	-	-	-	-	-	-	-	-	-	-	-	-
Colobus badius tephrosecles	-	-	-	-	-	-	-	-	-	-	-	-
Colobus guereza	-	-	1.000	-	1.000	2.5	-	-	-	-	1.000	12
Colobus guereza	-	-	-	-	-	-	-	-	-	-	-	-
Colobus guereza	-	-	-	-	-	-	-	-	-	-	-	-
Colobus guereza	-	-	-	-	-	-	-	-	-	-	-	-
Colobus guereza	-	-	-	-	4.000	-	3.000	-	2.000	-	2.000	-
Erythrocebus patas	-	-	-	-	-	-	-	-	-	-	-	-
Gorilla gorilla berengei	-	-	-	-	-	-	-	-	-	-	-	-
Gorilla gorilla berengei	2.000	87.000	0.000	-	-	-	-	-	-	-	-	-
Gorilla gorilla berengei	-	-	-	-	-	-	-	-	-	-	-	-
Gorilla gorilla gorilla	-	-	-	-	-	-	-	-	-	-	-	-
Gorilla gorilla gorilla	-	-	-	-	-	-	-	-	-	-	-	-
Gorilla gorilla gorilla	-	-	-	-	-	-	-	-	-	-	-	-
Hylobates lar	-	-	-	-	-	-	-	-	-	-	-	-

Species	No. sub-adult males	Age sub-adult males	No. sub-adult females	Age sub-adult females	No. adol-escent males	age adol-escent males	no. adol-escent females	age adol-escent females	No. juv-enile males	Age juv-enile males (mo)	No. juv-enile females	Age juv-enile females (mo)
Hylobates lar	-	-	-	-	-	-	-	-	-	-	-	-
Hylobates lar	-	-	-	-	-	-	-	-	-	-	-	-
Hylobates syndactylus	-	-	-	-	-	-	-	-	-	-	-	-
Hylobates syndactylus	-	-	-	-	-	-	-	-	2.000	-	-	-
Hylobates syndactylus	-	-	-	-	-	-	-	-	-	-	-	-
Lemur catta	-	-	-	-	-	-	-	-	-	-	-	-
Lemur catta	-	9.000	-	9.000	-	-	-	-	0.000	-	5.000	-
Macaca arctoides	-	-	-	-	-	-	-	-	-	-	-	-
Macaca arctoides	-	-	-	-	-	-	-	-	-	-	-	-
Macaca arctoides	-	-	-	-	-	-	-	-	8.000	12-25	6.000	18-25
Macaca arctoides	-	-	-	-	-	-	-	-	-	-	-	-
Macaca arctoides	-	-	-	-	-	-	-	-	-	-	-	-
Macaca arctoides	-	-	-	-	-	-	-	-	-	-	-	-
Macaca arctoides	-	-	-	-	-	-	-	-	-	-	-	-
Macaca arctoides	-	-	-	-	-	-	-	-	-	-	-	-
Macaca brunnescens	-	-	-	-	-	-	-	-	4.000	-	1.000	-
Macaca fuscicularis	-	-	-	-	-	-	-	-	-	-	-	-
Macaca fuscicularis	-	-	-	-	-	-	-	-	-	-	-	-
Macaca fuscata	-	-	-	9.000	3.000	-	-	-	5.000	4	-	-
Macaca fuscata	-	-	-	-	-	-	-	-	9.000	-	9.000	-
Macaca fuscata	-	-	-	-	-	-	-	-	52.000	-	34.000	-
Macaca fuscata	-	-	-	-	-	-	-	-	8.000	-	10.000	-
Macaca fuscata	-	-	-	-	-	-	-	-	-	-	-	-
Macaca fuscata	-	-	-	-	21.000	4	15.000	4	31.000	1-3	41.000	1-3
Macaca fuscata	-	-	-	-	-	-	-	-	-	-	-	-
Macaca fuscata	-	-	-	-	-	-	-	-	-	-	-	-
Macaca mulatta	-	-	-	-	-	-	-	-	4.000	-	2.000	-

Species	No. sub-adult males	Age sub-adult males	No. sub-adult females	Age sub-adult females	No. adol-escent males	age adol-escent males	no. adol-escent females	age adol-escent females	No. juv-enile males	Age juv-enile males (mo)	No. juv-enile females	Age juv-enile females (mo)
Macaca mulatta	-	-	9.000	-	9.000	-	-	-	-	-	-	-
Macaca mulatta	-	-	-	-	-	-	-	-	-	-	-	-
Macaca mulatta	-	-	-	-	-	-	-	-	-	-	-	-
Macaca mulatta	-	-	-	-	-	-	-	-	-	-	-	-
Macaca mulatta	-	-	-	-	-	-	5.000	3-4	2.000	2-3	-	-
Macaca mulatta	-	-	-	-	-	-	-	-	-	-	-	-
Macaca nemestrina	-	-	-	-	-	-	-	-	-	-	-	-
Macaca nemestrina	-	-	-	-	-	-	-	-	-	-	-	-
Macaca nemestrina	-	-	-	-	-	-	-	-	-	-	-	-
Macaca nemestrina	-	-	-	-	-	-	-	-	-	-	-	-
Macaca nigra	-	-	-	-	-	-	-	-	-	-	-	-
Macaca nigra	1.000	-	-	-	-	-	-	-	3.000	-	2.000	-
Macaca radiata	2.000	-	2.000	-	-	-	-	-	3.000	-	5.000	-
Macaca radiata	-	-	-	-	-	-	-	-	-	-	-	-
Macaca silenus	-	-	-	-	-	-	-	-	-	-	-	-
Macaca sinica	-	-	-	-	-	-	-	-	-	-	-	-
Macaca sylvanus	-	-	-	-	-	-	-	-	-	-	-	-
Macaca sylvanus	-	-	-	-	-	-	-	-	-	-	-	-
Macaca sylvanus	-	-	-	-	-	-	-	-	-	-	-	-
Macaca sylvanus	-	-	-	-	1.000	-	-	-	2.000	-	-	-
Macaca sylvanus	-	-	-	-	-	-	-	-	-	-	-	-
Macaca thibetana	-	-	-	-	-	-	-	9	-	-	-	-
Mandrillus sphinx	-	-	-	-	-	-	-	-	-	-	-	-
Mandrillus sphinx	-	-	-	-	-	-	-	-	-	-	-	-
Nycticebus coucang	-	-	-	-	-	-	-	-	-	-	-	-
Pan paniscus	-	-	-	-	-	-	-	-	-	-	-	-
Pan paniscus	-	-	-	-	3.000	-	1.000	-	2.000	-	1.000	-

Species	No. subadult males	Age subadult males	No. subadult females	Age subadult females	No. adolescent males	age adolescent males	no. adolescent females	age adolescent females	No. juvenile males	Age juvenile males (mo)	No. juvenile females	Age juvenile females (mo)
Pan troglodytes	-	-	-	-	-	-	-	-	5.000	-	2.000	-
Pan troglodytes	-	-	-	-	-	-	-	-	-	-	-	-
Pan troglodytes	-	-	-	-	-	-	-	-	8.000	-	13.000	-
Pan troglodytes	-	-	-	-	-	-	-	-	-	-	-	-
Pan troglodytes	-	-	-	-	-	-	-	-	-	-	-	-
Pan troglodytes	-	-	-	-	-	-	-	-	-	-	-	-
Pan troglodytes	-	-	-	-	-	-	-	-	-	-	-	-
Pan troglodytes	-	-	-	-	-	-	-	-	12.000	-	9.000	-
Pan troglodytes	-	-	-	-	-	-	-	-	-	-	-	-
Pan troglodytes	-	-	-	-	-	-	-	-	3.000	3-4	-	-
Pan troglodytes	1.000	8.000	1.000	9.000	-	-	-	-	-	-	-	-
Pan troglodytes	-	-	-	-	-	-	-	-	-	-	-	-
Pan troglodytes	0.000	-	-	-	-	-	-	-	2.000	-	1.000	-
Pan troglodytes	1.000	9.000	1.000	8.000	1.000	6.000	3.000	7,6, 6	1.000	44.000	3.000	41, 51, 52
Pan troglodytes	-	-	-	-	5.000	-	1.000	-	1.000	-	2.000	-
Pan troglodytes	-	-	-	-	-	-	-	-	-	-	-	-
Papio	-	-	-	-	-	-	-	-	-	-	-	-
Papio anubis	-	-	-	-	-	-	-	-	-	-	-	-
Papio anubis	-	-	-	-	-	-	-	-	-	-	-	-
Papio anubis	-	-	-	-	6.000	-	2.000	-	13.000	-	3.000	-
Papio anubis	-	-	-	-	-	-	-	-	-	-	-	-
Papio c. ursinus	3.000	4.000	-	-	2.000	3	1.000	3	3.000	1.5	3.000	1.5
Papio cynocephalus	-	-	-	-	-	-	-	-	-	-	-	-
Papio cynocephalus/anubis (mixed)	-	-	-	-	-	-	-	-	-	-	-	-
Papio hamadryas	-	-	-	-	-	-	-	-	1.000	48	1.000	24
Pithecia pithecia	-	-	-	-	-	-	-	-	-	-	-	-

Species	No. sub-adult males	Age sub-adult males	No. sub-adult females	Age sub-adult females	No. adol-escent males	age adol-escent males	no. adol-escent females	age adol-escent females	No. juv-enile males	Age juv-enile males (mo)	No. juv-enile females	Age juv-enile females (mo)
Pithecia pithecia	-	-	-	-	-	-	-	-	-	-	-	-
Pongo pygmaeus	-	-	-	-	-	-	-	-	1.000	48.000	-	-
Presbytis entellus	-	-	-	-	-	-	-	-	-	-	-	-
Presbytis entellus	8.000	-	0.000	0.000	0.000	-	0.000	-	9.000	-	0.000	-
Presbytis johnii	9.000	-	3.000	-	-	-	-	-	3.000	-	3.000	-
Presbytis pileatus	-	-	-	-	-	-	-	-	-	-	-	-
Pygathrix nemaeus	-	-	-	-	-	-	-	-	1.000	15	-	-
Saguinus fuscicollis	1.000	-	-	-	-	-	-	-	-	-	-	-
Saguinus fuscicollis	1.000	-	-	-	-	-	-	-	-	-	-	-
Saguinus midas	-	-	-	-	-	-	-	-	-	-	-	-
Saguinus midas	-	-	-	-	-	-	-	-	3.000	-	1.000	-
Saguinus oedipus	-	-	-	-	-	-	-	-	-	-	-	-
Saimiri boliviensis	-	-	-	-	-	-	-	-	2.000	12	2.000	12
Saimiri sciureus	-	-	-	-	-	-	-	-	-	-	-	-
Saimiri sciureus	-	-	-	-	2.000	2.5	-	-	2.000	12	-	-
Saimiri sciureus	-	-	-	-	-	-	-	-	-	-	-	-
Theropithecus gelada	-	-	-	-	-	-	-	-	-	-	-	-

Species	No. of infant males	Age infant males (mo)	No infant females	Age infant females (mo)	Un-known sex	Total no. males	Total no. females	Total adults	Total adoles-cents	Total juv-eniles	Total inf-ants
Allenopithecus nigroviridis	-	-	-	-	-	-	-	-	-	-	-
Alouatta caraya	-	-	-	-	-	2.000	3.000	3.000	2.000	0.000	0.000
Alouatta palliata	6.000	-	5.000	-	-	11.000	13.000	12.000	-	5.000	11.000
Alouatta palliata	-	-	-	-	-	-	-	95.000	-	56.000	-
Ateles geoffroyi	-	-	-	-	-	-	-	-	-	-	-
Cacajao rubicundus	-	-	-	-	-	-	-	-	-	-	-
Cacajao rubicundus	-	-	-	-	-	-	-	-	-	-	-
Callicebus moloch	1.000	-	2.000	-	-	3.000	5.000	4.000	-	1.000	3.000
Callithrix geoffroyi	-	-	-	-	-	-	-	-	-	-	-
Callithrix jacchus	-	-	-	-	2.000	12.000	7.000	14.000	2.000	3.000	2.000
Callithrix jacchus	3.000	3	3.000	3	-	10.000	11.000	8.000	1.000	6.000	6.000
Cebus albifrons	-	-	-	-	-	-	-	-	-	-	-
Cebus apella	-	-	-	-	2.000	7.000	11.000	9.000	3.000	4.000	2.000
Cebus apella	-	-	-	-	-	-	-	-	-	-	-
Cebus apella	-	-	-	-	-	8.000	9.000	8.000	2.000	7.000	-
Cebus capucinus	-	-	-	-	-	-	-	-	-	-	-
Cebus capucinus	-	-	-	-	-	-	-	-	-	-	-
Cebus olivaceus	-	-	-	-	-	-	-	-	-	-	-
Cercocebus atys	-	-	-	-	-	-	-	-	-	-	-
Cercopithecus aethiops	3.000	6	1.000	6.000	-	6.000	6.000	5.000	-	3.000	4.000
Cercopithecus aethiops	9.000	-	5.000	-	-	25.000	30.000	22.000	11.000	8.000	14.000
Cercopithecus aethiops	-	-	-	-	-	-	-	-	-	-	-
Cercopithecus aethiops	-	-	-	-	3.000	8.000	6.000	4.000	3.000	7.000	3.000
Cercopithecus aethiops	1.000	-	2.000	-	-	8.000	8.000	4.000	5.000	4.000	3.000
Cercopithecus diana	-	-	1.000	-	1.000	2.000	4.000	2.000	1.000	2.000	2.000
Cercopithecus diana	-	-	-	-	-	-	-	-	-	-	-
Cercopithecus diana	2.000	-	1.000	-	-	3.000	5.000	4.000	-	1.000	3.000

Species	No. of infant males	Age infant males (mo)	No infant females	Age infant females (mo)	Un-known sex	Total no. males	Total no. females	Total adults	Total adoles-cents	Total juv-eniles	Total inf-ants
Cercopithecus diana	-	-	-	-	-	-	-	-	-	-	-
Cercopithecus hamlyni	-	-	-	-	-	-	-	-	-	-	-
Cercopithecus hamlyni	-	-	1.000	-	-	3.000	4.000	2.000	2.000	2.000	1.000
Cercopithecus mitis	-	-	-	-	-	-	-	-	-	-	-
Cercopithecus neglectus	-	1	-	-	-	6.000	4.000	3.000	2.000	4.000	1.000
Colobus badius	-	-	-	-	-	-	-	-	-	-	-
Colobus badius	-	-	-	-	-	-	-	-	-	-	-
Colobus badius	-	-	-	-	-	-	-	-	-	-	-
Colobus badius	-	-	-	-	-	-	-	-	-	-	-
Colobus badius rufomitratus	-	-	-	-	-	-	-	-	-	-	-
Colobus badius tephrosecles	-	-	-	-	-	-	-	-	-	-	-
Colobus badius tephrosecles	-	-	-	-	-	-	-	-	-	-	-
Colobus badius tephrosecles	-	-	-	-	-	-	-	-	-	-	-
Colobus guereza	-	-	-	-	2.000	1.000	4.000	3.000	2.000	1.000	2.000
Colobus guereza	-	-	-	-	-	-	-	-	-	-	-
Colobus guereza	-	-	-	-	-	-	-	-	-	-	-
Colobus guereza	-	-	-	-	-	-	-	-	-	-	-
Colobus guereza	1.000	-	2.000	-	-	9.000	10.000	5.000	7.000	4.000	3.000
Erythrocebus patas	-	-	-	-	-	11.000	9.000	-	-	-	-
Gorilla gorilla berengei	-	-	-	-	-	-	-	-	-	-	32.000
Gorilla gorilla berengei	-	-	-	-	-	6.000	0.000	4.000	2.000	-	-
Gorilla gorilla berengei	-	-	-	-	-	-	-	-	-	-	-
Gorilla gorilla gorilla	-	-	-	-	-	12.000	14.000	-	-	-	-
Gorilla gorilla gorilla	2.000	4	1.000	4.000	-	3.000	4.000	4.000	-	-	3.000
Gorilla gorilla gorilla	-	-	-	-	-	-	-	4.000	-	-	-
Hylobates lar	-	-	-	-	-	-	-	-	-	-	-
Hylobates lar	-	-	-	-	-	-	-	-	-	-	-
Hylobates lar	-	-	-	-	9.000	2.000	2.000	4.000	-	9.000	-

Species	No. of infant males	Age infant males (mo)	No infant females	Age infant females (mo)	Unknown sex	Total no. males	Total no. females	Total adults	Total adolescents	Total juveniles	Total infants
Hylobates syndactylus	-	-	-	-	-	1.000	1.000	2.000	-	-	-
Hylobates syndactylus	-	-	-	-	-	3.000	1.000	2.000	-	2.000	-
Hylobates syndactylus	-	-	-	-	-	-	-	-	-	-	-
Lemur catta	-	-	-	-	-	-	-	-	-	-	-
Lemur catta	-	-	-	-	2.000	0.000	9.000	2.000	-	5.000	2.000
Macaca arctoides	-	-	-	-	-	-	-	-	-	-	-
Macaca arctoides	-	-	-	-	-	-	-	-	-	-	-
Macaca arctoides	3.000	1-5	6.000	1-5	-	14.000	21.000	12.000	-	10.000	9.000
Macaca arctoides	-	-	-	-	-	-	-	-	-	-	-
Macaca arctoides	-	-	-	-	-	24.000	16.000	-	-	-	-
Macaca arctoides	-	-	-	-	-	-	-	-	-	-	-
Macaca arctoides	-	-	-	-	-	-	-	-	-	-	-
Macaca arctoides	4.000	-	3.000	-	-	4.000	3.000	-	-	-	7.000
Macaca brunnescens	1.000	-	-	-	-	7.000	5.000	6.000	-	5.000	1.000
Macaca fascicularis	-	-	-	-	-	9.000	-	-	-	-	-
Macaca fascicularis	-	-	-	-	-	-	-	-	-	-	-
Macaca fuscata	-	-	-	-	-	16.000	0.000	8.000	3.000	5.000	-
Macaca fuscata	-	-	-	-	-	9.000	9.000	-	-	18.000	-
Macaca fuscata	19.000	-	29.000	-	-	128.000	176.000	170.000	-	86.000	48.000
Macaca fuscata	-	-	-	-	-	-	-	-	-	-	-
Macaca fuscata	-	-	-	-	-	-	-	-	-	-	-
Macaca fuscata	17.000	0	25.000	0.000	-	111.000	163.000	124.000	36.000	72.000	42.000
Macaca fuscata	10.000	-	12.000	-	-	10.000	34.000	22.000	-	-	22.000
Macaca fuscata	-	-	-	-	-	45.000	80.000	-	-	-	-
Macaca mulatta	-	-	-	-	-	8.000	12.000	14.000	-	6.000	-
Macaca mulatta	-	-	-	-	-	-	-	-	-	-	-
Macaca mulatta	-	-	-	-	-	-	-	-	-	-	-
Macaca mulatta	-	-	-	-	-	-	-	-	-	-	-

Species	No. of infant males	Age infant males (mo)	No infant females	Age infant females (mo)	Un-known sex	Total no. males	Total no. females	Total adults	Total adoles-cents	Total juv-eniles	Total inf-ants
Macaca mulatta	-	-	-	-	-	-	-	-	-	-	-
Macaca mulatta	-	-	-	-	-	-	-	-	-	-	-
Macaca mulatta	-	-	-	-	-	-	-	-	-	-	-
Macaca nemestrina	-	-	-	-	-	-	-	-	-	-	-
Macaca nemestrina	2.000	1, .75	3.000	211.000	-	2.000	3.000	-	-	-	5.000
Macaca nemestrina	-	-	-	-	-	-	-	-	-	-	-
Macaca nemestrina	-	-	-	-	-	-	-	-	-	-	-
Macaca nigra	4.000	-	6.000	-	-	10.000	13.000	13.000	-	-	10.000
Macaca nigra	-	-	-	-	-	5.000	5.000	4.000	1.000	5.000	-
Macaca radiata	-	-	-	-	-	-	-	-	-	-	-
Macaca radiata	-	-	-	-	-	-	-	-	-	-	-
Macaca silenus	-	-	-	-	-	-	-	-	-	-	-
Macaca sinica	-	-	-	-	-	-	-	-	-	-	-
Macaca sylvanus	-	-	-	-	-	16.000	11.000	-	-	-	-
Macaca sylvanus	-	-	-	-	-	-	-	-	-	-	-
Macaca sylvanus	-	-	-	-	-	-	-	-	-	-	-
Macaca sylvanus	1.000	-	-	-	-	5.000	3.000	4.000	1.000	2.000	1.000
Macaca sylvanus	-	-	-	-	-	-	-	-	-	-	-
Macaca thibetana	-	-	-	-	-	-	-	-	-	-	-
Mandrillus sphinx	-	-	-	-	-	-	-	-	-	-	-
Mandrillus sphinx	2.000	-	1.000	-	-	3.000	3.000	3.000	-	-	3.000
Nycticebus coucang	-	-	-	-	-	-	-	-	-	-	-
Pan paniscus	-	-	-	-	-	-	-	-	-	-	-
Pan paniscus	-	-	-	-	-	-	-	-	-	-	-
Pan troglodytes	-	-	-	-	-	5.000	2.000	-	-	7.000	-
Pan troglodytes	-	-	-	-	-	-	-	-	-	-	-
Pan troglodytes	-	-	-	-	-	-	-	-	-	21.000	-
Pan troglodytes	-	-	-	-	-	3.000	3.000	6.000	-	-	-

Species	No. of infant males	Age infant males (mo)	No infant females	Age infant females (mo)	Un-known sex	Total no. males	Total no. females	Total adults	Total adoles-cents	Total juv-eniles	Total inf-ants
Pan troglodytes	1.000	12	2.000	18,21	-	2.000	5.000	4.000	-	-	3.000
Pan troglodytes	-	-	-	-	-	-	-	-	-	-	-
Pan troglodytes	2.000	-	3.000	-	-	-	-	5.000	-	-	5.000
Pan troglodytes	-	-	-	-	-	-	-	-	-	21.000	-
Pan troglodytes	4.000	18,28,50, 44	2.000	33,40	-	5.000	10.000	9.000	-	-	6.000
Pan troglodytes	4.000	6-24	1.000	6-24	-	-	-	-	-	-	-
Pan troglodytes	-	-	1.000	4.000	-	3.000	4.000	4.000	2.000	0.000	1.000
Pan troglodytes	-	-	-	-	-	-	-	-	-	-	-
Pan troglodytes	1.000	-	-	-	0.000	7.000	5.000	8.000	0.000	2.000	2.000
Pan troglodytes	2.000	13, 18	1.000	8.000	-	7.000	18.000	11.000	6.000	4.000	4.000
Pan troglodytes	-	-	-	-	-	6.000	3.000	-	6.000	3.000	-
Pan troglodytes	-	-	-	-	-	-	-	-	-	-	-
Papio	-	-	-	-	-	45.000	42.000	-	-	-	-
Papio anubis	-	-	-	-	-	-	-	26.000	-	-	8.000
Papio anubis	-	-	-	-	-	-	-	-	-	-	-
Papio anubis	8.000	-	7.000	-	-	34.000	31.000	26.000	8.000	16.000	15.000
Papio anubis	-	-	-	-	-	-	-	-	-	-	-
Papio c. ursinus	8.000	-	-	-	-	-	-	10.000	6.000	6.000	8.000
Papio cynocephalus	11.000	0-3	14.000	0-3	-	11.000	14.000	-	-	-	25.000
Papio cynocephalus/anubis (mixed)	-	-	-	-	-	46.000	31.000	-	-	-	-
Papio hamadryas	-	-	-	-	-	3.000	4.000	5.000	-	2.000	-
Pithecia pithecia	-	-	-	-	-	-	-	-	-	-	-
Pithecia pithecia	-	-	-	-	-	1.000	1.000	2.000	-	-	-
Pithecia pithecia	-	-	-	-	-	-	-	-	-	-	-
Pongo pygmaeus	-	-	-	-	-	2.000	2.000	3.000	0.000	1.000	0.000
Presbytis entellus	15.000	-	4.000	-	-	-	-	-	-	-	-
Presbytis entellus	0.000	-	0.000	-	0.000	20.000	0.000	5.000	8.000	9.000	0.000

Species	No. of infant males	Age infant males (mo)	No infant females	Age infant females (mo)	Un-known sex	Total no. males	Total no. females	Total adults	Total adoles-cents	Total juv-eniles	Total inf-ants
Presbytis johnii	6.000	-	4.000	-	62.000	45.000	41.000	98.000	17.000	13.000	20.000
Presbytis pileatus	-	-	-	-	-	-	-	-	-	-	-
Pygathrix nemaeus	-	-	1.000	4.5	-	2.000	4.000	4.000	-	1.000	1.000
Saguinus fuscicollis	-	-	1.000	-	4.000	2.000	3.000	2.000	1.000	-	6.000
Saguinus fuscicollis	3.000	-	4.000	-	-	5.000	5.000	2.000	1.000	-	7.000
Saguinus midas	-	-	-	-	-	-	-	-	-	-	-
Saguinus midas	-	-	-	-	2.000	4.000	2.000	2.000	-	4.000	2.000
Saguinus oedipus	-	-	-	-	-	-	-	-	-	-	-
Saimiri boliviensis	-	-	-	-	-	3.000	8.000	7.000	-	4.000	-
Saimiri sciureus	-	-	-	-	-	-	-	-	-	-	-
Saimiri sciureus	-	-	-	-	-	4.000	-	-	2.000	2.000	-
Saimiri sciureus	-	-	-	-	-	-	-	-	-	-	-
Theropithecus gelada	-	-	-	-	-	-	-	-	-	-	-

Species	Adult play? (yes 1 rare 2 no 0)	Adult-adult play?	Sex play? (yes 1 no 0)	Length of study (mo)	No. of observ-ation hours	No. of play behav-iours	No. of play inter-actions	Average length of play bout (sec)	Male play Freq-uency per hour	Female play freq-uency per hour	Group play frequ-ency per hour
Allenopithecus nigroviridis	-	-	-	-	-	-	-	-	-	-	-
Alouatta caraya	1	1	1	0.50	40.000	-	176.000	-	-	-	176.000
Alouatta palliata	-	-	-	22.00	1456.000	-	-	-	-	-	-
Alouatta palliata	1	0	-	2.50	-	-	-	15.000	-	-	-
Ateles geoffroyi	-	-	-	-	-	-	-	-	0.230	0.620	-
Cacajao rubicundus	-	-	-	-	-	-	-	-	-	-	-
Cacajao rubicundus	-	-	-	-	-	-	-	-	-	-	-
Callicebus moloch	1	-	-	-	-	-	-	-	-	-	-
Callithrix geoffroyi	-	-	-	-	-	-	-	-	-	-	-
Callithrix jacchus	1	1	-	-	-	38.0	950.000	231.000	-	-	0.777
Callithrix jacchus	1	1	1	-	720.000	43.0	17.000	30.000	-	-	-
Cebus albifrons	-	-	-	-	-	-	-	-	-	-	-
Cebus apella	-	-	-	6.00	75.000	-	-	-	-	-	-
Cebus apella	-	-	-	-	-	-	-	-	-	-	-
Cebus apella	-	-	-	3.00	77.500	-	3060.000	-	-	-	-
Cebus capucinus	-	-	-	-	-	-	-	-	-	-	-
Cebus capucinus	-	-	-	-	-	-	-	-	0.180	0.240	-
Cebus olivaceus	-	-	-	-	-	-	-	-	-	-	-
Cercocebus atys	-	-	-	-	-	-	-	-	-	-	-
Cercopithecus aethiops	-	-	-	7.00	425.000	-	-	34.100	11.475	7.800	-
Cercopithecus aethiops	-	-	1	8.00	840.000	-	-	-	-	-	-
Cercopithecus aethiops	-	-	-	-	-	-	-	-	5.160	3.083	11.100
Cercopithecus aethiops	2	-	-	6.00	198.000	26.0	-	-	-	-	-
Cercopithecus aethiops	0	-	-	-	-	-	-	-	-	-	-
Cercopithecus diana	2	0	0	2.50	-	-	-	-	-	-	-

Species	Adult play? (yes 1 rare 2 no 0)	Adult-adult play?	Sex play? (yes 1 no 0)	Length of study (mo)	No. of observation hours	No. of play behaviours	No. of play interactions	Average length of play bout (sec)	Male play Frequency per hour	Female play frequency per hour	Group play frequency per hour
Cercopithecus diana	-	-	-	-	-	-	-	-	-	-	-
Cercopithecus diana	2	-	-	-	-	-	-	-	-	-	-
Cercopithecus diana	-	-	-	-	-	-	-	-	-	-	-
Cercopithecus hamlyni	-	-	-	-	-	-	-	-	-	-	-
Cercopithecus hamlyni	2	0	0	2.50	-	-	-	-	-	-	-
Cercopithecus mitis	0	0	-	-	-	-	-	-	-	-	-
Cercopithecus neglectus	0	0	-	-	-	6.0	-	-	-	-	-
Colobus badius	-	-	-	-	-	-	-	-	-	-	-
Colobus badius	-	-	-	-	-	-	-	-	-	-	-
Colobus badius	2	-	-	-	-	-	-	-	-	-	-
Colobus badius	-	-	-	-	-	-	-	-	-	-	-
Colobus badius rufomitratus	2	0	-	14.00	-	-	-	-	-	-	-
Colobus badius tephrosecles	0	0	0	2.00	-	-	-	-	-	-	-
Colobus badius tephrosecles	0	0	0	2.00	-	-	-	-	-	-	-
Colobus badius tephrosecles	0	0	0	14.00	-	-	-	-	-	-	-
Colobus guereza	1	-	-	8.00	-	3.0	-	-	-	-	3.909
Colobus guereza	-	-	-	-	-	-	-	-	-	-	-
Colobus guereza	-	-	-	-	-	-	-	-	-	-	-
Colobus guereza	0	0	-	-	-	-	-	-	-	-	-
Colobus guereza	0	-	-	6.00	1184.000	-	43.000	3.000	-	-	-
Erythrocebus patas	-	-	-	-	-	-	-	4.040	10.200	6.125	-
Gorilla gorilla berengei	1	2	-	84.00	413.000	23.0	-	-	-	-	-
Gorilla gorilla berengei	2	2	1	9.00	-	-	364.000	-	0.450	-	-
Gorilla gorilla berengei	-	-	-	-	-	-	91.000	-	-	-	-
Gorilla gorilla gorilla	-	-	-	-	-	-	-	-	1.250	0.616	-
Gorilla gorilla gorilla	1	-	0	16.00	-	-	-	-	-	-	-

Species	Adult play? (yes 1 rare 2 no 0)	Adult-adult play?	Sex play? (yes 1 no 0)	Length of study (mo)	No. of observ-ation hours	No. of play behav-iours	No. of play inter-actions	Average length of play bout (sec)	Male play Freq-uency per hour	Female play freq-uency per hour	Group play frequ-ency per hour
Gorilla gorilla gorilla	1	2	-	7.00	80.000	-	-	972.000	-	0.063	0.063
Hylobates lar	1	1	-	-	-	4.0	-	-	-	-	-
Hylobates lar	-	-	-	-	-	-	-	-	-	-	-
Hylobates lar	-	-	-	-	-	-	-	-	-	-	-
Hylobates syndactylus	1	1	1	1.50	117.700	4.0	-	-	-	-	5.830
Hylobates syndactylus	1	-	-	2.50	-	-	-	-	-	-	-
Hylobates syndactylus	-	-	-	-	-	-	-	-	-	-	-
Lemur catta	-	-	-	-	-	-	-	-	-	-	-
Lemur catta	2	0	0	2.50	-	9.0	-	-	-	-	-
Macaca arctoides	-	-	-	-	-	-	-	-	-	-	-
Macaca arctoides	-	-	-	-	-	-	-	-	-	-	-
Macaca arctoides	2	0	-	-	-	-	-	-	-	-	9.600
Macaca arctoides	-	-	-	-	-	-	-	-	-	-	-
Macaca arctoides	-	-	1	36.00	-	-	-	-	-	-	-
Macaca arctoides	1	1	-	-	-	-	-	-	-	-	-
Macaca arctoides	-	-	-	-	-	-	-	-	-	-	-
Macaca arctoides	2	-	-	2.00	-	14.0	-	-	-	-	-
Macaca brunnescens	-	-	-	0.55	150.000	-	-	-	-	-	-
Macaca fascicularis	2	0	-	-	-	-	-	-	-	-	-
Macaca fascicularis	-	-	-	-	-	-	-	-	-	-	-
Macaca fuscata	0	0	-	6.00	-	-	9.000	-	-	-	-
Macaca fuscata	-	-	1	16.00	-	-	-	9.000	-	-	-
Macaca fuscata	-	-	1	10.00	-	-	-	-	-	-	-
Macaca fuscata	2	-	-	-	-	-	-	9.000	-	-	-
Macaca fuscata	-	1	-	-	-	-	-	9.000	-	-	-
Macaca fuscata	-	-	-	15.00	-	-	-	-	19.380	12.660	-

Species	Adult play? (yes 1 rare 2 no 0)	Adult-adult play?	Sex play? (yes 1 no 0)	Length of study (mo)	No. of observation hours	No. of play behaviours	No. of play interactions	Average length of play bout (sec)	Male play Frequency per hour	Female play frequency per hour	Group play frequency per hour
Macaca fuscata	1	-	-	-	-	-	-	9.000	-	-	-
Macaca fuscata	0	0	-	-	-	-	6068.000	-	-	-	-
Macaca mulatta	1	0	0	7.00	-	-	-	-	-	-	-
Macaca mulatta	-	-	-	2.00	-	-	-	9.000	-	-	-
Macaca mulatta	-	-	-	-	-	-	-	-	-	-	-
Macaca mulatta	1	-	-	-	-	-	-	-	-	-	-
Macaca mulatta	2	0	-	-	-	-	-	-	-	-	-
Macaca mulatta	2	0	-	-	-	-	-	-	-	-	-
Macaca mulatta	-	-	-	-	-	-	-	-	-	-	-
Macaca nemestrina	-	-	-	-	-	-	-	-	-	-	-
Macaca nemestrina	-	-	-	5.00	-	-	-	-	-	-	-
Macaca nemestrina	-	-	-	-	-	-	-	-	-	-	-
Macaca nemestrina	-	-	-	-	-	-	-	-	-	-	-
Macaca nigra	-	-	-	-	-	-	-	-	-	-	-
Macaca nigra	1	-	-	7.50	9.000	14.0	-	-	-	-	-
Macaca radiata	-	-	-	-	-	-	-	-	-	-	-
Macaca radiata	1	-	-	-	-	-	-	-	-	-	-
Macaca silenus	-	-	-	-	-	-	-	-	-	-	-
Macaca sinica	1	-	-	-	-	-	-	-	-	-	-
Macaca sylvanus	1	-	-	1.80	-	-	-	-	-	-	-
Macaca sylvanus	1	0	-	-	-	-	-	-	-	-	-
Macaca sylvanus	-	-	-	-	-	-	-	-	-	-	-
Macaca sylvanus	1	0	-	2.50	-	-	-	-	-	-	-
Macaca sylvanus	-	-	-	-	-	-	-	-	-	-	-
Macaca thibetana	0	0	-	-	-	-	-	-	-	-	-
Mandrillus sphinx	-	-	-	-	-	-	-	-	-	-	-

Species	Adult play? (yes 1 rare 2 no 0)	Adult-adult play?	Sex play? (yes 1 no 0)	Length of study (mo)	No. of observation hours	No. of play behaviours	No. of play interactions	Average length of play bout (sec)	Male play Frequency per hour	Female play frequency per hour	Group play frequency per hour
Mandrillus sphinx	1	1	-	-	-	-	-	-	-	-	-
Nycticebus coucang	1	-	-	-	-	-	-	-	-	-	-
Pan paniscus	1	1	1	-	-	19.0	-	-	-	-	-
Pan paniscus	-	-	-	-	-	-	-	-	-	-	42.000
Pan troglodytes	-	-	-	-	-	-	13.000	-	-	-	-
Pan troglodytes	-	-	-	-	-	-	-	-	-	-	-
Pan troglodytes	-	-	-	60.00	792.000	-	-	-	-	-	-
Pan troglodytes	1	1	-	-	18.500	24.0	-	-	-	-	-
Pan troglodytes	1	2	1	15.00	-	7.0	-	-	-	-	-
Pan troglodytes	-	-	-	-	-	-	-	-	-	-	-
Pan troglodytes	1	-	-	-	-	-	-	-	-	-	-
Pan troglodytes	1	1	-	7.00	225.500	-	-	-	3.700	-	-
Pan troglodytes	-	-	-	2.00	-	-	-	-	-	-	-
Pan troglodytes	1	-	1	12.00	-	-	-	-	-	-	-
Pan troglodytes	1	-	-	11.00	-	17.0	-	-	-	-	-
Pan troglodytes	1	-	-	10.00	311.000	-	-	-	9.660	-	-
Pan troglodytes	1	1	1	2.50	-	-	-	-	-	-	-
Pan troglodytes	-	-	-	4.00	44.000	-	1651.000	27.700	-	-	-
Pan troglodytes	1	-	-	11.00	384.000	12.5	661.000	60.000	-	-	-
Pan troglodytes	1	-	1	-	-	-	-	-	-	-	-
Papio	-	-	-	-	-	4.0	2100.000	-	33.850	15.950	-
Papio anubis	-	-	-	6.00	231.000	30.0	-	-	-	-	-
Papio anubis	1	-	1	16.00	-	6.0	-	-	-	-	-
Papio anubis	2	0	-	1.00	140.000	-	-	180.000	-	-	-
Papio anubis	1	0	1	16.00	-	-	-	5.000	-	-	-
Papio c. ursinus	-	-	-	15.00	-	-	-	-	-	-	-

Species	Adult play? (yes 1 rare 2 no 0)	Adult-adult play?	Sex play? (yes 1 no 0)	Length of study (mo)	No. of observation hours	No. of play behaviours	No. of play interactions	Average length of play bout (sec)	Male play Frequency per hour	Female play frequency per hour	Group play frequency per hour
Papio cynocephalus	-	-	-	12.00	98.000	-	-	-	-	-	-
Papio cynocephalus/anubis (mixed)	1	-	1	24.00	-	11.0	-	-	12.100	5.920	-
Papio hamadryas	0	-	-	0.50	17.000	-	21.000	-	-	-	-
Pithecia pithecia	-	-	-	-	-	-	-	-	-	-	-
Pithecia pithecia	1	1	1	5.00	-	-	-	-	34.778	25.778	33.667
Pithecia pithecia	-	-	-	-	-	-	-	-	-	-	-
Pongo pygmaeus	1	-	-	3.00	100.000	10.0	30.000	-	-	-	-
Presbytis entellus	1	-	-	-	-	-	-	-	-	-	2.404
Presbytis entellus	0	0	-	12.00	515.000	-	1429.000	114.000	0.767	-	0.767
Presbytis johnii	1	0	-	12.00	1250.000	-	-	-	-	-	7.000
Presbytis pileatus	-	-	-	-	-	-	-	-	-	-	-
Pygathrix nemaeus	2	-	-	-	-	-	-	-	-	-	-
Saguinus fuscicollis	1	1	-	14.00	-	-	-	-	-	-	-
Saguinus fuscicollis	1	1	-	7.50	-	-	-	-	-	-	-
Saguinus midas	-	-	-	-	-	-	-	-	-	-	-
Saguinus midas	2	0	0	2.50	-	-	-	-	-	-	-
Saguinus oedipus	-	-	-	-	-	-	-	-	-	-	-
Saimiri boliviensis	1	-	-	3.00	-	-	54.000	-	-	-	-
Saimiri sciureus	-	-	-	-	-	-	-	-	-	-	-
Saimiri sciureus	-	-	-	2.00	-	7.0	109.000	15.000	-	-	-
Saimiri sciureus	-	-	-	-	-	-	-	-	-	-	-
Theropithecus gelada	-	-	-	-	-	-	-	-	-	-	-

Species	% play performed by males	% play performed by females	Mean male time budget of play %	Mean female time budget of play %	Mean play wrest-ling %	Mean play chasing %	Mean total play %	Mean Solitary play %	Mean Social play %	Mean Object play %
Allenopithecus nigroviridis	-	-	-	-	-	-	2.500	-	-	-
Alouatta caraya	-	-	-	-	-	-	-	-	-	-
Alouatta palliata	-	-	-	-	-	-	14.533	-	-	-
Alouatta palliata	-	-	-	-	-	-	1.560	1.040	0.083	-
Ateles geoffroyi	-	-	9.000	-	-	-	1.000	-	-	-
Cacajao rubicundus	-	-	-	-	-	-	-	-	-	-
Cacajao rubicundus	-	-	-	-	-	-	-	-	-	-
Callicebus moloch	-	-	-	-	-	-	1.440	-	-	-
Callithrix geoffroyi	-	-	-	-	-	-	5.830	-	-	-
Callithrix jacchus	-	-	-	-	-	-	1.075	-	-	-
Callithrix jacchus	-	-	-	-	-	-	-	-	-	-
Cebus albifrons	-	-	-	-	-	-	1.000	-	-	-
Cebus apella	-	-	-	-	-	-	14.705	-	-	-
Cebus apella	-	-	-	-	-	-	2.000	-	-	-
Cebus apella	45.400	40.500	-	-	4.000	1.100	20.528	17.070	18.870	9.550
Cebus capucinus	-	-	-	-	-	-	3.500	-	-	-
Cebus capucinus	-	-	-	-	-	-	-	-	-	-
Cebus olivaceus	-	-	-	-	-	-	3.500	-	-	-
Cercocebus atys	-	-	-	-	-	-	9.000	-	-	-
Cercopithecus aethiops	-	-	9.125	6.000	-	-	7.562	-	-	-
Cercopithecus aethiops	-	-	-	-	-	-	10.330	6.000	4.400	-
Cercopithecus aethiops	-	-	-	-	-	-	-	-	-	-
Cercopithecus aethiops	84.200	15.800	-	-	-	-	-	-	-	-
Cercopithecus aethiops	-	-	-	-	-	-	-	-	-	-
Cercopithecus diana	-	-	5.200	17.300	-	-	13.260	12.500	5.300	1.700
Cercopithecus diana	-	-	5.765	5.925	-	-	-	8.300	3.700	1.200

Species	% play performed by males	% play performed by females	Mean male time budget of play %	Mean female time budget of play %	Mean play wrest-ling %	Mean play chasing %	Mean total play %	Mean Solitary play %	Mean Social play %	Mean Object play %
Cercopithecus diana	-	-	-	-	-	-	2.910	-	-	-
Cercopithecus diana	-	-	-	-	-	-	0.140	-	-	-
Cercopithecus hamlyni	-	-	7.550	2.350	-	-	-	0.200	3.800	1.100
Cercopithecus hamlyni	-	-	7.550	6.625	-	-	6.940	3.100	5.700	1.400
Cercopithecus mitis	-	-	-	-	-	-	4.000	-	-	-
Cercopithecus neglectus	-	-	7.930	0.700	0.590	0.470	5.040	0.030	1.860	3.150
Colobus badius	-	-	-	-	-	-	2.700	-	-	-
Colobus badius	-	-	-	-	-	-	2.600	-	-	-
Colobus badius	-	-	-	-	-	-	2.600	-	-	-
Colobus badius	-	-	-	-	-	-	4.200	-	-	-
Colobus badius rufomitratus	-	-	-	-	-	-	3.400	-	-	-
Colobus badius tephrosecles	-	-	-	-	-	-	3.300	-	3.300	-
Colobus badius tephrosecles	-	-	-	-	-	-	1.000	-	1.000	-
Colobus badius tephrosecles	-	-	-	-	-	-	4.000	-	2.925	-
Colobus guereza	-	-	-	-	-	-	-	-	-	-
Colobus guereza	-	-	-	-	-	-	-	-	-	-
Colobus guereza	-	-	-	-	-	-	4.600	-	-	-
Colobus guereza	-	-	-	-	-	-	-	-	-	-
Colobus guereza	-	-	-	-	-	-	-	-	-	-
Erythrocebus patas	-	-	8.499	5.104	0.556	0.335	12.582	-	-	-
Gorilla gorilla berengei	-	-	-	-	-	-	13.260	3.450	22.187	9.213
Gorilla gorilla berengei	-	-	-	-	-	-	-	-	-	-
Gorilla gorilla berengei	-	-	-	-	-	-	-	-	-	-
Gorilla gorilla gorilla	-	-	-	-	-	-	-	-	-	-
Gorilla gorilla gorilla	-	-	-	-	-	-	-	-	-	-

Species	% play performed by males	% play performed by females	Mean male time budget of play %	Mean female time budget of play %	Mean play wrest-ling %	Mean play chasing %	Mean total play %	Mean Solitary play %	Mean Social play %	Mean Object play %
Gorilla gorilla gorilla	-	-	-	1.688	-	-	6.750	1.647	5.103	-
Hylobates lar	-	-	-	-	-	-	4.185	0.500	3.685	-
Hylobates lar	-	-	-	-	-	-	-	-	-	-
Hylobates lar	-	-	-	-	-	10.000	23.000	-	-	-
Hylobates syndactylus	-	-	-	-	-	-	-	-	-	-
Hylobates syndactylus	-	-	24.833	0.600	-	-	18.760	15.000	21.000	0.500
Hylobates syndactylus	-	-	12.667	0.600	-	-	-	-	11.000	0.300
Lemur catta	-	-	0.000	0.700	-	-	-	2.600	1.200	0.000
Lemur catta	-	-	0.000	0.500	-	-	3.850	5.700	2.000	0.000
Macaca arctoides	-	-	-	-	-	-	13.000	-	-	-
Macaca arctoides	-	-	-	-	-	-	1.400	-	-	-
Macaca arctoides	-	-	-	-	-	-	-	-	-	-
Macaca arctoides	-	-	-	-	-	-	12.500	8.000	17.000	-
Macaca arctoides	-	-	-	-	-	-	10.000	-	-	-
Macaca arctoides	-	-	-	-	-	-	-	-	-	-
Macaca arctoides	-	-	-	-	-	-	5.000	-	-	-
Macaca arctoides	-	-	-	-	-	-	7.290	-	-	-
Macaca brunnescens	-	-	-	-	-	-	5.100	-	-	-
Macaca fascicularis	-	-	-	-	-	-	-	-	-	-
Macaca fascicularis	-	-	-	-	-	-	4.000	-	-	-
Macaca fuscata	-	-	10.200	-	-	-	10.200	-	-	-
Macaca fuscata	-	-	26.328	16.230	-	-	21.279	-	21.279	-
Macaca fuscata	-	-	15.375	8.125	-	-	23.500	-	23.500	-
Macaca fuscata	-	-	-	-	-	-	-	-	-	-
Macaca fuscata	-	-	-	-	-	-	-	-	-	-
Macaca fuscata	-	-	-	-	-	-	-	-	-	-

Species	% play performed by males	% play performed by females	Mean male time budget of play %	Mean female time budget of play %	Mean play wrest-ling %	Mean play chasing %	Mean total play %	Mean Solitary play %	Mean Social play %	Mean Object play %
Macaca fuscata	-	-	-	-	-	-	-	-	-	-
Macaca fuscata	-	-	-	-	-	-	-	-	-	-
Macaca mulatta	-	-	3.850	6.150	-	-	5.000	-	5.000	-
Macaca mulatta	-	-	-	-	-	-	-	-	-	-
Macaca mulatta	-	-	-	-	-	-	-	-	-	-
Macaca mulatta	-	-	18.200	5.450	-	-	10.914	-	-	-
Macaca mulatta	-	-	-	-	-	-	-	-	-	-
Macaca mulatta	-	-	-	-	-	-	4.500	-	-	-
Macaca mulatta	-	-	-	-	-	-	12.125	18.250	6.000	-
Macaca nemestrina	-	-	4.500	2.400	-	-	3.400	-	-	-
Macaca nemestrina	-	-	-	-	-	-	-	-	-	-
Macaca nemestrina	-	-	-	-	-	-	-	-	-	-
Macaca nemestrina	-	-	-	-	-	-	8.160	-	-	-
Macaca nigra	-	-	-	-	-	-	8.000	-	-	-
Macaca nigra	-	-	6.233	5.400	-	-	5.816	-	-	-
Macaca radiata	-	-	-	-	-	-	6.196	16.850	36.267	-
Macaca radiata	-	-	-	-	-	-	-	-	-	-
Macaca silenus	-	-	-	-	-	-	3.500	-	-	-
Macaca sinica	-	-	-	-	-	-	-	-	-	-
Macaca sylvanus	-	-	7.280	4.950	-	-	5.687	-	-	-
Macaca sylvanus	-	-	-	-	-	-	-	-	-	-
Macaca sylvanus	-	-	-	-	-	-	20.900	-	-	-
Macaca sylvanus	-	-	21.080	1.130	-	-	13.570	5.200	4.100	17.000
Macaca sylvanus	-	-	5.285	1.130	-	-	-	2.800	8.900	2.100
Macaca thibetana	-	-	-	-	-	-	-	-	-	-
Mandrillus sphinx	-	-	-	-	-	-	13.750	8.830	18.650	-

Species	% play performed by males	% play performed by females	Mean male time budget of play %	Mean female time budget of play %	Mean play wrestling %	Mean play chasing %	Mean total play %	Mean Solitary play %	Mean Social play %	Mean Object play %
Mandrillus sphinx	-	-	18.653	3.736	-	-	13.430	2.980	18.650	-
Nycticebus coucang	-	-	-	-	-	-	1.200	1.200	0.000	0.000
Pan paniscus	-	-	-	-	-	-	-	-	-	-
Pan paniscus	-	-	-	-	-	-	-	-	-	-
Pan troglodytes	-	-	-	-	-	-	-	-	-	-
Pan troglodytes	-	-	-	-	-	-	-	-	-	-
Pan troglodytes	-	-	20.140	17.755	-	-	18.962	12.335	6.628	-
Pan troglodytes	-	-	-	-	-	-	4.100	0.510	3.590	0.220
Pan troglodytes	-	-	15.358	12.320	2.589	0.327	13.188	7.875	5.313	-
Pan troglodytes	-	-	9.504	9.066	-	-	-	6.060	9.400	3.400
Pan troglodytes	-	-	-	-	-	-	32.611	-	-	-
Pan troglodytes	-	-	11.083	-	-	-	11.083	-	11.083	-
Pan troglodytes	-	-	-	-	-	-	-	-	-	-
Pan troglodytes	-	-	-	-	-	-	-	-	-	-
Pan troglodytes	-	-	-	-	-	-	6.940	-	-	-
Pan troglodytes	-	-	3.733	-	-	-	3.733	-	-	-
Pan troglodytes	-	-	19.770	14.000	-	-	18.940	22.100	21.500	11.200
Pan troglodytes	-	-	16.026	13.402	13.120	9.372	19.000	4.985	14.200	6.140
Pan troglodytes	64.145	35.854	-	-	82.000	29.000	-	-	-	-
Pan troglodytes	-	-	7.500	7.800	-	-	7.667	-	7.667	-
Papio	-	-	-	-	-	-	-	-	-	-
Papio anubis	-	-	-	-	2.400	-	7.500	-	-	-
Papio anubis	-	-	-	-	24.250	10.875	-	-	-	-
Papio anubis	-	-	5.050	2.900	-	-	3.100	-	-	-
Papio anubis	-	-	3.738	2.194	-	-	5.932	-	-	-
Papio c. ursinus	-	-	-	-	-	-	20.940	-	-	-

Species	% play performed by males	% play performed by females	Mean male time budget of play %	Mean female time budget of play %	Mean play wrestling %	Mean play chasing %	Mean total play %	Mean Solitary play %	Mean Social play %	Mean Object play %
Papio cynocephalus	-	-	13.900	11.100	-	-	12.500	-	12.500	-
Papio cynocephalus/anubis (mixed)	-	-	-	-	-	-	-	-	-	-
Papio hamadryas	71.420	85.714	-	-	57.142	-	-	-	-	-
Pithecia pithecia	-	-	-	-	-	-	2.630	4.200	3.000	0.700
Pithecia pithecia	-	-	-	-	-	-	-	-	-	-
Pithecia pithecia	-	-	-	-	-	-	3.000	-	-	-
Pongo pygmaeus	-	-	-	-	-	-	19.563	-	-	-
Presbytis entellus	-	-	-	-	-	-	-	-	-	-
Presbytis entellus	-	-	-	-	-	-	-	-	-	-
Presbytis johnii	-	-	-	-	-	-	-	-	-	-
Presbytis pileatus	-	-	-	-	-	-	3.120	-	-	-
Pygathrix nemaeus	-	-	-	-	-	-	-	-	-	-
Saguinus fuscicollis	-	-	-	-	3.870	3.910	16.140	0.200	7.780	8.160
Saguinus fuscicollis	-	-	23.550	-	4.050	3.300	23.550	-	7.350	16.200
Saguinus midas	-	-	3.413	0.600	-	-	-	4.600	2.500	0.000
Saguinus midas	-	-	6.825	0.600	-	-	7.130	4.200	3.200	0.000
Saguinus oedipus	-	-	-	-	-	-	1.870	-	-	-
Saimiri boliviensis	-	-	-	-	-	-	-	-	-	-
Saimiri sciureus	-	-	-	-	-	-	-	-	-	-
Saimiri sciureus	100.000	0.000	-	-	-	-	-	-	-	-
Saimiri sciureus	-	-	-	-	-	9.000	-	-	-	-
Theropithecus gelada	-	-	-	-	-	-	11.167	-	-	-

Species	Play by infants %	Play by juv-eniles %	Play by adoles cents %	Play by sub-adults %	Play by adults %	Play at 3 mo %	Play at 6 mo %	Play at 9 mo %	Play at 12-14 mo %	Play at 18 mo %	Play at 24 mo %	Play at 30 mo %	Play at 36 mo %
Alouatta palliata	14.533	-	-	-	-	6.250	4.500	36.000	27.428	-	-	-	-
Alouatta palliata	-	2.083	-	-	-	-	-	-	-	-	-	-	-
Ateles geoffroyi	-	-	-	-	-	-	-	-	-	-	9.000	-	-
Callithrix jacchus	-	12.113	-	10.273	0.193	-	-	-	-	-	-	-	-
Callithrix jacchus	-	-	-	-	-	-	-	-	-	-	-	-	-
Cebus apella	-	-	-	-	-	-	-	-	-	-	-	-	-
Cebus apella	-	-	-	-	-	-	-	-	-	-	-	-	-
Cebus apella	-	43.537	12.866	-	-	-	-	-	-	-	-	-	-
Cercocebus atys	-	-	-	-	-	-	-	-	-	-	-	-	-
Cercopithecus aethiops	-	-	-	-	-	-	-	-	-	-	-	-	-
Cercopithecus aethiops	9.000	-	-	-	-	-	-	-	-	-	-	-	-
Cercopithecus aethiops	-	-	-	-	-	-	-	-	-	-	-	-	-
Cercopithecus aethiops	-	-	-	-	-	-	-	-	-	-	-	-	-
Cercopithecus aethiops	-	-	-	-	-	-	-	-	-	-	-	-	-
Cercopithecus diana	35.100	16.550	-	10.100	0.650	-	-	-	-	-	-	-	-
Cercopithecus diana	-	-	-	-	-	-	-	-	-	-	-	-	-
Cercopithecus diana	-	6.610	-	-	0.300	-	-	-	-	-	-	-	-
Cercopithecus diana	-	-	-	-	-	-	-	-	-	-	-	-	-
Cercopithecus hamlyni	-	-	-	-	-	-	-	-	-	-	-	-	-
Cercopithecus hamlyni	23.500	15.000	-	1.050	0.500	-	-	-	-	-	-	-	-
Cercopithecus mitis	-	4.000	-	-	-	-	-	-	-	-	-	-	-
Cercopithecus neglectus	18.400	7.300	-	1.350	0.030	-	-	-	-	-	-	-	-
Colobus badius	-	-	-	-	-	-	-	-	-	-	-	-	-
Colobus badius	-	-	-	-	-	-	-	-	-	-	-	-	-
Colobus badius	-	-	-	-	-	-	-	-	-	-	-	-	-
Colobus badius	-	-	-	-	-	-	-	-	-	-	-	-	-
Colobus badius rufomitratus	23.100	15.200	-	0.200	0.100	-	-	-	-	-	-	-	-

Species	Play by infants %	Play by juv-eniles %	Play by adoles cents %	Play by sub-adults %	Play by adults %	Play at 3 mo %	Play at 6 mo %	Play at 9 mo %	Play at 12-14 mo %	Play at 18 mo %	Play at 24 mo %	Play at 30 mo %	Play at 36 mo %
Colobus badius tephrosecles	-	-	-	-	-	-	-	-	-	9.000	-	-	-
Colobus badius tephrosecles	-	-	-	-	-	-	-	-	-	-	-	-	-
Colobus badius tephrosecles	0.000	0.000	14.000	0.000	0.000	-	-	-	-	9.000	-	-	-
Erythrocebus patas	-	-	-	1.670	-	-	-	-	27.080	-	-	-	-
Gorilla gorilla berengei	36.800	12.707	-	1.702	0.525	-	-	-	-	-	-	-	-
Gorilla gorilla berengei	-	-	-	-	-	-	-	-	-	-	-	-	-
Gorilla gorilla berengei	-	-	-	-	-	-	-	-	-	-	-	-	-
Gorilla gorilla gorilla	-	-	-	-	-	-	-	-	-	-	-	-	-
Gorilla gorilla gorilla	-	-	-	-	-	-	-	-	-	-	-	-	-
Gorilla gorilla gorilla	-	-	-	-	1.688	-	-	-	-	-	-	-	-
Hylobates lar	7.700	6.050	-	-	1.210	-	-	-	-	-	-	-	-
Hylobates lar	-	-	-	-	-	-	-	-	-	-	-	-	-
Hylobates lar	-	-	-	-	-	-	-	-	-	-	-	-	-
Hylobates syndactylus	-	-	-	-	-	-	-	-	-	-	-	-	-
Hylobates syndactylus	-	36.500	-	-	1.050	-	-	-	-	-	-	-	-
Hylobates syndactylus	-	-	-	-	-	-	-	-	-	-	-	-	9.000
Lemur catta	-	-	-	-	-	-	-	-	-	-	-	-	-
Lemur catta	15.600	0.000	-	-	0.700	-	-	-	-	-	-	-	-
Macaca arctoides	-	-	-	-	-	-	-	-	-	-	-	-	-
Macaca arctoides	-	-	-	-	-	-	-	-	-	-	-	-	-
Macaca arctoides	-	-	-	-	-	-	-	-	-	-	-	-	-
Macaca arctoides	12.500	-	-	-	-	-	27.000	-	23.000	-	-	-	-
Macaca arctoides	-	-	-	-	-	-	-	-	-	-	-	-	-
Macaca arctoides	-	-	-	-	-	-	-	-	-	-	-	-	-
Macaca arctoides	-	-	-	-	-	-	-	-	-	-	-	-	-
Macaca arctoides	2.480	0.040	-	-	-	-	-	-	-	-	-	-	-

Species	Play by infants %	Play by juv-eniles %	Play by adoles cents %	Play by sub-adults %	Play by adults %	Play at 3 mo %	Play at 6 mo %	Play at 9 mo %	Play at 12-14 mo %	Play at 18 mo %	Play at 24 mo %	Play at 30 mo %	Play at 36 mo %
Macaca fuscata	-	9.800	0.400	-	-	-	-	-	-	-	-	-	-
Macaca fuscata	-	21.279	-	-	-	-	-	-	-	-	21.779	-	-
Macaca fuscata	-	23.500	-	-	-	-	-	-	19.750	23.000	45.000	-	-
Macaca fuscata	-	-	-	-	-	-	-	-	-	-	-	-	-
Macaca fuscata	-	-	-	-	-	-	-	-	-	-	-	-	-
Macaca fuscata	-	-	-	-	-	-	-	-	-	-	-	-	-
Macaca fuscata	-	-	-	-	-	-	-	-	-	-	-	-	-
Macaca fuscata	-	-	-	-	-	-	-	-	-	-	-	-	-
Macaca mulatta	-	9.450	-	-	0.550	-	-	-	-	-	-	-	-
Macaca mulatta	-	-	-	-	-	-	-	-	-	-	-	-	-
Macaca mulatta	-	-	-	-	-	-	-	-	-	-	-	-	-
Macaca mulatta	17.850	16.600	3.300	0.900	-	-	-	-	-	-	-	-	-
Macaca mulatta	-	-	-	-	-	-	-	-	-	-	-	-	-
Macaca mulatta	-	-	-	-	-	-	-	-	-	-	-	-	-
Macaca mulatta	12.125	-	-	-	-	-	23.000	-	25.500	-	-	-	-
Macaca nemestrina	-	-	-	-	-	-	-	-	-	-	-	-	-
Macaca nemestrina	-	-	-	-	-	-	-	-	-	-	-	-	-
Macaca nemestrina	-	-	-	-	-	-	-	-	-	-	-	-	-
Macaca nemestrina	-	15.000	-	-	-	-	-	-	-	-	-	-	-
Macaca nigra	-	-	-	-	-	-	-	-	-	-	-	-	-
Macaca nigra	-	25.000	-	4.000	3.125	-	-	-	-	-	-	-	-
Macaca radiata	18.300	51.300	-	-	-	-	-	-	-	-	-	-	-
Macaca radiata	-	-	-	-	-	-	-	-	-	-	-	-	-
Macaca sinica	-	-	-	-	-	-	-	-	-	-	-	-	-
Macaca sylvanus	-	18.900	-	2.700	1.150	-	-	-	-	-	-	-	-
Macaca sylvanus	-	-	-	-	-	-	-	-	-	-	-	-	-
Macaca sylvanus	20.900	-	-	-	-	39.600	-	-	-	-	-	-	-

Species	Play by infants %	Play by juv-eniles %	Play by adoles cents %	Play by sub-adults %	Play by adults %	Play at 3 mo %	Play at 6 mo %	Play at 9 mo %	Play at 12-14 mo %	Play at 18 mo %	Play at 24 mo %	Play at 30 mo %	Play at 36 mo %
Macaca sylvanus	45.600	26.400	9.000	6.900	0.875	-	-	-	-	-	-	-	-
Macaca sylvanus	-	-	-	-	-	-	-	-	-	-	-	-	-
Macaca thibetana	-	-	-	-	-	-	-	-	-	-	-	-	-
Mandrillus sphinx	-	-	-	-	-	-	-	-	-	-	-	-	-
Mandrillus sphinx	37.740	-	-	-	2.550	-	-	-	-	-	-	-	-
Nycticebus coucang	-	-	-	-	-	-	-	-	-	-	-	-	-
Pan troglodytes	-	-	-	-	-	-	-	-	-	-	-	-	-
Pan troglodytes	-	-	-	-	-	-	-	-	-	-	-	-	-
Pan troglodytes	29.260	20.155	6.280	-	-	-	-	-	-	-	-	-	-
Pan troglodytes	-	-	-	-	4.100	-	-	-	-	-	-	-	-
Pan troglodytes	25.711	-	-	-	3.796	-	-	-	-	-	-	-	-
Pan troglodytes	-	-	-	-	-	-	-	-	-	-	-	-	-
Pan troglodytes	-	-	-	-	-	-	-	-	-	-	-	-	-
Pan troglodytes	-	-	-	-	-	-	-	-	-	-	-	-	-
Pan troglodytes	-	-	-	-	-	-	-	-	-	-	-	-	-
Pan troglodytes	-	-	-	-	-	-	-	-	-	-	-	-	-
Pan troglodytes	5.860	-	-	-	-	0.840	-	-	10.950	-	-	-	-
Pan troglodytes	-	-	-	-	3.733	-	-	-	-	-	-	-	-
Pan troglodytes	57.350	50.100	-	-	5.450	-	-	-	-	-	-	-	-
Pan troglodytes	13.930	47.910	28.528	9.630	-	-	-	-	-	-	-	-	-
Pan troglodytes	-	-	-	-	-	-	-	-	-	-	-	-	-
Pan troglodytes	11.000	18.500	7.000	-	2.250	-	-	-	-	-	-	-	-
Papio	-	-	-	-	-	-	-	-	-	-	-	-	-
Papio anubis	-	-	-	-	-	9.500	9.000	9.000	16.000	-	-	-	-
Papio anubis	-	-	-	-	-	-	-	-	-	9.000	-	-	-
Papio anubis	5.742	1.050	0.000	0.000	0.000	-	-	-	-	-	-	-	-
Papio anubis	-	-	0.830	0.830	0.028	-	7.638	8.889	8.330	-	-	-	-

Species	Play by infants %	Play by juveniles %	Play by adolescents %	Play by sub-adults %	Play by adults %	Play at 3 mo %	Play at 6 mo %	Play at 9 mo %	Play at 12-14 mo %	Play at 18 mo %	Play at 24 mo %	Play at 30 mo %	Play at 36 mo %
Papio c. ursinus	29.360	5.000	-	-	-	29.800	43.670	-	-	-	-	-	-
Papio cynocephalus	12.500	-	-	-	-	-	-	-	-	-	-	-	-
Papio cynocephalus/anubis (mixed)	-	-	-	-	-	-	-	-	-	-	-	-	-
Papio hamadryas	-	-	-	-	0.000	-	-	-	-	-	-	-	-
Saguinus fuscicollis	19.565	-	-	2.110	5.410	14.700	11.700	10.700	24.550	-	-	-	-
Saguinus fuscicollis	23.550	-	-	-	-	-	-	-	-	-	-	-	-
Saguinus midas	-	-	-	-	-	-	-	-	-	-	-	-	-
Saguinus midas	14.400	8.300	-	-	1.200	-	-	-	-	-	-	-	-
Saguinus oedipus	-	-	-	-	-	-	-	-	-	-	-	-	-

Species	Mo play appears	Mo at 1st play peak	Mo at 2nd play peak	Males play more? yes 1, no 0	Same sex preference? Yes 1, no 0	Significant age difference? Yes 1	Same age preference?	Vocalisation?y es 1 no 0	Sibling preference? Yes 1 no 0	Relatedness? (1=sig/0=n.s)
Allenopithecus nigroviridis	-	-	-	-	-	-	-	-	-	-
Alouatta caraya	-	-	-	-	-	1	-	-	-	-
Alouatta palliata	2.500	6.500	12.500	1	-	-	-	-	-	-
Alouatta palliata	-	-	-	-	-	1	-	0	-	-
Ateles geoffroyi	-	-	-	2	-	-	-	-	-	-
Cacajao rubicundus	-	-	-	-	-	-	-	-	-	-
Cacajao rubicundus	-	-	-	-	-	-	-	-	-	-
Callicebus moloch	3.750	-	-	-	-	1	-	-	1	1
Callithrix geoffroyi	-	-	-	-	-	-	-	-	-	-
Callithrix jacchus	-	9.000	-	1	-	1	-	-	-	-
Callithrix jacchus	-	-	-	-	-	-	-	1	-	-
Cebus albifrons	-	-	-	-	-	-	-	-	-	-
Cebus apella	-	-	-	-	-	-	-	-	-	-
Cebus apella	-	-	-	-	-	-	-	-	-	-
Cebus apella	-	-	-	0	-	0	-	-	-	-
Cebus capucinus	-	-	-	-	-	-	-	-	-	-
Cebus capucinus	-	-	-	0	-	-	-	-	-	-
Cebus olivaceus	-	-	-	-	-	-	-	-	-	-
Cercocebus atys	-	-	-	-	-	-	-	-	-	-
Cercopithecus aethiops	1.000	-	-	1	1	1	1	-	-	-
Cercopithecus aethiops	1.200	-	-	-	-	-	-	-	-	-
Cercopithecus aethiops	0.250	-	-	1	-	-	-	-	-	-
Cercopithecus aethiops	-	-	-	1	-	0	0	-	1	1
Cercopithecus aethiops	-	-	-	-	-	-	-	-	-	-
Cercopithecus diana	-	-	-	2	1	1	1	-	-	-

Species	Mo play appears	Mo at 1st play peak	Mo at 2nd play peak	Males play more? yes 1, no 0	Same sex preference? Yes 1, no 0	Signif-icant age differ-ence? Yes 1	Same age pref-erence?	Vocal-isation?yes 1 no 0	Sibling pref-erence? Yes 1 no 0	Related-ness? (1=sig/0=n.s)
Cercopithecus diana	-	-	-	-	-	-	-	-	-	-
Cercopithecus diana	-	-	-	-	-	-	-	-	-	-
Cercopithecus diana	-	-	-	-	-	-	-	-	-	-
Cercopithecus hamlyni	-	-	-	1	-	1	-	-	-	-
Cercopithecus hamlyni	-	-	-	-	-	-	-	-	-	-
Cercopithecus mitis	-	-	-	-	-	-	-	-	-	-
Cercopithecus neglectus	-	-	-	-	-	-	-	-	-	-
Colobus badius	3.500	-	-	-	-	-	-	0	-	-
Colobus badius	-	-	-	-	-	-	-	-	-	-
Colobus badius	-	-	-	-	-	-	-	-	-	-
Colobus badius	-	-	-	-	-	-	-	-	-	-
Colobus badius rufomitratus	-	-	-	-	-	1	-	-	-	-
Colobus badius tephrosecles	-	-	-	-	-	1	-	-	-	-
Colobus badius tephrosecles	-	-	-	-	-	1	-	-	-	-
Colobus badius tephrosecles	-	-	-	-	-	-	-	-	-	-
Colobus guereza	1.250	-	-	-	-	-	-	0	-	-
Colobus guereza	-	-	-	-	-	-	-	-	-	-
Colobus guereza	-	-	-	-	-	-	-	-	-	-
Colobus guereza	-	-	-	-	-	-	-	-	-	-
Colobus guereza	-	-	-	1	-	1	-	0	-	-
Erythrocebus patas	2.000	8.000	-	1	-	1	-	1	0	-
Gorilla gorilla berengei	-	-	-	-	-	-	-	1	-	-
Gorilla gorilla berengei	-	-	-	-	-	1	-	1	-	-
Gorilla gorilla berengei	-	3.000	14.000	1	-	1	-	-	-	-
Gorilla gorilla gorilla	4.000	12.000	-	-	-	-	-	-	-	-
Gorilla gorilla gorilla	-	-	-	-	1	-	-	-	-	1

Species	Mo play appears	Mo at 1st play peak	Mo at 2nd play peak	Males play more? yes 1, no 0	Same sex preference? Yes 1, no 0	Significant age difference? Yes 1	Same age preference?	Vocalisation?yes 1 no 0	Sibling preference? Yes 1 no 0	Relatedness? (1=sig/0=n.s)
Gorilla gorilla gorilla	-	-	-	-	-	1	-	-	1	1
Hylobates lar	-	-	-	-	-	-	-	-	-	-
Hylobates lar	-	-	-	2	0	-	-	-	-	-
Hylobates lar	-	-	-	1	1	1	-	-	1	1
Hylobates syndactylus	-	-	-	-	-	-	-	-	-	-
Hylobates syndactylus	-	-	-	-	-	-	-	-	-	-
Hylobates syndactylus	9.000	-	-	2	1	1	0	-	1	1
Lemur catta	-	-	-	-	-	-	-	-	-	-
Lemur catta	-	-	-	-	-	-	-	-	-	-
Macaca arctoides	1.000	-	-	1	1	1	1	-	-	-
Macaca arctoides	-	-	-	-	-	-	-	-	-	-
Macaca arctoides	-	-	-	1	-	1	-	-	-	-
Macaca arctoides	-	-	-	-	-	-	-	-	-	-
Macaca arctoides	-	-	-	-	-	-	-	-	-	-
Macaca arctoides	1.000	2.000	-	1	-	1	-	-	-	-
Macaca arctoides	-	-	-	-	-	-	-	-	-	-
Macaca arctoides	-	-	-	1	-	1	-	-	-	-
Macaca brunnescens	-	-	-	-	-	-	-	-	9	-
Macaca fascicularis	-	-	-	1	1	-	-	-	-	-
Macaca fascicularis	-	-	-	1	1	1	1	-	1	1
Macaca fuscata	-	23.750	-	1	-	1	-	-	-	-
Macaca fuscata	-	-	-	1	1	1	1	-	1	1
Macaca fuscata	-	-	-	0	-	0	-	-	-	-
Macaca fuscata	-	-	-	1	1	1	1	-	1	-
Macaca fuscata	-	-	-	1	1	1	-	-	-	1
Macaca fuscata	-	-	-	1	1	1	1	-	1	1

Species	Mo play appears	Mo at 1st play peak	Mo at 2nd play peak	Males play more? yes 1, no 0	Same sex preference? Yes 1, no 0	Significant age difference? Yes 1	Same age preference?	Vocalisation? yes 1 no 0	Sibling preference? Yes 1 no 0	Relatedness? (1=sig/0=n.s)
Macaca fuscata	-	-	-	2	-	1	-	-	-	-
Macaca fuscata	-	-	-	1	1	1	1	1	-	-
Macaca mulatta	-	2.000	-	-	-	-	-	-	-	-
Macaca mulatta	-	-	-	1	1	1	1	-	1	1
Macaca mulatta	0.750	-	-	1	-	-	-	-	-	-
Macaca mulatta	-	-	-	-	-	1	-	-	-	-
Macaca mulatta	-	-	-	-	-	-	-	-	-	-
Macaca mulatta	-	-	-	-	-	-	-	-	-	-
Macaca mulatta	1.000	-	-	-	-	-	-	-	-	-
Macaca mulatta	3.000	-	-	-	-	-	-	-	1	1
Macaca nemestrina	-	-	-	1	-	1	-	-	-	-
Macaca nemestrina	-	-	-	-	-	-	-	-	-	-
Macaca nemestrina	-	-	-	-	-	-	-	-	-	-
Macaca nemestrina	-	-	-	-	-	-	1	-	-	-
Macaca nigra	2.000	-	-	1	-	1	-	-	-	-
Macaca nigra	-	-	-	-	-	-	-	-	-	-
Macaca radiata	-	-	-	-	-	-	-	-	-	-
Macaca radiata	-	-	-	-	-	-	-	-	-	-
Macaca silenus	3.000	-	-	1	-	1	-	-	-	-
Macaca sinica	-	-	-	-	-	-	-	-	-	-
Macaca sylvanus	-	-	-	1	1	1	-	-	1	1
Macaca sylvanus	-	-	-	-	-	-	-	-	-	-
Macaca sylvanus	0.750	1.500	-	1	-	1	-	-	-	-
Macaca sylvanus	-	-	-	-	-	-	-	-	-	-

Species	Mo play appears	Mo at 1st play peak	Mo at 2nd play peak	Males play more? yes 1, no 0	Same sex preference? Yes 1, no 0	Significant age difference? Yes 1	Same age preference?	Vocalisation?yes 1 no 0	Sibling preference? Yes 1 no 0	Relatedness? (1=sig/0=n.s)
Macaca sylvanus	-	-	-	1	-	1	-	-	-	-
Macaca thibetana	-	-	-	-	-	-	-	-	-	-
Mandrillus sphinx	-	-	-	-	-	-	-	1	-	-
Mandrillus sphinx	-	-	-	-	-	-	-	-	-	-
Nycticebus coucang	-	-	-	1	-	1	-	-	-	-
Pan paniscus	-	-	-	-	-	-	-	-	-	-
Pan paniscus	-	-	-	1	-	1	-	-	-	-
Pan troglodytes	-	-	-	1	-	1	-	-	-	-
Pan troglodytes	-	-	-	-	-	-	-	-	-	-
Pan troglodytes	-	-	-	-	-	1	-	-	-	-
Pan troglodytes	-	-	-	-	-	-	-	-	-	-
Pan troglodytes	-	-	-	-	-	1	-	-	-	-
Pan troglodytes	-	-	-	-	-	-	-	-	1	-
Pan troglodytes	-	-	-	1	-	-	-	-	-	-
Pan troglodytes	-	-	-	1	-	1	-	-	-	0
Pan troglodytes	-	-	-	1	-	1	-	1	-	-
Pan troglodytes	-	-	-	1	1	1	1	1	-	-
Pan troglodytes	-	-	-	-	-	-	-	1	-	-
Pan troglodytes	-	-	-	-	-	1	-	-	-	-
Pan troglodytes	-	-	-	1	1	1	1	-	-	-
Pan troglodytes	1.000	4.000	-	-	-	1	-	0	-	-
Pan troglodytes	-	-	-	1	-	1	-	1	-	-
Pan troglodytes	-	-	-	-	-	-	-	-	-	-
Papio	0.500	4.500	14.000	1	1	1	1	1	-	-
Papio anubis	0.500	6.750	12.750	0	0	1	1	-	1	-
Papio anubis	-	-	-	0	-	-	-	-	-	-

Species	Mo play appears	Mo at 1st play peak	Mo at 2nd play peak	Males play more? yes 1, no 0	Same sex preference? Yes 1, no 0	Significant age difference? Yes 1	Same age preference?	Vocalisation?yes 1 no 0	Sibling preference? Yes 1 no 0	Relatedness? (1=sig/0=n.s)
Papio anubis	1.000	3.000	17.000	1	-	1	-	0	-	-
Papio anubis	-	-	-	0	-	0	-	0	-	-
Papio c. ursinus	-	-	-	-	-	-	-	-	-	-
Papio cynocephalus	-	-	-	1	-	-	-	-	-	-
Papio cynocephalus/anubis (mixed)	-	-	-	-	-	-	-	-	-	-
Papio hamadryas	-	-	-	-	-	-	-	-	-	-
Pithecia pithecia	1.000	2.250	-	-	-	1	-	-	-	-
Pithecia pithecia	-	-	-	-	-	1	-	-	-	-
Pithecia pithecia	-	-	-	1	1	1	0	-	-	-
Pongo pygmaeus	-	-	-	-	-	-	-	-	-	-
Presbytis entellus	1.000	2.000	13.000	-	1	1	-	-	1	1
Presbytis entellus	-	-	-	-	-	-	-	-	-	-
Presbytis johnii	-	-	-	-	-	-	-	-	-	-
Presbytis pileatus	-	-	-	1	-	1	-	-	-	-
Pygathrix nemaeus	-	-	-	-	-	-	-	-	-	-
Saguinus fuscicollis	-	-	-	1	-	1	-	1	-	-
Saguinus fuscicollis	-	-	-	-	-	-	-	-	-	-
Saguinus midas	-	-	-	-	-	-	-	1	-	-
Saguinus midas	-	-	-	-	-	-	1	-	-	-
Saguinus oedipus	-	-	-	-	-	-	-	-	-	-
Saimiri sciureus	-	-	-	-	-	-	-	-	-	-
Saimiri sciureus	-	-	-	-	-	1	-	-	-	-
Saimiri sciureus	2.500	6.500	12.500	1	-	-	-	-	-	-
Theropithecus gelada	-	-	-	-	-	1	-	0	-	-

Species	Dyadic play?	Poly-adic play?	Inter-specific play?	Preferred time of day	Dominance significant?	Play-parenting?	Place pref. (0=grnd/ 1=tree	dawn	early a.m	mid-a.m	noon	early p.m
Allenopithecus nigroviridis	-	-	-	-	-	-	-	-	-	-	-	-
Alouatta caraya	1	-	-	-	-	-	-	-	-	-	-	-
Alouatta palliata	-	-	-	-	-	-	-	-	-	-	-	-
Alouatta palliata	1	0	-	-	-	-	-	-	-	-	-	-
Ateles geoffroyi	-	-	-	-	-	-	-	-	-	-	-	-
Cacajao rubicundus	-	-	1	-	-	-	-	-	-	-	-	-
Cacajao rubicundus	-	-	1	-	-	-	-	-	-	-	-	-
Callicebus moloch	-	-	-	-	-	-	-	-	-	-	-	-
Callithrix geoffroyi	-	-	-	-	-	-	-	-	-	-	-	-
Callithrix jacchus	1	-	-	-	-	-	-	-	-	-	-	-
Callithrix jacchus	-	-	-	-	-	-	-	-	-	-	-	-
Cebus albifrons	-	-	-	-	-	-	-	-	-	-	-	-
Cebus apella	-	-	-	5	-	-	-	-	-	14.446	-	-
Cebus apella	-	-	-	-	-	-	-	-	-	-	-	-
Cebus apella	-	-	-	-	-	-	-	-	-	-	-	-
Cebus capucinus	-	-	-	-	-	-	-	-	-	-	-	-
Cebus capucinus	-	-	-	-	-	-	-	-	-	-	-	-
Cebus olivaceus	-	-	-	-	-	-	-	-	-	-	-	-
Cercocebus atys	-	-	-	6	-	-	-	9.000	8.000	7.000	10.000	-
Cercopithecus aethiops	1	0	-	-	0	-	-	-	-	-	-	-
Cercopithecus aethiops	1	-	-	-	-	1	-	-	-	-	-	-
Cercopithecus aethiops	-	-	-	-	-	-	-	-	-	-	-	-
Cercopithecus aethiops	1	1	-	2	0	-	-	-	-	-	-	-
Cercopithecus aethiops	1	1	1	5	-	-	-	-	-	-	-	-
Cercopithecus diana	1	-	-	-	-	1	-	-	-	-	-	-
Cercopithecus diana	-	-	-	-	-	-	-	-	-	-	-	-
Cercopithecus diana	-	-	-	-	-	-	-	-	-	-	-	-
Cercopithecus diana	-	-	-	-	-	-	-	-	-	-	-	-

Species	Dyadic play?	Poly-adic play?	Inter-specific play?	Preferred time of day	Domin-ance signif-icant?	Play-parenting?	Place pref. (o=grnd/ 1=tree	dawn	early a.m	mid-a.m	noon	early p.m
Cercopithecus hamlyni	1	0	-	-	-	-	-	-	-	-	-	-
Cercopithecus hamlyni	-	-	1	-	-	-	-	-	-	-	-	-
Cercopithecus mitis	-	-	-	-	-	-	-	-	-	-	-	-
Cercopithecus neglectus	-	-	-	-	-	-	-	-	-	-	-	-
Colobus badius	1	-	1	-	-	-	1	-	-	-	-	-
Colobus badius	-	-	-	-	-	-	-	-	-	-	-	-
Colobus badius	-	-	-	-	-	-	-	-	-	-	-	-
Colobus badius	-	-	-	-	-	-	-	-	-	-	-	-
Colobus badius rufomitratus	-	-	-	-	-	-	-	-	-	-	-	-
Colobus badius tephrosecles	-	-	-	-	-	-	-	-	-	-	-	-
Colobus badius tephrosecles	-	-	-	-	-	-	-	-	-	-	-	-
Colobus badius tephrosecles	-	-	-	-	1	-	-	-	-	-	-	-
Colobus guereza	1	-	-	-	-	-	-	-	-	-	-	-
Colobus guereza	-	-	-	-	-	-	-	-	-	-	-	-
Colobus guereza	-	-	-	-	-	-	-	-	-	-	-	-
Colobus guereza	1	1	1	2	-	-	-	-	-	-	-	-
Colobus guereza	-	1	-	-	-	-	-	-	-	-	-	-
Erythrocebus patas	1	1	-	-	-	-	-	-	-	-	-	-
Gorilla gorilla berengei	-	-	-	-	-	-	-	-	-	-	-	-
Gorilla gorilla berengei	1	1	-	3	-	-	0	-	-	-	-	-
Gorilla gorilla berengei	-	-	-	-	-	-	-	-	-	-	-	-
Gorilla gorilla gorilla	-	-	-	-	-	-	-	-	-	-	-	-
Gorilla gorilla gorilla	1	0	-	-	-	-	-	-	-	-	-	-
Gorilla gorilla gorilla	1	-	-	-	-	-	-	-	-	-	-	-
Hylobates lar	-	-	0	-	-	-	-	-	-	-	-	-

Species	Dyadic play?	Poly-adic play?	Inter-specific play?	Preferred time of day	Dominance significant?	Play-parenting?	Place pref. (o=grnd/ 1=tree	dawn	early a.m	mid-a.m	noon	-
Hylobates lar	1	0	-	-	-	-	-	-	-	-	-	-
Hylobates lar	1	-	-	-	-	-	-	-	-	-	-	-
Hylobates syndactylus	-	-	-	-	-	-	-	-	-	-	-	-
Hylobates syndactylus	-	-	-	-	-	-	-	-	-	-	-	-
Hylobates syndactylus	1	-	-	-	-	-	-	-	-	-	-	-
Lemur catta	-	-	-	-	-	-	-	-	-	-	-	-
Lemur catta	-	-	-	-	-	-	-	-	-	-	-	-
Macaca arctoides	-	-	-	-	-	-	-	-	-	-	-	-
Macaca arctoides	-	-	-	-	-	-	-	-	-	-	-	-
Macaca arctoides	1	-	-	7	-	-	-	10.000	9.000	11.000	8.000	-
Macaca arctoides	-	-	-	-	-	-	-	-	-	-	-	-
Macaca arctoides	-	-	-	-	-	-	-	-	-	-	-	-
Macaca arctoides	1	-	-	-	-	-	-	-	-	-	-	-
Macaca arctoides	-	-	-	-	-	-	-	-	-	-	-	-
Macaca arctoides	-	-	-	-	-	-	-	-	-	-	-	-
Macaca brunnescens	-	-	-	-	-	-	-	-	-	-	-	-
Macaca fascicularis	1	1	-	-	-	-	-	-	-	-	-	-
Macaca fascicularis	1	1	-	-	1	-	-	-	-	-	-	-
Macaca fuscata	1	-	-	-	-	-	-	-	-	-	-	-
Macaca fuscata	1	1	-	-	-	-	-	-	-	-	-	-
Macaca fuscata	-	-	-	-	-	-	-	-	-	-	-	-
Macaca fuscata	1	1	-	-	1	-	-	-	-	-	-	-
Macaca fuscata	1	-	-	-	1	-	-	-	-	-	-	-
Macaca fuscata	1	1	-	-	1	-	-	-	-	-	-	-
Macaca fuscata	1	-	-	6	-	-	-	5.600	5.400	2.600	4.600	5.900
Macaca fuscata	-	-	-	-	1	-	-	-	-	-	-	-
Macaca mulatta	-	-	-	-	-	-	-	-	-	-	-	-

Species	Dyadic play?	Polyadic play?	Interspecific play?	Preferred time of day	Dominance significant?	Play-parenting?	Place pref. (0=grnd/ 1=tree	dawn	early a.m	mid-a.m	noon	early p.m
Macaca mulatta	1	1	-	-	-	-	-	-	-	-	-	-
Macaca mulatta	-	-	-	-	-	-	-	-	-	-	-	-
Macaca mulatta	-	-	-	-	-	-	-	-	-	-	-	-
Macaca mulatta	-	-	-	-	-	-	-	-	-	-	-	-
Macaca mulatta	-	-	-	-	1	-	-	-	-	-	-	-
Macaca mulatta	-	-	-	-	-	-	-	-	-	-	-	-
Macaca nemestrina	-	-	-	7	-	-	-	8.000	5.000	9.000	6.000	-
Macaca nemestrina	-	-	-	7	-	-	-	9.000	9.000	11.000	4.000	-
Macaca nemestrina	-	-	-	-	-	-	-	-	-	-	-	-
Macaca nemestrina	-	-	-	-	-	-	-	-	-	-	-	-
Macaca nigra	1	1	-	-	-	-	-	-	-	-	-	-
Macaca nigra	-	-	-	-	-	-	-	-	-	-	-	-
Macaca radiata	-	-	-	-	-	-	-	-	-	-	-	-
Macaca radiata	1	-	1	2	-	-	-	-	4.000	8.500	4.000	3.500
Macaca silenus	-	-	-	-	-	-	-	-	-	-	-	-
Macaca sinica	-	-	-	-	-	-	-	-	-	-	-	-
Macaca sylvanus	1	1	-	-	-	-	0	-	-	-	-	-
Macaca sylvanus	-	-	-	-	-	-	-	-	-	-	-	-
Macaca sylvanus	-	-	-	-	-	-	-	-	-	-	-	-
Macaca sylvanus	-	-	-	-	-	-	-	-	-	-	-	-
Macaca sylvanus	-	-	-	-	-	-	-	-	-	-	-	-
Macaca thibetana	0	0	-	-	-	-	-	-	-	-	-	-
Mandrillus sphinx	-	-	-	-	-	1	-	-	-	-	-	-
Mandrillus sphinx	-	-	-	-	-	-	1	-	-	-	-	-
Nycticebus coucang	-	-	-	-	-	-	-	-	-	-	-	-
Pan paniscus	-	-	1	-	-	-	-	-	-	-	-	-
Pan paniscus	1	1	-	-	-	-	-	-	-	-	-	-
Pan troglodytes	1	1	-	-	-	-	-	-	-	-	-	-

Species	Dyadic play?	Poly-adic play?	Inter-specific play?	Preferred time of day	Dominance significant?	Play-parenting?	Place pref. (0=grnd/ 1=tree	dawn	early a.m	mid-a.m	noon	early p.m
Pan troglodytes	-	-	-	-	-	-	-	-	-	-	-	-
Pan troglodytes	-	-	-	-	-	-	-	-	-	-	-	-
Pan troglodytes	-	-	-	-	-	-	-	-	-	-	-	-
Pan troglodytes	1	-	-	-	1	-	-	-	-	-	-	-
Pan troglodytes	1	1	-	-	-	1	-	-	-	-	-	-
Pan troglodytes	-	-	-	-	-	-	-	-	-	-	-	-
Pan troglodytes	1	-	-	-	1	-	-	-	-	-	-	-
Pan troglodytes	1	1	-	-	-	-	-	-	-	-	-	-
Pan troglodytes	1	1	-	-	-	-	0	-	-	-	-	-
Pan troglodytes	1	1	-	-	-	-	-	-	-	-	-	-
Pan troglodytes	-	-	-	-	-	-	-	-	-	-	-	-
Pan troglodytes	-	-	-	-	-	-	-	-	-	-	-	-
Pan troglodytes	-	-	-	-	-	-	-	-	-	-	-	-
Pan troglodytes	-	-	-	-	-	-	-	-	-	-	-	-
Pan troglodytes	1	-	-	7	-	-	1	-	-	-	-	-
Papio	1	2	-	-	-	-	-	-	-	-	-	-
Papio anubis	-	-	-	-	-	-	-	-	-	-	-	-
Papio anubis	-	-	-	-	-	-	-	-	-	-	-	-
Papio anubis	-	-	-	-	-	-	-	-	-	-	-	-
Papio anubis	1	-	-	-	-	-	-	-	-	-	-	-
Papio c. ursinus	-	-	-	-	-	-	-	-	-	-	-	-
Papio cynocephalus	1	-	-	3	-	-	-	-	-	-	-	-
Papio cynocephalus/anubis (mixed)	-	-	-	-	-	-	-	-	-	-	-	-
Papio hamadryas	-	-	-	-	-	-	-	-	-	-	-	-
Pithecia pithecia	-	-	-	-	-	-	-	-	-	-	-	-
Pithecia pithecia	1	1	-	2	-	-	-	-	-	-	-	-
Pithecia pithecia	-	-	-	-	-	-	-	-	-	-	-	-

Species	Dyadic play?	Poly-adic play?	Inter-specific play?	Preferred time of day	Dominance significant?	Play-parenting?	Place pref. (0=grnd/ 1=tree	dawn	early a.m	mid-a.m	noon	early p.m
Pongo pygmaeus	1	-	-	-	-	-	0	-	-	-	-	-
Presbytis entellus	1	-	-	-	-	-	-	-	-	-	-	-
Presbytis entellus	-	-	-	-	-	1	-	-	-	-	-	-
Presbytis johnii	-	-	-	-	-	-	-	-	-	-	-	-
Presbytis pileatus	1	-	-	-	-	-	-	-	-	-	-	-
Pygathrix nemaeus	-	-	-	-	-	-	-	-	-	-	-	-
Saguinus fuscicollis	1	0	-	-	-	-	-	-	-	-	-	-
Saguinus fuscicollis	-	-	1	-	-	-	-	-	-	-	-	-
Saguinus midas	-	-	-	-	-	-	-	-	-	-	-	-
Saguinus midas	1	-	1	-	-	-	-	-	-	-	-	-
Saguinus oedipus	-	-	-	7	-	-	-	3.000	13.000	8.000	9.000	-
Saimiri sciureus	-	-	-	-	-	-	-	-	-	-	-	-
Saimiri sciureus	1	-	-	-	-	-	-	-	-	-	-	-
Saimiri sciureus	-	-	-	-	-	-	-	-	-	-	-	-
Theropithecus gelada	1	0	-	-	-	-	-	-	-	-	-	-

Appendix E. Carnivore play database

Species	Data type	Source	Captive=o/wild=1	No. in study group	No. observed	Adult play? (yes=1,rare2, noo)	Adult-adult play?	Sex play? (yes=1)	Length of study (mo)	No. of observation hours
Helogale undulata rufula	Paper	Rasa 1984	0	9.000	9.000	-	-	-	3.00	-
Thalarctos maritimus	Paper	Latour 1980	1	-	-	1	1	0	1.00	-
Felis catus	Paper	Martin & Bateson 1985b	0	39.000	28.000	-	-	-	-.00	-
Felis catus	Paper	Hall & Bradshaw 1998	0	9.000	9.000	1	1	0	-.00	-
Felis catus	Paper	Bateson et al. 1990	0	54.000	50.000	-	-	-	-.00	-
Felis catus	Paper	Martin & Bateson 1985a	0	21.000	21.000	1	-	-	-.00	-
Lutra canadensis	Paper	Beckel 1991	0	16.000	16.000	1	1	-	21.00	521.000
Anonyx cinerea	Paper	Pellis 1991	0	12.000	12.000	-	-	-	1.00	-
Phoca vitulina	Paper	Renouf & Lawson 1986	1	-	-	1	-	-	2.50	120.000
Mustela putorius	Paper	Poole 1978	0	36.000	-	-	-	-	-.00	-
Mustela vison	Paper	Poole 1978	0	18.000	-	-	-	-	-.00	-
Crocuta crocuta	Paper	Drea et al. 1996	0	21.000	21.000	-	-	-	-.00	-
Canis latrans	Paper	Bekoff & Wells 1986	1	-	56.000	-	-	-	-.00	-
Canis aureus	Paper	Wilkomm 1990	-	-	-	-	-	-	-.00	-
Thalarctos maritimus	Paper	Grittinger 1997	0	2.000	2.000	1	1	-	19.50	140.000
Acinonyx jubatus	Paper	Caro 1995	1	-	-	0	0	0	45.00	2600.000
Panthera leo	Book	Schaller 1972	-	-	-	-	-	-	-.00	-
Panthera leo	Book	Schaller 1972	-	-	-	-	-	-	-.00	-
Panthera leo	Book	Schaller 1972	-	-	-	-	-	-	-.00	-
Arctocephalus australis	Paper	Harcourt 1991	-	-	-	-	-	-	-.00	-
Arctocephalus australis	Paper	Harcourt 1991	-	-	-	-	-	-	-.00	-

Cerdocyon thous	Paper	Biben 1982	0	-	9.000	-	-	-	6.00	-

Species	**Data type**	**Source**	**Captive= 0/wild=1**	**No. in study group**	**No. observed**	**Adult play? (yes=1,rare2, noo)**	**Adult-adult play?**	**Sex play? (yes=1)**	**Length of study (mo)**	**No. of observation hours**
Speothos venaticus	Paper	Biben 1982	0	-	9.000	-	-	-	6.00	-
Thalarctos maritimus	Paper	Ramsay & Waterman 1999	1	-	18.000	1	1	-	0.75	-
Phoca vitulina	Paper	Wilson 1974	1	-	84.000	-	-	2	3.00	-
Halichoerus grypus	Paper	Wilson 1974	1	-	44.000	-	-	-	3.00	-
Phoca vitulina	Paper	Wilson 1974	0	6.000	6.000	-	-	-	0.75	40.000
Haliochoerus grypus	Paper	Wilson 1974	0	2.000	2.000	-	-	-	0.75	40.000
Ailuropoda melanoleuca	Paper	Wilson & Kleiman 1974	0	-	-	1	1	-	9.00	9.000
Phoca vitulina	Paper	Wilson & Kleiman	0	-	-	1	0	-	1.00	-
Canis familiaris	Paper	Rooney et al. 2000	0	-	-	-	-	-	-.00	-
Ursus americanus	Paper	Henry & Herrero 1974	0	3.000	3.000	-	-	1	1.50	-
Melursus ursinus	Paper	Henry & Herrero 1974	0	-	-	-	-	-	-.00	-
Selenarctos thibetanus	Paper	Henry & Herrero 1974	0	-	-	-	-	-	-.00	-
Thalarctos maritimus	Paper	Henry & Herrero 1974	0	-	-	-	-	-	-.00	-
Ursus arctos	Paper	Henry & Herrero 1974	0	-	-	-	-	-	-.00	-

Species	No. of play behaviours	No. of play interactions	Average length of play bouts	Mean total play %	Mean Solitary play %	Mean Social play %	Mean Object play %	Sig. sex difference? yes 1, females more=2	Same sex preference? yes=1	Sig. age difference? yes=1	Same age preference? yes=1	Vocalisation? yes=1	Adult male play?
Helogale undulata rufula	36.0	78.000	630.000	5.150	-	-	5.150	-	-	-	-	1	-
Thalarctos maritimus	14.0	73.000	221.000	-	-	-	-	-	-	-	-	0	1
Felis catus	4.0	-	-	11.000	-	-	-	-	-	1	-	-	-
Felis catus	11.0	-	-	-	-	-	-	-	-	-	-	-	-
Felis catus	2.0	-	-	14.317	-	10.175	4.140	0	-	-	-	-	-
Felis catus	13.0	-	-	9.100	9.100	-	-	-	-	1	-	2	-
Lutra canadensis	10.0	-	282.000	15.510	-	15.510	-	2	-	-	-	1	-
Anonyx cinerea	-.0	-	-	-	-	-	-	-	-	-	-	-	-
Phoca vitulina	13.0	345.000	16.130	15.700	12.560	0.722	0.000	0	1	0	0	-	-
Mustela putorius	19.0	-	0.907	19.455	0.831	16.000	2.624	-	-	-	-	-	-
Mustela vison	-.0	-	-	-	-	4.000	-	-	-	-	-	-	-
Crocuta crocuta	13.0	-	2.625	-	-	-	-	0	-	-	-	-	-
Canis latrans	-.0	-	-	1.000	-	-	-	-	-	-	-	-	-
Canis aureus	-.0	-	-	-	-	-	-	-	-	-	-	-	-
Thalarctos maritimus	7.0	-	-	9.000	11.000	7.000	-	1	0	-	-	-	1
Acinonyx jubatus	15.0	-	-	3.400	0.347	2.958	0.503	-	-	1	-	-	-
Panthera leo	-.0	-	-	1.500	-	-	-	-	-	-	-	-	-
Panthera leo	-.0	-	-	1.600	-	-	-	-	-	-	-	-	-
Panthera leo	-.0	-	-	6.000	-	-	-	-	-	-	-	-	-
Arctocephalus australis	-.0	-	-	6.100	-	-	-	-	-	-	-	-	-
Cerdocyon thous	18.0	236.000	-	13.500	-	10.000	3.500	-	-	-	-	-	-
Speothos venaticus	9.0	849.000	-	21.375	-	8.750	12.625	-	-	-	-	-	-
Thalarctos maritimus	18.0	-	330.000	-	-	-	-	-	-	-	-	-	1
Phoca vitulina	11.0	-	40.000	-	-	-	-	-	-	-	-	1	-

Species	No. of play behaviours	No. of play interactions	Average length of play bouts	Mean total play %	Mean Solitary play %	Mean Social play %	Mean Object play %	Sig. sex difference? yes 1, females more=2	Same sex preference? yes=1	Sig. age difference? yes=1	Same age preference? yes=1	Vocalisation? yes=1	Adult male play?
Halichoerus grypus	6.0	133.000	-	-	-	-	-	-	-	-	-	1	-
Phoca vitulina	11.0	-	-	5.625	-	5.625	-	1	-	-	-	1	-
Halichoerus grypus	6.0	-	-	1.458	-	1.458	-	0	-	-	-	1	-
Ailuropoda melanoleuca	11.0	95.000	140.000	22.037	-	4.812	17.225	-	-	-	-	-	-
Phoca vitulina	16.0	-	990.000	5.779	-	-	-	-	-	-	-	-	-
Canis familiaris	-.0	-	-	-	-	-	-	-	-	-	-	-	-
Ursus americanus	31.0	508.000	-	10.550	1.477	8.862	-	-	-	-	-	0	-
Melursus ursinus	-.0	-	-	-	-	-	-	-	-	-	-	0	-
Selenarctos thibetanus	-.0	-	-	-	-	-	-	-	-	-	-	0	-
Ursus maritimus	-.0	-	-	-	-	-	-	-	-	-	-	0	-
Ursus arctos	-.0	-	-	-	-	-	-	-	-	-	-	0	-

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