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A comparison of habitat use by the mountain lion (*Puma concolor*) and kodkod (*Oncifelis guigna*) in the southern Neotropics with implications for the assessment of their vulnerability status

by

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This thesis is submitted in
candidature for the degree of

Master of Science

Declaration

The material contained within this thesis has not previously been submitted for a degree at the University of Durham or any other university. The research reported within this thesis has been conducted by the author unless indicated otherwise.

Abstract

This study investigates the population density and habitat utilisation of two felid species in the southern Neotropics, the kodkod *Oncifelis guigna* and the mountain lion *Puma concolor.* Information on habitat utilisation provides an insight into which landscape features or disturbances are likely to influence overall species' distribution and density and is relevant to the identification of key habitats for these predators. A variety of data are discussed including population density, body size, and species resilience in the assessment of the vulnerability status of each species and the likely effect of habitat fragmentation and impoverishment on their populations.

The mountain lion was studied in an area subject to a high level of human activity in a commercial forestry system in Southern Brazil. Density in a 100 km^2 core area was calculated based using track counts and camera-trap methods, resulting in an estimate of 0.06-0.09 and 0.09-0.12 individuals per km^2 respectively, including adults and sub-adults. Home range of one female mountain lion was estimated 75.5 km^2 based on radio-tracking. The diet of the mountain lion was analysed, and a model for calculating standing prey biomass and numbers were derived from it.

The density of kodkod estimated from radio-tracking data was 0.97 individuals per km^2. Mean home ranges of sub-adult males and a juvenile male was 2.2 km^2, and two adult females averaged 2.5 km^2; one adult male had a range size of 4.4 km^2. Kodkods did not seem disturbed by the presence of humans. Circumstantial evidence suggests that small patches of preferred habitat are not utilised if beyond a minimum threshold distance from neighboring patches.

An attempt was made to generate a crude density estimate for mountain lions and kodkods throughout their geographic ranges; and according to which mountain lion population numbers do not differ greatly from kodkods'. However, while both species seem to be adaptable to different habitats within their ranges, they seem to be affected by different pressures which affect their vulnerability status. Kodkods have a restricted geographic range and probably low dispersal capability although their high density in suitable habitats and their adaptability to exist in modified habitats possibly compensates for this. The dispersal capability of mountain lions in the southern Neotropics may be hampered because their populations are far apart due to habitat fragmentation and lack of prey as a result of hunting and persecution. Their ability to disperse through modified landscapes and adapt to changing environments may compensate this disadvantage.

Acknowledgements

Although completely written and analysed by myself this thesis is the culmination of a joint effort, involving different participants at different stages.

In chronological order, the project started with the commitment from the Klabin Paper Company in southern Brazil to support research on mountain lions on the company lands. Several persons were involved at this stage; Ralf Andreas Berndt gave the companies initial support for the project. Paulo Kikuti and other executive directors including Raul M. Speltz approved and supported the project during the course of the study. The Park staff provided help with traps, including Sérgio A. Filipak, and I shared many leisure hours with Alceu B. Mello, Lauredi J. Mello, Donizete L. Bueno, Anastácio T. de Oliveira, and Eliane F. Leite. Nilton L. Venturi kindly provided me with maps of the study area. Eliane F. Young Blood helped with the company's library.

Assistance in data collection was provided by Catherine B.Ryan (Katy), who also assisted with invaluable veterinarian support, and helped draft a final report of the project to the company. Many memorable moments were spent on the trails of the study area. I particularly I recall tracking mountain lions or checking traps accompanied by my very enthusiastic three year old daughter Kimberly.

The UK Foreign Office and the British Council provided me with a Chevening scholarship to study for a Masters degree in Biological Sciences in England. I am particularly grateful to Ann Lipe and Judith Elliot. Their assistance and enthusiasm and support in the UK since the day I arrived were much appreciated.

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My supervisor Dr. Nigel Dunstone encouraged me from the start, and has been always ready to help and participate since my arrival at the University of Durham. He

supervised the research on kodkod and allowed access to field data on kodkod which was collected by Leon Durbin, Ian Wyllie, Rachel Freer, Gerardo A. Jamett, and Sam Rose over the course of four years as part of a Darwin Initiative project.

In Durham I had the pleasure of sharing many working days with colleagues in laboratory 15, including Dr. Stephen G.Willis, Dr. Liam Simms, Natalie Walker, and Dr. Yih-Yia Liao. Dr. Stephen G.Willis helped me with Pythagoras theorem to determine consecutive distances between animal locations.

At Howlands Farm, my home while in Durham, friends helped make my life more enjoyable.

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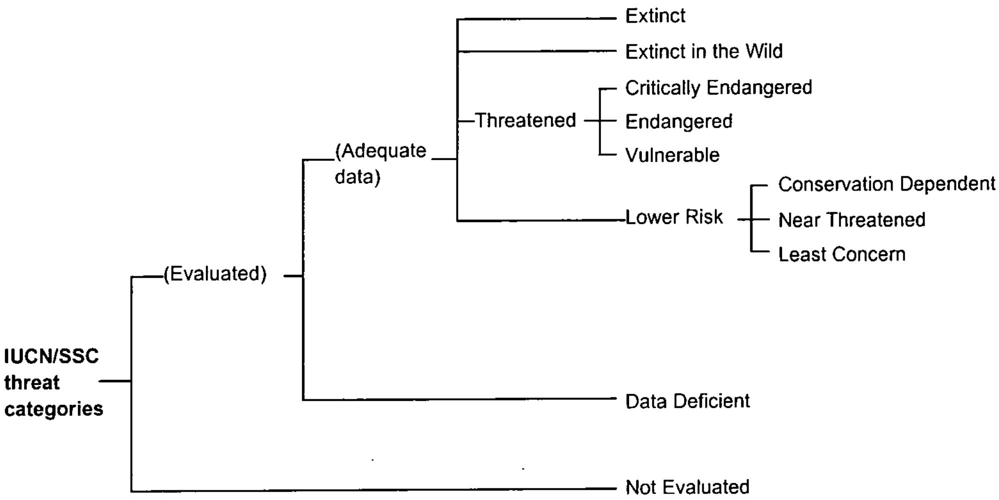
Chapter 1: General Introduction

There are 36 species of wild felids in the world, ranging in weight from 2 kg to over 300 kg, 19 of which are considered at risk in the International Union Conservation of Nature – Species Survival Commission (IUCN/SSC) Status Survey and Conservation Plan (Nowell and Jackson 1996). These authors assessed vulnerability of the various felids by ranking factors such as the number of habitat types the species is found in association with, total (geographic) range, body size and the level of persecution. Other approaches for vulnerability assessment have been developed (e.g. IUCN 1994, Weaver *et al.* 1996) which require biological data such as demographic information, food habits, recruitment, and dispersal. While such an approach aims to deliver a more thorough analysis of a species' vulnerability status, the necessary quantitative data are frequently not available. This lack of information is particularly evident when an attempt is made to compare a wide variety of species (Mace and Balmford 2000).

Weaver *et al.* (1996) considered vulnerability at three hierarchical levels: firstly at the individual level, involving behavioural plasticity in food acquisition; secondly at the population level, concerning demographic compensation; and thirdly at the level of the meta-population mainly concerning dispersal. However, the most widely used system to define a species' vulnerability status is that detailed in the IUCN Red List categorisation (see Figure 1, Mace and Balmford 2000). This system may be applied at species or sub-species level, or within specific areas of the species' range. The geographical approach can either be based on political areas (national and regional), or subspecies range (IUCN 1994). Main categories of vulnerability are *critically endangered, endangered* and *vulnerable*. Species assigned to any of these categories are described as "*threatened*". In order to list a particular taxon within any one category of threat, one of five criteria must be met. Each criterion utilises one or more of a combination of parameters, including overall population size, numeric trend, extent of occurrence (geographic range), population fragmentation, decline of habitat quality, and probability of extinction within specific time-frames based on quantitative analysis (e.g. PVA, Shaffer 1981, 1983, Boyce 1992, Lacy 1993). It is not necessary, however, to utilise PVA stochastic models for management decisions if the population decline is caused by deterministic processes. In these circumstances appropriate management would be to stop the forces leading to decline (Possingham 1996).

Figure 1.1. Threat categories (IUCN 1994)



In 1994, the IUCN (IUCN 1994) stated that *"the category of threat is not necessarily sufficient to determine priorities for conservation action. A system for assessing priorities will include numerous other factors concerning conservation action such as costs, logistics, chances of success, and even perhaps the taxonomic distinctiveness of the subject"*. This is illustrated by alternative approaches for conservation action that are not entirely species-oriented, but ecosystem and/or biodiversity oriented (e.g. Myers 1988, 1991).

MacKinnon (2000) has argued that it is likely that efforts will still continue to be directed towards saving those species which are most highly valued. Entwistle and Dunstone (2000) suggest a conciliatory approach between species-focused and biodiversity-focused conservation actions, and that means should be found to ensure that species-focused conservation programmes also provide as much added value for biodiversity in general.

This study investigates the density and habitat utilisation of two cat species inhabiting the Neotropics, the kodkod *Oncifelis guigna* and the mountain lion *Puma concolor*, and compares the validity and power of different vulnerability factors operating on these species. Habitat loss is the most common threat to mammals (Groombridge 1992, Mace and Balmford 2000). Research on habitat utilisation is intended to give an insight into which landscape features or disturbances are likely to influence overall species' distribution and density, and provide a contribution for management and maintenance of suitable habitats for these predators.

The mountain lion has a variety of popular names. In Brazil it is known as onça-parda, suçuarana, leão, and puma. In North America among other names, it is known as mountain lion, lion, cougar, puma, and in Florida as the Florida Panther. Anderson (1983) suggested that *puma* (a Quechua name originating in Peru) has several advantages over other names. In addition *puma* can be understood in any official language throughout the animal's range. However I shall use the common name *mountain lion* because in my study area it is generally called *leão* (lion) by rural people. As a field researcher I refer to the animals as lion, as is probably the case for colleagues in several areas of North America. Mountain lion is also often used in scientific journals.

The mountain lion and the kodkod differ in a number of ways, the must obvious and fundamental of which is body size. The kodkod rarely weights in excess of 2 kg, whereas the mountain lion varies in weight according to the subspecies, but generally males weight from 55 to 65 kg, and females from 35 to 45 kg (Currier 1983). There are many differences in the behaviour and ecology of the two species that are directly attributable to this difference in size. For example, it is the most important factor determining inter-specific differences in density (Eisenberg 1980, Gittleman and Harvey 1982). Size also determines the size of prey that the two species will be able to feed upon (Emmons 1987, Kitchener 1991). This will itself affect the predator's behaviour and ecology including habitat choice, which will, by necessity, influence the habitat utilisation of the predators at different geographic scales.

In the absence of inter-specific interference, prey availability seems to be the most important parameter determining intra-specific variation of home range size of carnivores (Gittleman and Harvey 1982), and of population density of large felids such as the tiger *Panthera tigris*, mountain lion, leopard *Panthera pardus*, and jaguar *Panthera onca* (Anderson 1983, Hoppe-Dominik 1984, Seindesticker *et al.* 1990, Crawshaw and Quigley 1991, Miquele *et al.* 1999).

In the present study I was able to conduct an intensive investigation of mountain lion food habits based on dietary analysis and prey availability. Similar data for the kodkod are only now becoming available as this species has only recently been studied intensively (Dunstone *et al.* in submission). Hence, information on food habits of the kodkod have been generalised from the literature. In addition to the analysis of habitat utilisation and density, I have attempted to compare the vulnerability status of the two species by discussing parameters such as predator size and prey characteristics.

The status of kodkod to date is said to be *indeterminate* due to lack of adequate data to allow an evaluation under the IUCN Red List criteria. It may be at risk because of its restricted geographical range (Nowell and Jackson 1996). It has been suggested that there has been a population reduction in the north (Nowell and Jackson 1996), but there is no supportive information of a continuous population decline.

The mountain lion is not considered threatened as a species, but the subspecies *P. c. cougar* (eastern USA), and *P.c. coryi* (Florida) are considered vulnerable (IUCN 1976) and status information in the Neotropics is generally lacking (Nowell and Jackson 1996). Bernardes *et al.* (1990) suggests endangered status for mountain lions in Brazil, although, again, there is no quantitative information for evaluation under the IUCN Red List criteria. Populations are likely to be declining in Brazil at an unknown rate due to increasing settlement in frontier areas.

The mountain lion has disappeared from most of eastern North America due to government pest control programs. Nonetheless, their dispersal and population recruitment potential has enabled them to endure severe persecution in some western States. In Arizona, for example, on average 328 mountain lions were hunted annually as a pest for 51 consecutive years (from 1918 to 1969). In this State mountain lions were also hunted from 1971 to 1987 as a game animal at an average rate of 235/year. In British Columbia mountain lions were persecuted as pests for 25 years at a rate of 530/year (from Smith 1989).

At the species level, vulnerability is mainly determined by variations in population density throughout the species range. At this level of resolution, body size, which is the most important factor in determining inter-specific differences in home range size, becomes a minor parameter due to low intra-specific variation. Instead, the availability and utilisation of resources (mainly habitat and prey) along with inter-specific interference (including anthropogenic factors) assumes a major role in determining population density. Population density is a critical factor because it may be correlated with the likelihood of extinction (Eisenberg 1980, Fagan *et al.* 1999).

The current study was conducted on a mountain lion population in southern Brazil and a kodkod population inhabiting southern Chile. Although the ranges of the two species overlap, it was not possible to conduct the investigation in the area of sympatry. Within the Brazilian study area it was possible to investigate the mountain lion's response to human interference within a fragmented landscape of forest plantations and areas influenced by other disturbances. However, in the kodkod study area (Chile), human and animal interference are virtually non-existent. Since the kodkod study site was naturally patchy it provided a pattern similar to that found in disturbed habitats, facilitating investigation of preference/avoidance for various habitats. The evaluation of the utilisation of forest fragments is important in our understanding of the conditions under which the effects of patch size on density are expected to occur (Bender *et al.* 1998).

Density is related to size and intra-specific overlap of home ranges. It is generally found that home ranges of felids *"... vary in time, position and space and may overlap considerably with those of conspecifics"* (Kitchener 1991), but the maintenance of exclusive male ranges is the most commonly observed pattern among solitary felids (Sunquist 1981). It has been shown, however, that the extent of home range overlap for males may even vary between different geographic ranges of the same cat species (e.g. bobcats, Bailey 1974, Lembeck 1986; jaguar, Rabinowitz and Nottingham 1986, Crawshaw and Quigley 1991; mountain lion, Hornocker 1970, Hopkins *et al.* 1986). Home-range size has been shown to correlate with the daily distance travelled by leopards (Hamilton 1976, Norton and Henley 1987). A similar correlation has been found for the brown hyena *Hyaena brunnea*, which has been attributed to the dispersal characteristics of their prey (Mills 1982). If the resource is clumped in distribution, the animal might be able to restrict its movements to a very small area (Krebs and Davies 1984). Home range overlap may thus be facilitated by low mobility of prey, as small transient feeding areas may facilitate avoidance and allow for a relatively dense population (Rabinowitz and Nottingham 1986, Crawshaw and Quigley 1991).

The seasonal movement of mountain lions in North America provides supporting evidence that predator movements are influenced by those of their prey (Rasmussen 1941, Seidensticker *et al.* 1973, Anderson *et al.* 1992).

It is thus reasonable to assume that there are greater chances of intra-specific confrontation and less territorial overlap when cats have to travel longer distances to find adequate prey within their ranges.

In assessing vulnerability it is also important to determine if felids will survive modification of habitats, and whether such changes imply fragmentation of the population or not. There is an increasing likelihood of population extinction with a decrease in the size of habitat fragments and the decreasing probability of recolonisation with increasing isolation (see Braak *et al.* 1998, Wiegand *et al.* 1999). This trend can only be reversed by the provision of additional habitat for cats. The extent of forest plantations, as opposed to natural forests, is increasing globally (Evans 1986), although this does not always imply the destruction of native forests (Mather 1990).

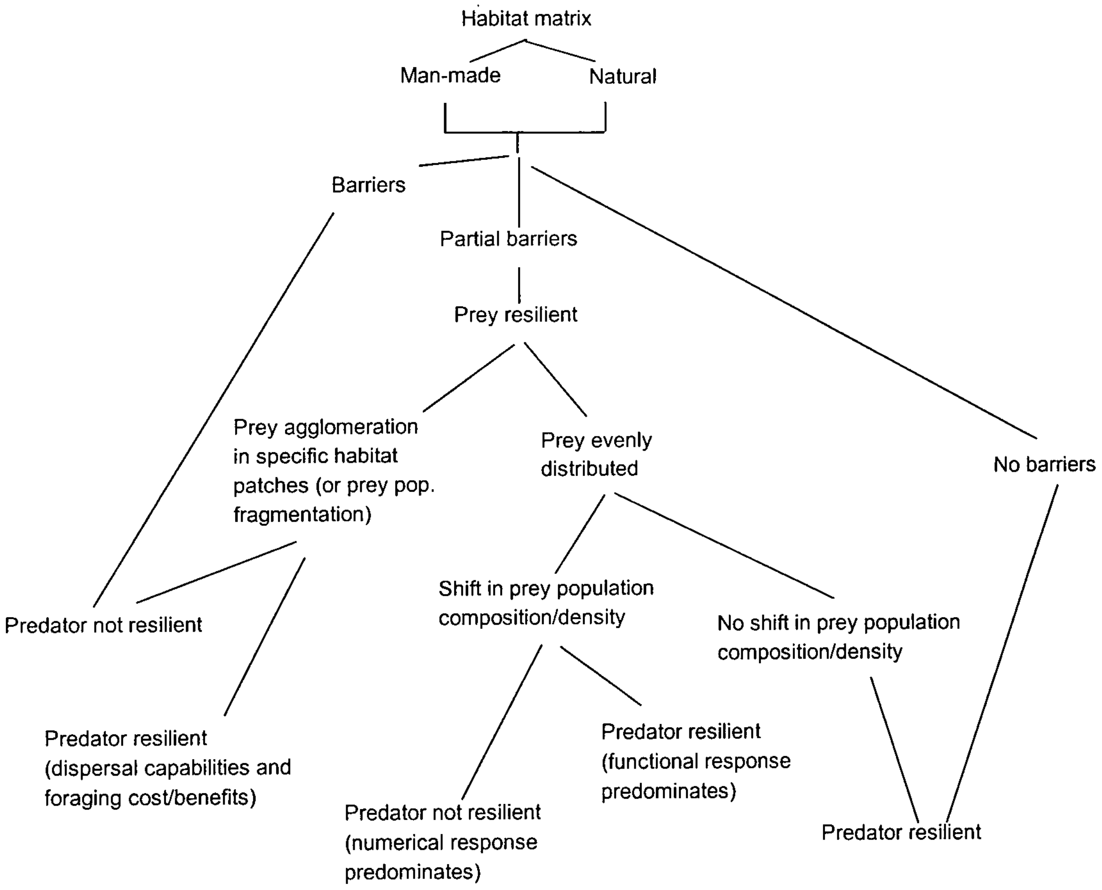
The evidence that felids make use of mono-culture forest plantations is scanty and contradictory and deserves further research (Nowell and Jackson 1996). The vegetation comprising the understory in such forests has, for example, benefited the tiger in teak plantations in India (Nowell and Jackson 1996), and in Nagarahole it supports a higher ungulate biomass than does dry deciduous forests (Karanth and Sunquist 1992). Although forest plantations may lack the diversity of native forests (Sawyer 1993), they are considered to relieve the pressure on natural forest (Sayer *et al.* 1992), and may provide additional habitat for those cat species that are tolerant of disturbance. Other wild cats, including the kodkod, (C.Weber *in litt.* 1993, J.Rottmann pers.comm. in Melquist 1984) and the leopard cat (*Prionailurus bengalensis*) (Harrison 1974, Payne *et al.* 1985), seem to utilise such forests.

It is desirable when assessing habitat tolerance to determine what will be the likely consequences on the density of felids and to investigate how these are influenced by habitat impoverishment compared to that caused by direct human interference. In reality, it is difficult to isolate one factor from the other, since they often operate together. This is because human-induced disturbances in habitats are frequently associated with a decline in the predator's wild prey due to hunting (Schaller 1983, Emmons 1987, Karanth and Sunquist 1992, Peres 1996, Cullen Jr. 2000) or direct persecution (e.g. Norton and Lawson 1985, Rabinowitz 1986, Norton and Henley 1987, Seindesticker *et al.* 1990, Oli *et al.* 1994, Mishra 1997, Franklin *et al.* 1999).

Human-induced landscape disturbances have also lead to habitat fragmentation on a global scale (Whitmore 1997, INPE 1998) which has resulted in fragmentation of the populations of several cat species, including the tiger, mountain lion, jaguar, and Iberian lynx *Felis pardinus* (Ximenez 1972, Seidensticker 1986, Swank and Teer 1987, Rodríguez and Delibes 1992, Beier 1995, Weber and Rabinowitz 1996, Rabinowitz 1999, Wikaramanayake *et al.* 1999; Cullen Jr. *et al.* unpubl. manuscr.) which may lead to population decline as a result of inbreeding depression (Bengtsson 1978, Waser *et al.* 1986), or by reducing the likelihood of recolonisation of habitats where local extinction has occurred (Hemker *et al.* 1984, Olivieri *et al.* 1995).

Fragmentation of habitat, however, does not necessarily relate to population fragmentation. With (1997) argues that connectivity does not need to entail physical linkage between patches, and considers functional connectivity to be more relevant. This depends on the scale at which individuals perceive and interact with landscape structure (Keitt *et al.* 1997). To understand this concept it is necessary to abandon the patch-based, binary view where only suitable and unsuitable habitat exists and where the interactions of individuals within the intervening areas are ignored (Wiens *et al.* 1993, Wiegand *et al.* 1999). Population fragmentation will most probably be related to the degree of disturbance and to the resilience of prey in the intervening areas. For example, a species highly associated with forest such as the jaguar has been recorded to occupy 10 to 100 ha forest fragments near ranches when preying on cattle (Cullen Jr. *et al.* unpubl.manuscr.). However, if the prey are associated with fragmented habitats the predator's dispersal capabilities, distance between habitat patches and foraging efficiency will play a major role in the survival of its population (see Fauchald 1999, Wiegand *et al.* 1999). I present a conceptual model for this approach (see Figure 1.2).

Figure 1.2. Conceptual model illustrating possible outcomes of predator persistence in fragmented patches. The model incorporates the interaction of multiple parameters including prey, foraging cost, and dispersal capabilities



The standard management approach to circumvent the problem caused by the aggregation of prey and the difficulties that the predator may encounter in hunting in several suitable but distant patches (prey accessibility) concerns the maintenance of continuous good quality habitats known as refugia or sources (Fahrig 1988, Pulliam and Danielson 1991). Ideally, such refugia should be physically linked by corridors, but this is not always the case. Under these circumstances the type, size and distribution of refugia needed across the landscape likely will vary according to the degree of disturbance in the intervening habitat matrix and between species (Weaver *et al.* 1996). The absolute size of refugia will vary according to variation in the diversity of prey species and the ratio predator/ prey across a predator's geographical range. Knick (1990) preferred to utilise non-absolute values to measure minimum size of refugia for bobcats (*Felis rufus*). He found that refugia for this species must be sufficiently large to encompass a total of 12-16 continuous territories, of which 3-5 are completely within the refugia. As a general rule, refugia are better habitats when suitable habitat fragments are larger and closer together (Diamond 1975).

Another crucial inter-specific difference between the kodkod and the mountain lion concerns the total geographic range of the species. The distribution of the mountain lion extends beyond South America into Central and North America, from latitudes 50ºN to 50ºS. In fact, the mountain lion has the largest distribution of any American mammal (Currier 1983). The kodkod on the other hand is geographically restricted to Chile and Argentina, a very narrow strip of habitat ranging from latitudes 30º to 50º S and 70º to 75ºW, and encompassing approximately 160,000 km^2 (Nowell and Jackson 1996).

The two species of cats differ also in the amount of research that has been conducted on their behaviour and ecology. While the mountain lion has been the subject of considerable study in North America, the kodkod has received little attention until recently. Although the mountain lion is not considered to be highly threatened as a species (Nowell and Jackson 1996) it is, nevertheless, losing habitat at a fast rate throughout its range. Furthermore, there remain critical gaps in our knowledge of its general ecology (Anderson 1983), particularly with respect to its utilisation of human disturbed landscapes (Nowell and Jackson 1996), and of other factors that influence its population density (Smallwood 1997).

Until recently much of the published information on the kodkod was anecdotal in nature. This lack of fundamental knowledge concerning its biology and the fact that it inhabits such a restricted geographic range is responsible for it being considered at risk relative to other felids (Nowell and Jackson 1996). This study analyses some data on kodkod acquired by field scientists during an extensive study that remains in progress (see Dunstone *et al.* in submission). This investigation provides data on kodkod which can be compared with that I collected on the mountain lion thus allowing a comparison of habitat utilisation and density for the two species.

1.1 Aims

To investigate the population density, habitat utilisation and diet of the mountain lion and kodkod. These data are used to evaluate direct causal effects of these parameters on species' vulnerability. Other intrinsic parameters such as body size and species resilience, and extrinsic parameters such as fragmentation and impoverishment of habitats are also discussed.

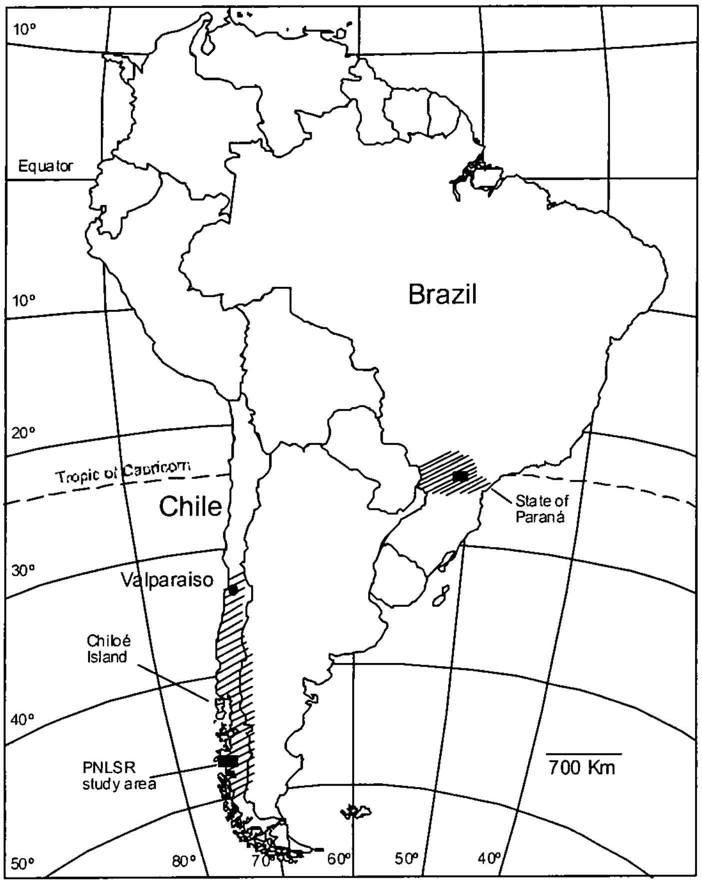
This thesis is divided in two main sections linked by a General Introduction and Discussion. Part one will investigate mountain lion food habits, prey distribution, density, and habitat utilisation (Chapters 3, 4, 5, and 6, respectively), preceded by an introduction to these chapters. Chapter 7 will evaluate habitat utilisation and density of the kodkod. This will serve as the basis for a comparison of the main vulnerability factors operating on the two cat species.

1.2 Overview of the study areas

Despite being separated by 3,200 km, the study area for the kodkod in southern Chile and the mountain lion in southern Brazil are very similar in habitat composition. Similarities exist among many taxa including plants, birds, frogs, butterflies, beetles and Hymenoptera from southern Brazil's highlands "campos de altitude" (also natural grasslands or steppe) and Andean highlands (e.g. Rambo 1951, 1953, Brade 1956, Lynch 1979, Sick 1984, Brown 1987, Haffer 1987, Erwin and Pogue 1988, Willink 1988, Clark 1992). This evidence suggests that they have been connected by corridors a number of times in the past e.g. during the Cenozoic and the Pleistocene (Safford 1999). Cool-temperate Austral-Antarctic tree species (e.g. *Araucaria, Podocarpus*, and possibly *Drymis*) reached eastern and southern Brazil no later than the Miocene (Rambo 1951, Menendez 1969, Beurlen 1970, Landrum 1981, Romero 1986), expanding at higher altitudes when climate gradually became warmer from 5,000 years BP (Ab'Sáber 1977, 1980, Ledru *et al.* 1998, Salgado-Labouriau *et al.* 1998). While the contemporary climate in south-eastern Brazil is the most pluvial for the past 30,000 years (Behling 1998), today the forests of both southern Chile and Argentina are separated from all other forests by more than a thousand kilometers (Pearson and Pearson 1982). The high altitude mountains of Andes and desert surrounding it are responsible for its isolation (Osgood 1943).

Figure 1.3 shows both study areas. More detailed maps including habitat information are provided in the chapters concerning each of the studied species.

Figure 1.3. Location of the study area s in Chile and Brazil. Study areas are black rectangles. Shaded areas in Chile represent the geographical range of the kodkod. Shaded areas in Brazil roughly represent the political boundaries of Paraná State.



Part I: Ecology of the mountain lion

Chapter 2: Introduction and study area

2.1 Overview

The mountain lion has a wide distribution, ranging form northern Canada to southern South America (Currier 1983), varying in size and color according to the area (Young and Goldman 1946, Kurtén 1973, Anderson 1983). This variation is usually recognised in sub-specific status. Although the sub-species of mountain lion in my study area is believed to be *Puma concolor concolor* (Herskovitz 1959), most mountain lion sub-species in South America are yet to be adequately described. Although genetic variation of micro-satellites are currently popular to assign subspecies status (e.g. Culver *et al.* 1997), the validity of molecular or DNA techniques which disregard phenotype and behaviour parameters is controversial (see King and Wilson 1975).

The mountain lion is one of the most studied of the large felids, yet little is known of its life history in the Neotropics. It is considered endangered in Brazil by some (e.g. Bernardes 1990), but the quantitative information required to evaluate its true vulnerability status is not available .

In an era of rapid destruction of natural habitats, researchers are currently trying to identify the factors that define species distribution and abundance. Such knowledge is important in order to predict where target species are most likely to survive in the face of habitat disturbance, and where conservation efforts should be focused. Little is known of the responses of large cats to human interference and their survival in disturbed habitats (Nowell and Jackson 1996). The following chapters aim to improve our current understanding of the biology of the mountain lion, particularly with respect to human interference by investigating its population density, habitat use and prey availability in a commercial forestry system in southern Brazil.

The structure of the mountain lion population was assessed by discriminating individuals on the basis of their tracks and by automatic photography using camera traps. One female mountain lion was radio-collared and monitored to investigate movement parameters and habitat utilisation. Population density estimates were then cross-checked using a theoretical approach which included formulating a model to generate estimates of prey density. The minimum population numbers of prey animals predicted by the model were then compared to field observations and the literature to determine the validity and reliability of the mountain lion density estimate.

2.2 The mountain lion study area

The study was conducted in a private area in southern Brazil. This area is owned by Klabin, a ecologically oriented paper mill company which recently received the Stewardship Forest Council 'green' seal. It encompasses 1,255 km^2, of which 513 km^2 (41 %) are native forests and the remainder comprises planted stands of *Pinus* spp., *Eucalyptus* spp., and *A. angustifolia*. Only the planted forests are harvested, either for timber or cellulose extraction. Non-native stands are harvested at intervals of approximately 7 years during which time there is a substantial growth of underbrush, and a clear fell is carried out in 3rd interval (i.e. after c. 21 years).

The investigation on mountain lion density and movements was carried out within a 100 km^2 area of the 1,255 km^2 private property. The study site included the 'Park', an area containing a high proportion of native forest (60%). Whereas the mountain lion and its prey range throughout the 1,255 km^2 reserve, their densities are likely to vary; hence, a conservative approach was adopted when extrapolating mountain lion population numbers. Prey assessments were done throughout the whole property.

The area is a mosaic of natural vegetation types and is thus classified as "transitional" (IBGE 1992), with patches of natural grasslands (Steppe), Coniferous

(*Araucaria*) Forest (also called Mixed Ombrofilous Forest), and Atlantic Rain Forest (also called Moist Ombrofilous Forest).

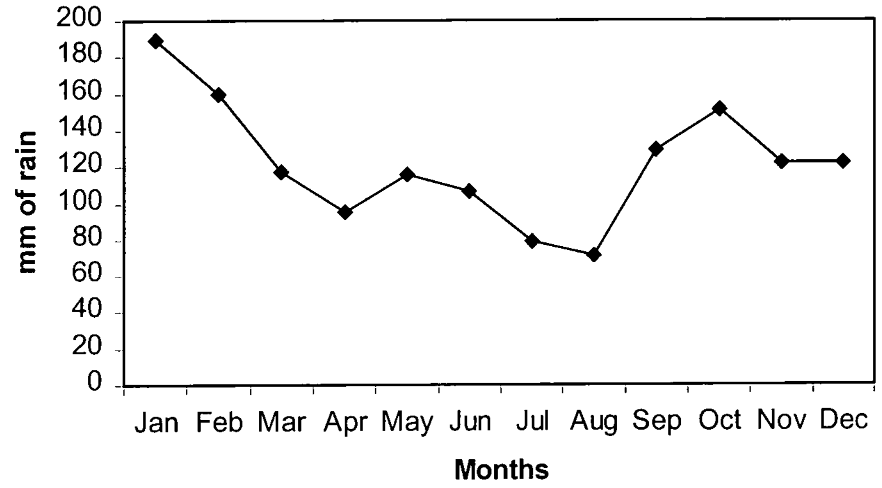
The Atlantic forest is the second most endangered tropical forest in the world (IUCN 1990), and the highest priority for biodiversity conservation in the Americas (CONAMA 1997). About 5-12% of the Atlantic Forest remains (Brown and Brown 1992), and of the *Araucaria* forest only 3% were left in 1978 of which 0.6% were primary forests (IBDF/FUPEF 1978). Deforestation continues with 11% of the remaining Atlantic Forest areas destroyed between 1985 and 1990 (SOS Mata Atlântica and INPE 1993).

The most striking characteristic of the *Araucaria* forest concerns its high density and spread canopy, which gives the forest the appearance of pure stands of *A. angustifolia* when seen from above or from some distance, compared to the variety of "co-dominant" trees found in Atlantic Forest formations. Being transitional, early secondary stands of coniferous natural forests which contain a low density of *A. angustifolia* will have an aspect similar to the Atlantic Rain Forest.

Altitude in the study area varies from 700 to 960m, with temperatures averaging approximately 18°C in the summer (December to March) and 14°C in the winter (June to September). A dry season occurs in winter with precipitation falling to 71 mm/month (Fig. 2.1) interspersed with periods of dry, clear weather lasting for several weeks. Such dry seasons are characteristic of southern and south-eastern Brazilian mountains with drought increasing with both altitude and 'continentallity' (Safford 1999).

Natural forests are allowed to grow along watercourses or in steep valleys. The terrain is well irrigated and generally undulating. Creeks were situated between steep banks, some of which were deep, and provided well watered valleys.

Figure 2.1. Average precipitation in the study area in Brazil during the last 52 years. (source: Klabin).



2.3 Maps

Digitised maps of the study area were provided in ArcView format by the GIS department (ATEC/GIS) at Klabin, and included information on each of the forest covers extant in the area, including the ages of planted parcels and degree of trimming.

The whole property is divided into parcels that range in size from 31 to 97 km^2. Because these parcels vary in forest composition and thus in habitat suitability, percentages of native forest were assessed for each individual parcel. I needed to compare the natural and planted forest ratio across the whole property with that found in my intensive study area. If they did not differ substantially, then I would be able to extrapolate mountain lion densities with greater confidence. If parcels differed from the main site, I would try to verify whether the floristic variation affected prey availability and thus mountain lion density in these parcels. I used the available habitat mapping information along with recorded sightings of mammals to explore the possibility of habitat association for the most important prey species and to predict relative prey availability based on forest composition. The overall goal was to predict habitat suitability for the mountain lion based on prey availability and to provide information that would allow me to extrapolate mountain lion density estimates across the entire property.

2.4 Objectives

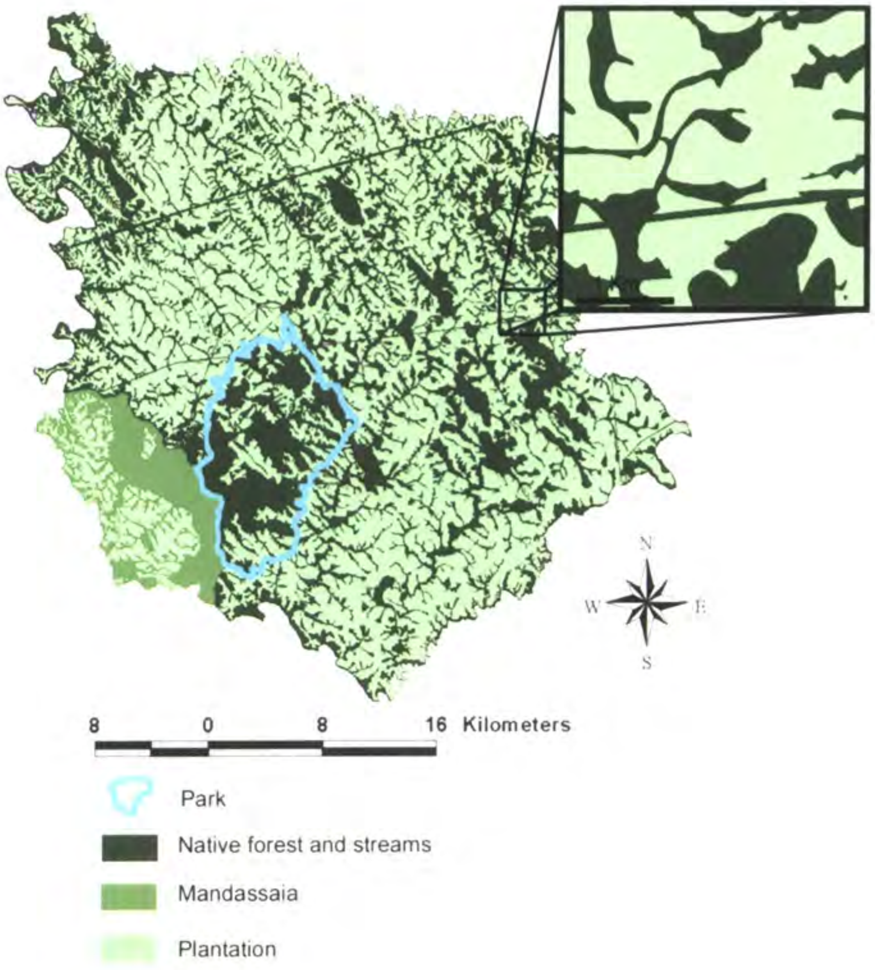
The major hypothesis to be tested concerned whether forest plantations have the same effect as habitat loss, by causing the mountain lion to completely avoid patches that they would otherwise use. Evidence of habitat and patch use derived from a radio-tracked mountain lion was analysed to provide information on preferential use of different forest types at a very fine scale. Beyond that, I aimed to investigate whether movements of this animal were modified by other human landscape changes, such as addition of paved roads, villages, and the presence of people within the felid's home range.

The overall density of mountain lions in this modified habitat will also be used as an indicator of habitat suitability by comparison with that found by other researchers in habitats with lower levels of disturbance.

An indirect method of obtaining habitat preferences involved the analysis of the frequency of occurrence of various prey in the diet. Dietary analysis can provide a useful tool for the investigation of habitat use based on prey habitat preferences.

From the information collected at my intensive study site I attempted to predict the density of mountain lion over the entire area. To do so I compared the ratio of availability of different forest types to their utilisation by mountain lions and their prey. Prey availability estimation was based on sightings across the entire area by company employees. In addition I attempted to evaluate the prey availability in different areas from sightings, the literature and observed habitat associations.

Figure 2.2. Map of the area showing the network of streams and belts of natural forest alongside.



Chapter 3: Food habits and prey density

3.1 Introduction

The mountain lion is known to take a wide range of prey, which varies according to the geographic area and availability. Food habits of mountain lions are well documented in North America, but for Latin America there are few published studies, all of which involve small sample sizes (e.g. Crawshaw and Quigley 1984, Emmons 1987, Aranda and Sánchez-Cordero 1996, Chinchilla 1997). The exception is Chile where a number of detailed investigations have taken place (Iriarte *et al.*1991, Rau *et al.* 1991, Frankin *et al.* 1999).

The purpose of this chapter is to provide an insight into the mountain lion's diet, the biomass consumed, and the density of available prey. This is investigated by identifying which prey species are consumed and how frequently they occur in the diet. These data can then be translated into biomass and number of animals consumed. The minimum stable size of the prey population capable of sustaining harvesting by mountain lions is then estimated.

The daily intake of meat by captive mountain lions varies from 1.6 to 3.6 kg (Hornocker 1970), 2.3 to 5.5 kg (Robinette *et al.* 1959), 4.4 kg (Presnall 1948, Ackerman *et al.* 1986). Hornocker (1970) estimated an annual intake ranging from 860 to 1,300 kg of deer per year assuming that 70 percent of the carcass is consumed. Meat yield from prey animals, including peccaries, deer, and capybara did not exceed 60% in my study area (pers.obs.).

Based on the consumption of a juvenile mountain lion raised in the park (pers. obs.), which was eating 2 kg per day of meat while still immature, and assuming a consumption of 60 percent of the kill, I considered a consumption rate of 3 kg of meat/day for a free ranging adult mountain lion, and an annual intake of 1,800 kg of standing prey.

3.2 Methodology

3.2.1 Collecting and processing scat samples

Mountain lion scats were collected during surveying and radio-tracking operations. The majority of the samples came from systematic collection alongside the railroad which traversed the Park. There was no potential error in identifying mountain lion scats compared to jaguar as the latter did not inhabit the area, and ocelot (*Leopardus pardalis*) scats are usually darker and much smaller. Nevertheless, any scats collected that might have come from this species were excluded from the following analyses.

Following collection scats were left to soak for two days to soften, they were then washed on a sieve with running water to extract the undigested remains, including hair, bones, claws, and hoofs, and dried at 50° C.

3.2.2 Prey identification

A reference collection of hair, bone, scales, hoofs, and claw samples from potential prey species known to inhabit the area was compiled and compared with that found in scats. Hair was sampled from different parts of the body of potential prey, and from both young and adult individuals when available. Most of the identification was carried out with the aid of a microscope at 10x or lower magnification. Hair was identified by comparison to the reference collection. In some occasions claws and bones were also used for species identification. Occasionally it was necessary to take an imprint of the cuticular scale pattern on the external surface of the hair in order to aid identification (Schemnitz 1980, Chehébar and Martín 1989).

The most easily identifiable prey remains were those from collared peccary *Tayassu tajacu*, deer *Mazama gouazoubira*, armadillo *Dasypus novemcinctus*, and porcupine *Coendu prehensilis*. Collared peccary hairs were easy to identify because of the longitudinal striped pattern which was observed under low power magnification and distinguished them from white-lipped peccary *Tayassu pecari* hairs which are black and required the scale patterns to be imprinted to aid identification. The brocket deer and the pampas deer *Ozotocerus bezoarticus* had hairs with similar scale patterns, but the hair of the latter was longer and not found in the samples examined. Scat samples containing armadillo remains were the most easily identifiable, because their claws, scales and hairs are unmistakable. Porcupine remains were also easily identified from their quills or claws, however their hair proved to be more difficult to distinguish from other species. Approximately 12% of all items remained unidentified, believed to be mostly small rodents and birds, which represented minor dietary components.

3.2.3 Estimates of biomass and number of prey consumed

Two basic terms are used to define presence of an item in the diet. The *percentage occurrence of prey*, which is the number of times a specific item was found expressed as a percentage of all the items found; and *frequency of occurrence* expressed as the percentage of total scats in which an item was found. Ackerman's (1984) method for calculating biomass consumed was used to derive a model for estimation of minimum prey densities from prey frequency of occurrence in the diet. Natural history parameters including estimated prey weight, estimated daily weight of prey consumed per mountain lion (here 3 kg/day of meat, or 5 kg/day of standing prey), density of mountain lions/km^2 (set at 0.05/km^2), and prey productivity were added to this model to derive the number of individual prey of the most representative species consumed per km^2. Density of mountain lions was set at a very conservative value relative to the calculated density (see Chapter 5) in order to account to variation in local population densities through time (Hornocker and Bailey 1986, Smallwood 1997) and due to intepretation design (Smallwood and Schonewald 1998).

Total density of prey populations was based on the same conceptual model utilised to manage populations for commercial harvesting or hunting (see Caugley 1977). It was assumed that culling of mountain lions was accomplished in such a way as not to exceed the maximum sustained yield (MSY), a maximum cropping rate that can be taken year after year without forcing the population into decline. Mortality factors of prey populations other than predation by mountain lions were not included in the calculation. This implies that the prey population will only be stable if the rate of increase (r) is greater than the culling rate.

The significance of this theory to my estimates is clear. Frequency of ocurrence prey (Table 3.1) is transformed into number of prey items consumed per year. Mountain lion culling rate never exceeds prey productivity, and is utilised as measure of minimum prey productivity. The culling rate (per year) can be used to calculate total prey numbers from reproductive parameters (Table 3.2). The variables presented in the table were calculated as follows:

a. *Estimated Prey Weight* (EPW kg), this was based on the size of hooves and claws, and the degree of bone ossification of the remains recovered from scats, rather than from average weight of adults from the literature. Errors in the calculation of biomass consumed were reduced utilising this approach since the bulk of the diet was represented by immature prey animals rather than by adults.

b. *Relative Biomass Consumed* (RBC %). This was obtained by multiplying a correction factor (*c.f*). by the frequency f of prey occurrence in the diet and dividing by the sum of multiplication for all prey items:

$$c.f. \times f / \sum c.f. \times f \qquad \textit{(from Ackerman et al. 1984)}$$

The correction factor is intended to compensate for the higher production of collectable scats derived from small prey in relation to prey body weight. It is calculated with the equation

$$Y=1.98+0.035X,\ R=0.77\ (p<0.05)$$

where Y is the weight of prey consumed per scat and X is the prey body weight (kg) (Ackerman *et al.* 1984). It is not applied for prey weighing 2 kg or less, in which case actual prey weight was used in the calculation instead.

c. *Annual Biomass Consumed per mountain lion* (ABC kg). Obtained by multiplying RBC × Annual prey biomass intake of one mountain lion. Annual prey biomass intake for one mountain lion is calculated as follows:

ABC = (3 kg (mean daily meat requirement) × 360 days × 100) percent of meat in carcass)
(assumed here to be 60%)

resulting in an annual intake of 1800 kg of standing prey.

d. *Number of Prey Consumed Annually per mountain lion per km^2* (NPCA):

$$(\text{ABC} / \text{EPW}) \times \text{density of mountain lions/km}^2 \text{ (set as 0.05)}.$$

e. *Female Productivity* (FP). The number of offspring produced per female per year, based on the literature (Nowak 1991, Robinson and Redford 1992).

f. *Total Prey Population Number (parents + offspring per km^2)* (TPPN*).*
Calculated by estimating a minimum threshold adult population number necessary to maintain mountain lion intake. In this I assumed that the entire prey production is culled by the mountain lions (NPCA) and at the end of the year only the minimum breeding adults necessary to produce an equivalent available off-take for the next year remains in the population. Hence, assuming no other source of mortality, NPCA equals the number of offspring produced during the year. Once NPCA is known, the number of adult females needed to produce this quantity of offspring can be calculated by dividing the number of offspring produced per year by female productivity (FP). In order to obtain the total adult population I added the male and female numbers. This is done by multiplying the number of females by two assuming a 50% sex ratio,

$$\text{i.e.,} \quad 2\,(\text{NPCA} / \text{OF}).$$

Once the population of adults has been calculated, I include the number of offspring to give the total population size (TPPN). The formula becomes

$$\text{TPPN} = 2\,(\text{NPCA} / \text{OF}) + \text{NPCA}$$

TPPN cannot be calculated for any given time because of the dynamic nature of population number, which is influenced by natality and mortality.

g. *Average Population Number per km^2(*APN).This was calculated by adding to the number of adults (2(NPCA / OF)) half the number of offspring (NPCA / 2):

$$\text{APN} = 2(\text{NPCA} / \text{OF}) + (\text{NPCA} / 2)$$

This is an arbitrary value halfway between the minimum population of breeding adults and the TPPN.

Because mountain lion predation is not the only source of prey mortality, a higher density than that estimated would be required to maintain stable prey populations.

3.3 Results

A total of 119 scat samples were analysed for prey content and found to contain 18 different prey items, 15 of which were identified to species level; 3 further items were classified to general categories (Table 3.1).

Table 3.1. Occurrence of prey items in mountain lion scats (n=119 scats). Percentage ocurrence of prey (a) represents the number of times a specific item was found expressed as a percentage of all the items found; and frequency of occurrence (b) is the percentage of total scats in which an item was found.

Prey item		Items (n)	Items occur.[a] (%)	Freq. occur.[b] (%)	summer/ spring occur. (%)	autumn/ winter occur. (%)
Artiodactyla						
Collared peccary	*Tayassu tajacu*	20	13.3	16	14.6	12.5
W. lip. Peccary	*Tayassu pecari*	7	4.7	5.6	14.6	8.0
Peccary	*Tayassu* ssp.	4	2.7	3.2	9.8	0.0
Deer	*Mazama gouazoubira*	15	10.0	12	2.4	5.4
Rodents						
Capybara	*Hydrochaeris hydrochaeris*	12	8.0	9.6	12.2	6.3
Prehensile-tailed porcupine	*Coendu prehensilis*	13	8.7	10.4	7.3	8.9
Agouti	*Dasyprocta*	4	2.7	3.2	2.4	2.7
Paca	*Agouti paca*	5	3.3	4	0.0	4.5
Small rodents	*Unidentified*	4				
Edentata						
Nine-banded armadillo	*Dasypus novemcinctus*	40	26.7	32	22.0	27.7
Collared ant-eater	*Tamandua tetradactyla*	4	2.7	3.2	2.4	2.7
Six-banded armadillo	*Euphractus sexcintus*	1	0.7	0.8	0.0	0.9
Giant ant-eater	*Mymercophaga tridactyla*	1	0.7	0.8	0.0	0.9
Lagomorpha						
Brazilian cottontail rabbit	*Sylvilagus brasiliensis*	3	2.0	2.4	2.4	1.8
Carnivora						
Coati	*Nasua nasua*	12	8.0	9.6	0.0	10.7
Small felid	*Felis* spp.	2	1.3	1.6	0.0	1.8
Maned Wolf	*Chrysocyon brachyurus*	1	0.7	0.8	0.0	0.9
Reptiles						
Lizard	*Tupinambis teguixin*	3	2.0	2.4	4.9	0.9
Birds	unidentified	2	1.3	1.6	4.9	0
Totals		150	100	119	100	100

Four prey species represented 61.2% of relative biomass consumed (RBC), including the armadillo (26.7%), the two peccary species (22.7%), and the brocket deer (11.8%). Other species also well represented in the samples were capybara, porcupine and coati, which together represented 24.8% of total biomass consumed (Table 3.2).

A standing biomass estimate of major prey for the study area based on my model would yield roughly 300 kg/km^2. This was calculated by adding the results of the multiplication of the prey population size per km^2 (APN) by their average weights in the wild (e.g. Eisenberg *et al.* 1979, Eisenberg 1980, Nowak 1991, Robson and Redford 1992).

Table 3.2. Model used to calculate % biomass consumed (RCB), number of prey consumed annually per km^2 (NPCA), and major prey population size per km^2 (APN). Abbreviations as in text.

Prey item	EPW [a]	RBC [b]	ABC [c]	NPCA [d]	FP [e]	TPPN [f]	APN [g]
Artiodactyla							
Collared peccary	10	14.7	264.5	1.3	2	2.6	2.0
White lipped peccary	10	5.1	92.6	0.5	2	0.9	0.7
Peccary	10	2.9	52.9	0.3	2	0.5	0.4
Deer	15	11.8	213.2	0.7	1	2.1	1.8
Rodents							
Capybara	6	8.3	149.1	1.2	4	1.9	1.2
Prehensile tailed porcupine	3	8.5	153.8	2.6	1	7.7	6.4
Agouti	3	2.6	47.3	0.8	2	1.6	1.2
Paca	6	3.5	62.1	0.5	2	1.0	0.8
Edentata							
9-banded armadillo	4	26.7	481.3	6.0	4	9.0	6.0
Collared ant-eater	5	2.7	48.9	0.5	1	1.5	1.2
Carnivora							
Coati	4	8.0	144.4	1.8	4	2.7	1.8

3.4 Discussion

In terms of contribution to biomass consumed the order of importance of prey in the diet of the mountain lion are: armadillo, peccaries and gray brocket deer.

Prey densities and biomass in habitats dominated by forests are much lower than in open areas where large herbivores have evolved. Wild herbivore biomass in Nagarahole, India, may reach up to 14,744 kg/km^2 (Karanth and Sunquist 1992), and over 19,000 kg/km^2 in savanna and swamp-savannas of Africa (Eltrigham 1979). In evergreen forests, forest-meadows, and forest-pasture however, herbivore biomass is usually lower than 3,600 kg/km^2 (e.g. Barro Colorado, Eisenberg 1980; Bardia, Dinerstein 1980, Chitwan, Tamang 1982, Pantanal, Schaller 1983; Manu, Terborgh *et al.* 1986; Gabon, Prins and Reitsma 1989).

The high density of mountain lions found in the present study (see chapter 5) suggests a relatively high density of prey animals required to sustain them. The annual off-take of prey by mountain lions was calculated to be 1,800 kg/year. This off-take can be translated into 90 kg prey/km^2 assuming a density of 0.05 moutain lions/km^2 (i.e., 1800 x 0.05=90). The total biomass of the area probably does not have to be necessarily very high because 43% of the biomass comes from prey which are capable of producing up to four offspring per year. On the other hand, in a situation where large cats feed mainly on large ungulates, the off-take may vary between 10 to 20 % standing biomass of the prey population per year (Schaller 1972, Sunquist 1981, Johnsingh 1983). Had this been the case in the present study, and considering a minimum mountain lion population of 0.05/km^2, the standing prey biomass would reach a value between 450 and 900 kg/km^2. A minimum biomass estimated for the study area based on my model would yield roughly 250 kg/km^2. This is a very minimum estimate, as it considers mountain lion predation as the only source of prey population mortality. Increasing the maximum sustained yield (MSY) by including other sources of mortality would require a larger prey population to prevent mountain lion populations from declining. In addition, only major prey items are included in this calculation, the biomass of prey in the study area is considerably higher than the minimum estimated.

For comparison, Schaller (1983) estimated a biomass of 380 kg/km^2 in the Pantanal of Brazil, based on the census data of 64 species of mammals. In his study area, large predators utilised an additional biomass of 3,750 kg/km^2 of livestock.

Densities of armadillos were expected to be high, given their high level of occurrence in the diet. Armadillos contributed some 26.7% of relative biomass consumed (RCB) by mountain lions. Minimum armadillo densities (APPS) derived from scat analysis suggest at least 6 animals per km^2 in order to sustain this level of consumption (ABC 481 kg) per mountain lion (Table 3.2). In the Pantanal, Schaller

(1983) estimated an armadillo density of 1.1 per km^2, and elsewhere they have been found to occur at densities ranging from 4 to 13/km^2 (Wetzel 1982). In the present study armadillo burrows were found mainly in natural forests, particularly on steeper slopes.

The occurrence of collared peccaries in the diet of mountain lions in North America may reach 24% (Cunningham *et al.* 1995) to 47% (Leopold and Krausman 1986), but they have not previously been recorded as a major prey item of mountain lions in Central or South America. In the current study, however, the two species of peccaries together comprised the second most important prey item in terms of biomass contribution, representing 22.7% RCB. Minimum peccary densities (APPS) derived from scat analysis suggest at least 3.1 animals per km^2 in order to sustain an annual biomass consumption (ABC) of 410 kg per mountain lion (Table 3.2).

The collared peccary was consumed almost three times more intensively than the white-lipped peccary. It may be that differences in predation rates between collared and white-lipped peccaries are associated with their respective densities. Signs and sightings of groups of collared peccaries were more frequent than those of white lipped peccaries (see Chapter 4).

Density of collared peccary can be as high as 8.8-11.6 individuals/km^2 (Peres 1996). On Barro Colorado Island where large predators are absent it ranged from 9.0 (Glanz 1982) to 12.4/km^2 (Wright *et al.* 1994). Densities of white-lipped peccaries have been recorded to vary from 1.9 to 6.6 km^2 in the Peruvian Amazon (Bodmer 2000).

In my study area collared peccaries give birth in summer (from November to February) and follow their mothers closely, until they are about 10 kg. After that they still remain in groups, but start to explore their surroundings more freely (pers. obs.) and are thus likely to be more susceptible to mountain lion attacks. Even so, mountain lion will prey on collared peccary throughout the year (Table 3.1).

Gray brocket deer were found singly or as females accompanied by their offspring. Minimum density derived from scat frequency is 0.6 per km^2. By comparison, Schaller (1983) estimated the density of gray brocket deer to be 0.9 individuals per km^2 in the Pantanal based on line transect sampling.

Capybara seem to be preferably taken during spring and summer, when the young are born. Analysis of scat samples confirmed the small size of capybaras consumed. This is supported by a visual record of a 5 kg capybara killed by a mountain lion. The density of capybara estimated in the study area was not very high (1.2/km^2), almost certainly due to the predominance of forested habitats. In open country capybara biomass can vary from 270 kg/km^2 to 6,240 kg/km^2 (Ojasti 1973). With an average weight of 63 kg (Eisenberg and Redford 1999) the biomass in Ojasti's (1973) study would yield a density of 4-99 animals per km^2.

There was no evidence of livestock depredation based on analysis of the scats collected. This is likely to be due to a number of reasons: the core study area is well supplied with wild prey, it is relatively distant from ranching areas, and forestry rather than ranching is the main economic activity in the region. Although no evidence of livestock predation was found in the core study area, it was verified in areas adjacent to the study area beyond the property boundaries. Even though, a low level of livestock predation was recorded despite the relatively high mountain lion densities (Chapter 5). Of the three ranches surveyed during the study which had suffered predation losses, all guarded their herds at night and suffered no further losses. One of these herds was afforded extra protection by the presence of six large mastiff-like dogs.

The "food niche breadth" of mountain lions in Central and South America is less than in North America, where prey species are generally larger (Iriarte *et al.* 1990). Particular prey items frequently represent a larger proportion of the diet in North America compared to Central and South America. For example in North America mule deer *Odocoileus hemionus* comprised up to 61% (Ackerman *et al.* 1984), 85% (Leopold and Krausman 1986), and 77% (Robinette *et al.* 1959) of the diet of mountain lions, while in the Neotropics single prey items found in scats tended to represent no more than 32% of occurrence in the diet (e.g. this study, Leite *et al.* unpubl. manuscr., Rau *et* *al.* 1991, Stallings pers.comm.), with the exception of lagomorphs in Chile (Yáñez *et al.* 1986, Rau *et al.* 1991).

Additionally, the importance of major prey species in the diet in the Neotropics varies regionally, possibly as a result of the wider array of prey choice available. For instance, cattle and capybaras are the most important prey items in the Brazilian Pantanal (Crawshaw and Quigley 1984); agoutis in the rain forests of Peru (Emmons 1987); armadillo in the Brazilian Atlantic forest (this study, Leite *et al.* unpubl. manuscr.) and Paraguayan Chaco (Stallings pers.comm.); and primates, small rodents and deer in Costa Rica (Chinchilla 1997).

A broader choice of prey helps to maintain mountain lion population stability, enabling the predator to shift to alternative prey when one of the major species suffers a significant decline in numbers. Such a functional response to a decline in the prey population has been noted for a number of wild felid species (Rudnay 1974, Beasom and Moore 1977, Bergerud 1983, Leopold and Krausman 1986).

Iriarte *et al.* (1990) hypothesised that interference by jaguar may be a possible cause of mountain lion predation on smaller prey species in South America. There is evidence that when the jaguar population is large, mountain lions tend to be less abundant, such as at Foz do Iguaçú (pers.obs., Crespo 1982), and spatial separation (avoidance) between the two predators has been reported in the Pantanal region (Schaller and Crawshaw 1980). Hunters have suggested that mountain lions follow herds of peccaries (pers.obs.), and this may also apply to jaguars. The constant presence of jaguars near peccary herds could be hampering the predation of mountain lion's on peccaries.

The importance of peccary in the diet of puma where jaguars do not occur, (e.g. current study, Leopold and Krausman 1986, Cunningham *et al.* 1995) supports Iriarte's *et al.* (1990) interference hypothesis. However, intensive studies of mountain lion food habits where they are sympatric with the jaguar are almost non-existent, and predator-prey relationships are well enough understood to allow for a more objective discussion.

Ambient temperature and disturbance caused by day-time human activity may affect prey intake by causing the mountain lion to use the moist, cooler and more secluded natural forested habitat as a refuge. If the mountain lion's search efficiency when hunting in natural habitats is equivalent or superior to that in altered habitats, then species more strongly associated with natural habitats are likely to be taken more frequently. As I demonstrate in the next chapter deer are found to be least associated with natural forest and taken less often than are armadillos and peccaries. However, prey abundance and vulnerability are also major factors determining intake. Coatis are found to be strongly associated with forest and provide a prey type which is equivalent in energetic terms to armadillos but are, nevertheless predated at lower rates. This is possibly due to their arboreal habits which render them less vulnerable to predation by mountain lions.

Chapter 4. Distribution of prey in the study area

4.1 Introduction

Investigation of the mountain lion's diet (Chapter 3) indicated that seven major prey species account for 86 percent of total biomass consumed, including three ungulate species (peccaries and deer), two rodents (capybara and porcupine), one edentate (nine-banded armadillo) and one carnivore (coati). In the absence of inter-specific competition or major landscape disturbances the distribution of predators is typically determined by that of their prey. A consequence of this is that predator density usually increases with increased prey density.

Investigation of mountain lion food habits (Chapter 3) and density (Chapter 5) are derived from sampling almost solely within one of the property sites. In this chapter I investigate whether an equivalent mountain lion density could be sustained throughout the property.

This was determined by examining the pattern of the prey distribution across the entire area by analysing sighting records of prey animals available from the company database. These were accumulated during a supervised program carried out by the company's environmental department involving employees working in the field. The program started in 1990 whereby company employees complete sighting sheets of all animals observed during the course of their routine duties in the forest and elsewhere, including information on location, parcel, habitat type (or forest cover) and the group size of the animals observed. The numbers of animals sighted were compared between areas of differing forest cover and between different areas within the property.

The habitat types available were natural forest, *Pinus* spp. plantations, eucalyptus plantations, *Araucaria* stands, natural field, scrub forest and aquatic systems. For the purposes of statistical analyses these habitat types were divided in four main groups, by including natural field, scrub forest and aquatic systems into the natural forest category because observations in these habitats were few and these habitats were not as well represented. Furthermore, they had not been recorded as distinct features in the companies mapping database, and it was difficult to assess their true availability, since they were also not mapped during this study.

Parcels are divisions within the whole property ranging from 32 to 105 km^2 ($\overline{X}$=65.8 km^2) and are reference units for logging operations (Appendix I). The entire study area (1,255.00 km^2) comprised twenty such parcels and were grouped for comparison into four categories (blocks) according to the percentage of natural forest incorporated, with *Araucaria* stands included as natural forest. Block 1 contained 60-69% of natural forest, block 2 contained 50-59%, block 3 contained 40-49%, and block 4 contained only 20-39% natural forest.

4.2 Assumptions and bias in the data set

The number of observations made in the different forest cover categories is prone to bias because most of the employee's field work is conducted in intensively managed zones, such as *Pinus* and eucalyptus plantations, and therefore almost certainly over-represents observations for these areas, and under-represents those where there is less or no human activity, such as old *Araucaria* plantations (herein referred to as *Araucaria* stands) and natural forests. Preliminary analysis of the data had demonstrated some biases, but since some of the results were pertinent to discussion, these data are included in this chapter.

A number of authors have employed different techniques for censusing wildlife, all invariably introduce sampling errors (Eisenberg and Seidensticker 1976). Estimating animal density based on more common procedures such as line transects and utilising computer programs does not ensure a dataset completely free of bias. They utilise coefficients in mathematical formulas that cannot fully capture the nuances and variations in animal behaviour or of terrain features. Such estimates may not reflect the true density of animals when there are obstacles that impair direct observation (e.g. due to dense vegetation) or when the animal avoids the observer. Estimates based on transects conducted in difficult terrain are referred to as a frequency of animals per plot instead, and its relationship with density is non-linear (Caughley 1977).

Since the forest patches are small and field activities of employees are widespread while carrying out their observations the bias is expected not to be extreme. Records also came also from tractor, truck, and car drivers whose observations are made on what are essentially line transects through several habitats. Another bias expected from sight recordings concerned differential visibility under different forest cover since this might under-represent counts made in closed habitats, particularly of smaller species. In order to cross-check the data collected I compared counts made within particular forest types with that found between blocks.

I found that observations for all the species were much more frequent within block 3. Consequently, this block was removed from the analysis of counts (but not from analyses of mean group size). The removal was necessary because there was concern that the higher number of observations in this block was due to employees reporting more frequently from here rather than as a result of animal abundance.

4.3 Methods

Sighting records of prey were analysed to verify association between different prey species with forest parcels and forest cover. A χ^2 Goodness of Fit analysis was performed to test the association of prey animals with habitats (*Pinus* spp., eucalyptus plantations or natural forest) and blocks. The null hypothesis tested was that the frequency of observations of each main prey species was proportional to the availability of blocks and habitat types. χ^2 analyses were always based on the same number of categories (n=4, thus $d.f$ =3), probability (α=0.10), and critical value (χ^2=6.25) for forest cover comparisons. For block comparisons χ^2 analyses were always based on three categories (n=3, thus df=2). Where the results were significant, forest cover and block preference or avoidance were then tested using individual confidence intervals involving Bonferroni z statistics, and constructed for each theoretical proportion of occurrence, using the formula below from Neu *et al.* (1974):

$$\overline{p}i - z_{(1-\alpha/2k)}\sqrt{\overline{p}i(1-\overline{p}i) \div n} \leq pi \leq \overline{p}i + z_{(1-\alpha/2k)}\sqrt{\overline{p}i(1-\overline{p}i) \div n}$$

Critical values for Bonferroni statistics were the same for most analysis unless otherwise noted, with critical $Z_{(1-\alpha/(2*n))}$ value for forest cover ($Z_{0.9875}$=2.24) and for blocks ($Z_{0.983}$=2.12) (α=0.10). To avoid repetition, only the resulting χ^2 values will be mentioned after each Goodness of Fit test, and in the case of Bonferroni tests only "Bonferroni" will be mentioned. If the proportion of availability of a particular forest cover or block was greater than the confidence intervals derived from Bonferroni statistics, the forest cover or block was considered to be used less than expected, and if proportion of availability of forest cover or block was smaller than the confidence interval, the area was used more than expected.

Gregarious prey animals were analysed both in terms of number (counts) of groups observed for each block or forest cover, and by comparing mean group size. Comparison of mean group size of gregarious animals between habitats and between blocks was tested using one-tailed ANOVA. When significant differences were found, a *post hoc* multiple comparison test was performed to determine which mean group sizes differed from each other. Groups that did not differ in the multiple comparison were then pooled together and a new test of comparison performed to obtain the pooled mean and standard deviation.

The mean group size found in different habitats and blocks was compared as an additional indicator of habitat suitability. Larger herds were expected in more suitable habitats.

4.4 Results

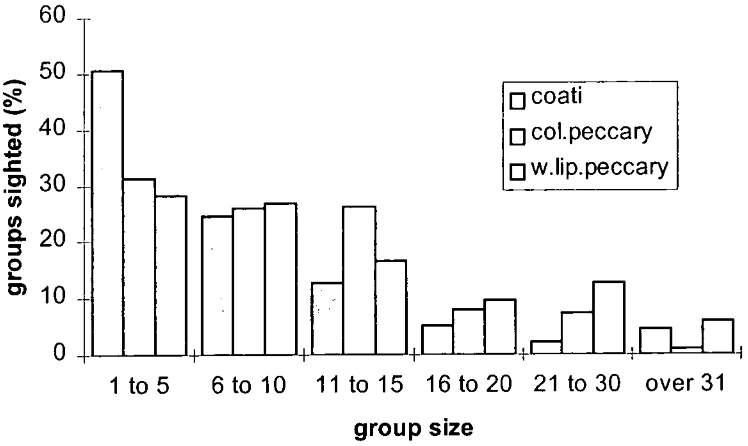
Average group sizes were found to be significantly different for the three species of gregarious prey, the coati ($\overline{X}=8$), the collared peccary ($\overline{X}=9.8$) and the white-lipped peccary ($\overline{X}=12.4$) (Kruskal-Wallis=63.4, *df*=2, $p<0.001$) (Table 4.1).

Table 4.1. Descriptive analysis of group size in gregarious animals found in the property.

Species	number of observations	Mean group size	SD	Min	Max
Coati	385	8.0	9.3	1	78
Collared peccary	541	9.8	7.2	1	36
White-lipped peccary	319	12.4	9.7	1	56

A comparison of frequency distributions of the group sizes of gregarious species indicated that coatis predominated in group sizes ranging from 1 to 5, peccaries in groups from 11 to 15, and white-lipped peccaries in groups of 16 or more (Figure 4.2).

Figure 4.2. Frequency distribution of observations of coati and peccary groups. Data are presented as the percentage of observations for each group class size.



4.4.1 The white-lipped peccary *Tayassu pecari*

A larger mean group size of this species was found in *Araucaria* stands ($\overline{X}=15.8$, SD=12.9) compared to *Pinus* spp. plantations ($\overline{X}=10.5$, SD=9) ($F=3.3$, $df=274$, $p<0.05$), whereas mean group sizes between blocks were significantly greater in block 1 ($\overline{X}=18$, SD=14) compared to the others ($\overline{X}=9.6$, SD=7.2) ($F=18.5$, $df=229$, $p<0.001$) (Table 4.2).

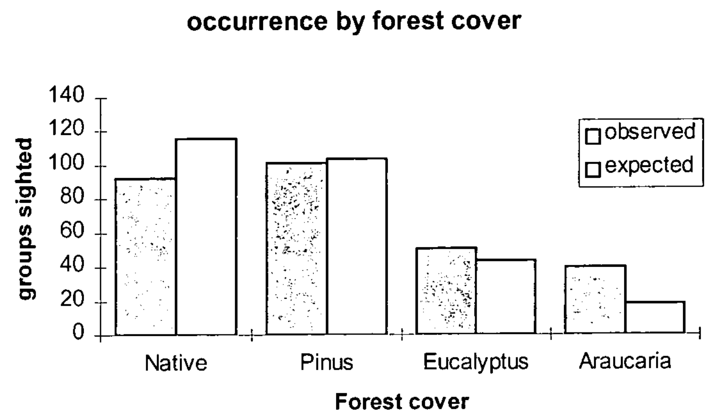
Table 4.2. Mean group size of white-lipped peccaries observed within blocks with different proportion of natural forest.

Block	Count	Mean group size	SD
1	33	18.36	14.06
2	42	8.59	6.17
3	110	10.52	8.12
4	41	8.15	4.90

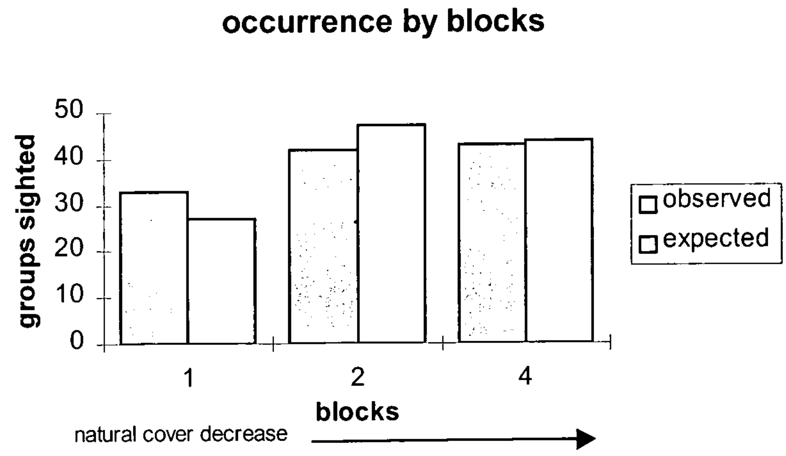
Groups were observed twice as frequently in *Araucaria* stands (n=40) than expected (n=19), somewhat less frequently than expected in native forest, and as expected in eucalyptus and *Pinus* spp. plantations ($\chi^2=30$ and Bonferroni) (Figure 4.3a). In order to demonstrate that this strong preference for *Araucaria* stands was related to *pinion* seed production during autumn and winter, a χ^2 Goodness of Fit test was carried out for each season. Only in summer were observed values similar to those expected ($\chi^2=4.6$), and *Araucaria* stands were preferred during autumn ($\chi^2=14$, Bonferroni) and winter ($\chi^2=13$, Bonferroni). There number of groups observed in blocks did not differ from expected ($\chi^2=2$) (Figure 4.3b).

4.3. Frequency distribution of observed and expected group counts of white-lipped peccaries by: a) forest cover, b) parcels grouped in blocks according to percentage of native forest, which decreases from block 1 (60-70%) to block 4 (20-40%).

a)



b)

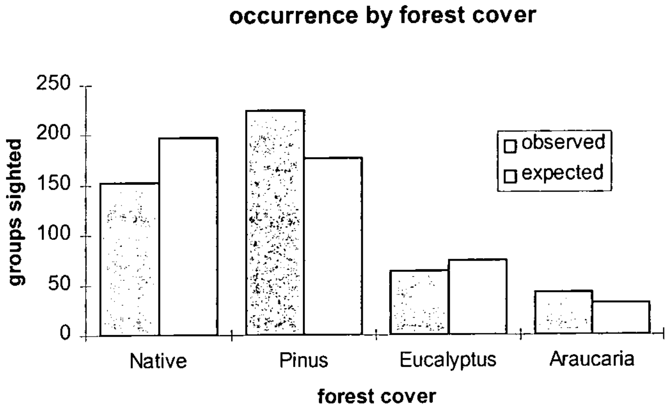


4.4.2 The collared peccary *Tayassu tayassu*

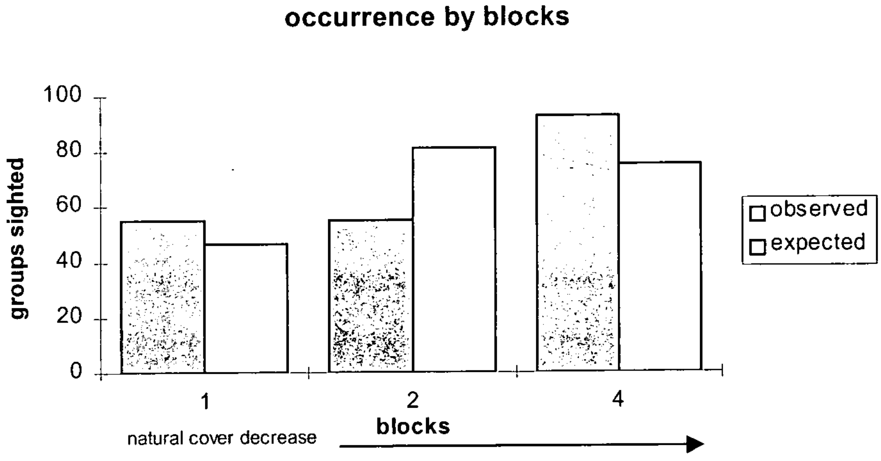
In this species mean group size did not differ between the various extents of forest cover (*F*=0.9, *df*=481, *p*>0.05), nor among blocks (*F*=1.9, *df*=404, *p*>0.05). The number of groups observed was less than expected in native and eucalyptus forests, and more than expected in *Pinus* spp. (χ^2=28, Bonferroni) (Figure 4.4a). All seasonal observations differed from those expected, except in spring (χ^2=4.2). *Araucaria* stands were frequented more often during autumn (χ^2=22, Bonferroni). The number of observations made in blocks differed from expected (χ^2=32), groups were observed more frequently than expected in block 4, and less than expected in block 2 (Bonferroni) (Figure 4.4b).

Figure 4.4. Frequency distribution of observed and expected group counts of collared peccaries in relation to: a) forest cover, b) parcels grouped in blocks according to percentage of native forest, which decreases from block 1 (60-70%) to block 4 (20-40%).

a)



b)

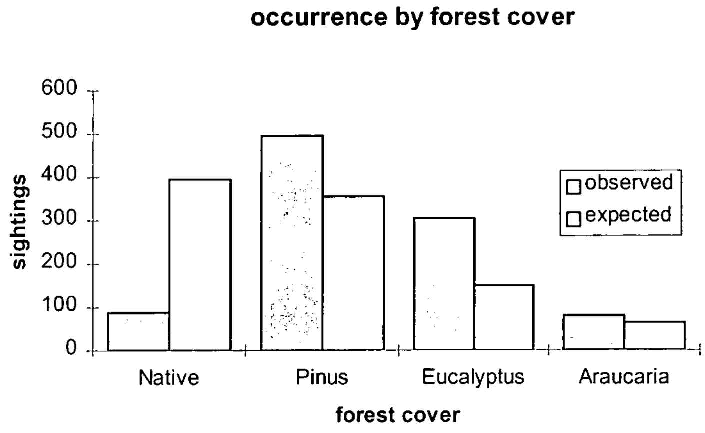


4.4.3 Grey brocket deer *M. gouazoubira*

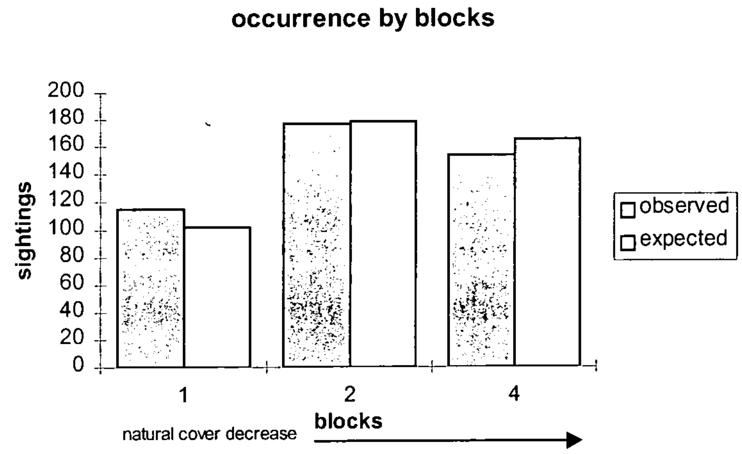
Deer were often sighted on paved and dirt roads, and occasionally killed while attempting to cross paved roads. They were also frequently seen at forest edges. The number of sightings of deer made in the areas of different forest cover did not fit an expected distribution (χ^2=459), with apparent avoidance of native forest, and preference for eucalyptus and *Pinus* spp. (Bonferrroni). In eucalyptus plantations individuals were observed almost twice (n=304) as frequently as expected from the χ^2 distribution (n=153) for this forest cover. Of all the species analysed, deer exhibited the strongest avoidance of natural forest with expected values almost four times (n=402) the observed distribution (n=104) (Figure 4.5a). In addition they were the subject of the highest number of observations made in natural grassland and scrub forest (n=45) from a total of 104 observations classified as native forest. The observed number of sightings per block did not differ from expected distribution of values (χ^2=2) (Figure 4.5b).

Figure 4.5. Frequency distribution of observed and expected counts of deer in relation to: a) forest cover, b) parcels grouped in blocks according to percentage of native forest, which decreases from block 1 (60-70%) to block 4 (20-40%).

a)



b)

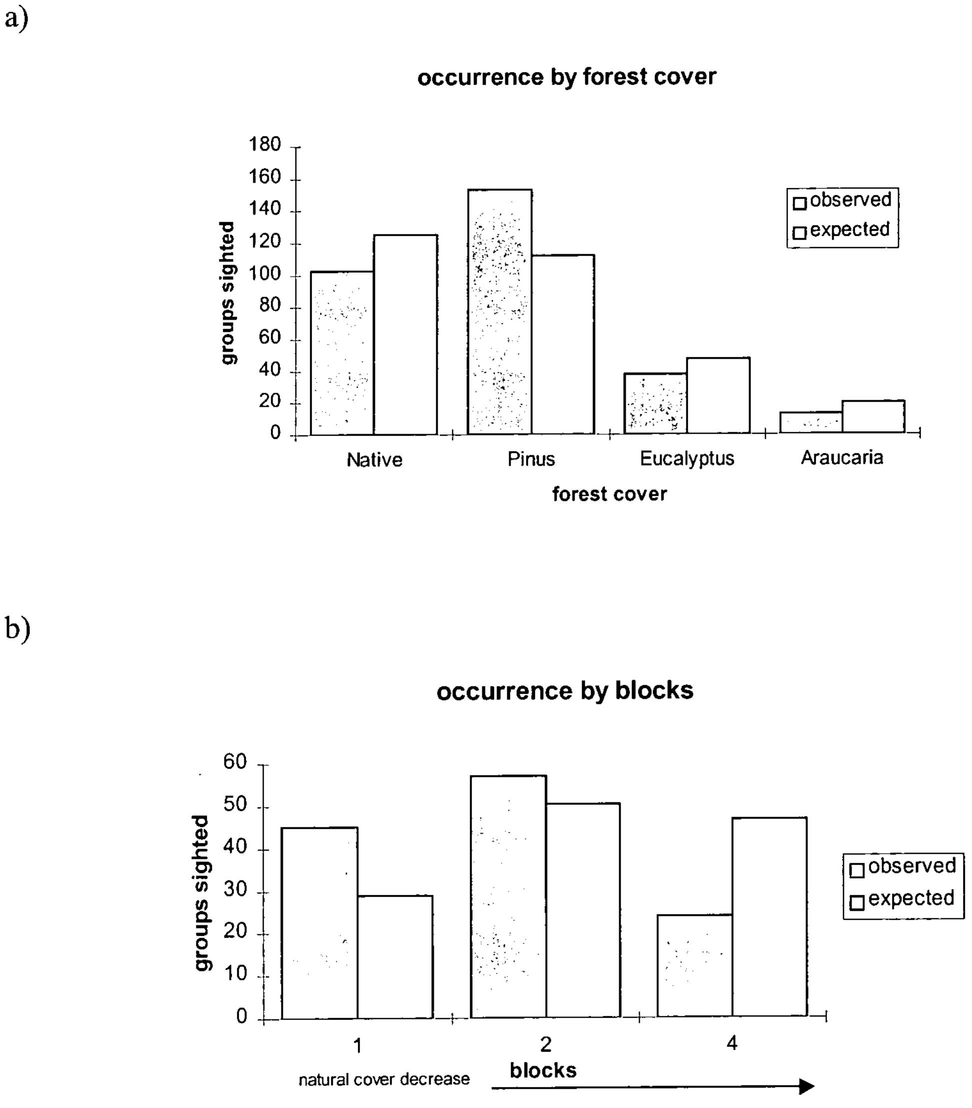


4.4.4 Coati *Nasua nasua*

Groups of coatis were observed more frequently than expected within *Pinus* spp. forest and less than expected within native forest (χ^2=23, Bonferroni) (Figure 4.6a). Coatis are notorious for their commensalism with humans. The company maintained a restaurant for the employees which was frequently visited by groups of coatis that had to be periodically translocated to other areas within the property boundaries, and they also visited household garbage sites within the local villages.

Mean group size of coatis did not vary between areas of different forest cover (*F*=1.8, *df*=481, *p*>0.05), but mean group size in block 3 ($\bar{X}$=10, SD=6.6) was slightly greater than in other blocks ($\bar{X}$=8, SD=7) (*F*=8.1, *df*=406, *p*<0.05). The number of groups observed differed from expected for observations in blocks (χ^2=21). Groups were seen more often at block 1 and less often within block 3 (Bonferroni) (Figure 4.6b).

Figure 4.6. Frequency distribution of observed and expected group counts of coati in relation to: a) forest cover, b) parcels grouped in blocks according to percentage of native forest, which decreases from block 1 (60-70%) to block 4 (20-40%).



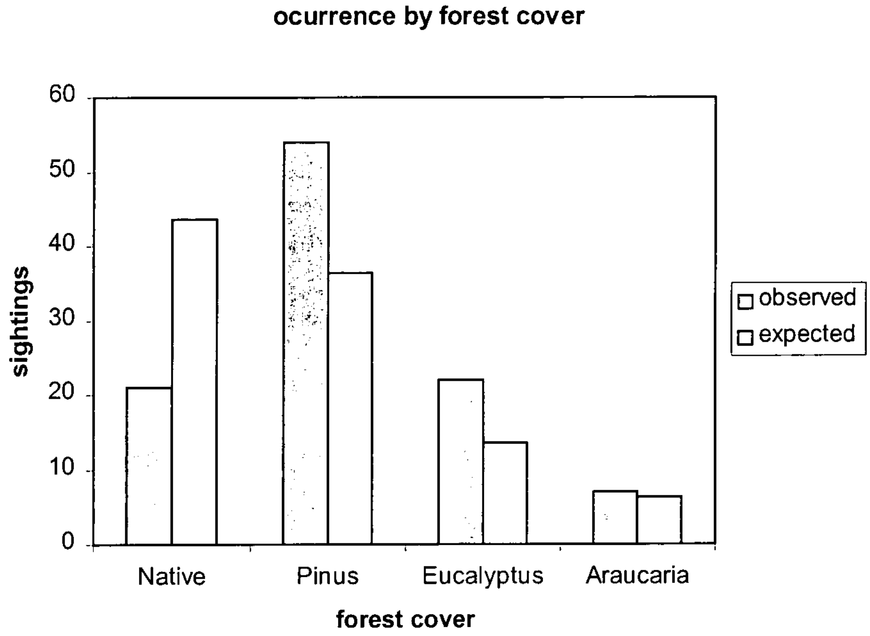
4.4.5 Prehensile-tailed porcupine *Coendu prehensilis*

Because of the low sample size of observations for this species the four original blocks were consolidated into two by combining blocks 1 and 2, and blocks 3 and 4. Expected values of χ^2 did not differ from the observed values of blocks ($\chi^2=0$, *df*=1, n=17) or forest cover ($\chi^2=2$, df=3, n=33), although the sample size (n=36) was too small for any detailed examination.

4.4.6 Nine-banded armadillo *Dasypus novemcinctus*

Armadillos were recorded less frequently than expected in natural forests, more than expected in *Pinus* spp. and eucalyptus plantations, and as expected in *Araucaria* stands (χ^2=25.7, Bonferroni) (Figure 4.7). The sample size for block comparison was too small to be analysed statistically.

Figure 4.7. Frequency distribution of observed and expected armadillo counts by forest cover.



4.4.7 Capybara *Hydochaeries hydrochaeris*

Capybara were recorded on 84 occasions, but parcel location was not mentioned in 41 cases limiting the possibilities for detailed analysis. Capybaras were found in 16 different parcels including Mandaçaia (near the town) and in all four block categories.

Capybara are well know to live near water, hence, not unexpectedly, native forest was the preferred forest cover occupied. They did not occur in association with dense vegetated narrow streams, but were concentrated in areas surrounding lakes (natural or artificial) and alongside the wider watercourses that flowed toward lakes.

Somewhat surprisingly however, 16 records were in *Pinus* spp. and only one from each of *Araucaria* stands and eucalyptus forests.

4.5 Discussion

As previously indicated the presumably non-random nature of data collection by the company's employees was expected to yield some biases, particularly by over-representing observations in intensively managed areas such as are the *Pinus* spp. and eucalyptus plantations. Such biases seem to have arisen since many species show a similar pattern of preference for these forest habitats. Comparison of blocks is intuitively more reliable since these include larger continuous areas comprising several vegetation types. However, all species displayed a pattern of strong preference for block 3 which comprised 40-50% of native forest, this necessitated its removal from the analysis to permit statistical comparison among blocks. A further evaluation applying alternative methodologies would prove useful to verify the validity of the exhibited preference for block 3.

Field signs of foraging activity by peccary were found mainly in native forests or *Araucaria* stands, but there is no doubt that they utilised other forest cover types, even if only for transit. One of the camera-traps photographed a white-lipped peccary within an eucalyptus plantation adjacent to natural forests. The results were cross-checked by analysing information unrelated to spatial analysis. For instance, the frequency distribution of group sizes for the two species of peccary are in accordance with that stated in the literature (e.g. Peres 1996, Fragoso 1999) with white-lipped peccary occurring in larger group sizes.

Fortunately, some results involving spatial relationships can be considered with more confidence, such as the greater than expected number of observations of white-lipped peccary in *Araucaria* stands, even when these areas are infrequently visited by employees, and where they represent a small fraction of the property's entire forests. Collared peccaries were found to prefer *Araucaria* stands during autumn, while white-lipped peccaries were found to prefer them both in autumn and winter. The frequency of observations here seems to be related to the availability of *pinion* seed in autumn and at the beginning of winter. Females were observed with new-born young in the summer, from November to February. Their gestation period is 145 days (Sowls 1966, Smith and Sowls 1975), so their reproductive season matches the abundance of the *Araucaria* seeds as food.

Peccaries were reported in all parcels but one (Mandaçaia), which is not contiguous with the remaining parcels due to a river (c.100 m wide), and is adjacent to the main city. This parcel was eliminated from the block ratings because the town area was not included in the maps used for analysis, so habitat availability could not be calculated.

Collared peccaries seem to be less affected by the availability of native forest cover than are white-lipped peccaries. They have shown a preference for the most disturbed block and were reported more frequently in *Pinus* spp. forests than were white-lipped peccaries, providing evidence of a stronger association of the latter to native forests. Additional evidence relating to habitat preference supports the association of white-lipped peccaries with native cover as shown by their larger mean group sizes found in block 1. The white-lipped peccary was also found less frequently in *Pinus* plantations than other prey species. This differences in habitat association is further supported by the differences found in their geographical distribution, the collared peccary ranging as far north as the semi-arid regions of south-western United States, whereas white-lipped peccaries only range up to southern Mexico (Nowak 1991).

Compared with the more gregarious and conspicuous prey animals (coati, peccaries, and capybara) the distribution of deer seems to be the least closely related to availability of native forest cover. Deer were found more frequently in eucalyptus plantations, but did not differ in their choice of blocks, and were also reported from all parcels including Mandaçaia. Deer were frequently spotted crossing open land between non-native plantations. Medellin and Redford (1992) reported, however, that *M.*

americana is dependent on the forest for their long term survival. Observation of deer near the park area indicated that they come out of the forest to browse in natural grasslands in the early morning and late afternoon, returning to the forest during the day and the night.

Coatis clearly display a higher preference for blocks with more native cover than did any other of the prey species. Coatis are found mainly in wooded areas (Nowak 1991) and forage on fruit as well as invertebrates, although adult males tend to prey on large rodents (Smythe 1970). Porcupine and armadillo were expected to yield even greater biases in forest cover comparisons than other, more conspicuous, prey species that either wander as groups or are larger in size. In this context, sightings in native forest are expected to be greatly under-represented, and possibly unreliable even for inter-species comparison. This is perhaps shown in the very marked avoidance of natural forest cover by armadillos as determined from sighting analysis, although this is unsupported by field observations whereby armadillo burrows were found mainly in native forest. The number of sightings in non-native plantations may be indicative of foraging activities in these areas. Block comparison would be a more appropriate method in this case because, since as mentioned earlier, these do not suffer the same type of bias as do forest cover comparison although such analyses were hampered by small sample sizes. The sample size of prehensile-tailed porcupine sightings was too small to judge presence/absence within blocks, but it was reported from Mandaçaia. There are also too few porcupine records (n=33) to allow for forest cover comparison, except maybe in *Pinus* spp. plantations (n=15). The prehensile-tailed porcupine is known to be mainly nocturnal and arboreal, and to live mainly in forests (Nowak 1991).

In summary, while I found some variations in the distribution of individual prey species within different blocks, and within different forest cover types, it did not suggest the existence of a strongly unbalanced distribution throughout the property, which might, in turn, be reflected in an uneven distribution of mountain lions. This similarity of prey distribution throughout the site may be attributed, in part, to the existence of a natural understory in the non-native forests which can be particularly dense in older stands that have been trimmed once or twice and where the trees are widely separated from each other. Another factor that must also be important in determining prey distribution and abundance is the dense network of streams that irrigate the entire area. No neighbouring streams were further than one kilometre from each other, and all were surrounded by a belt of natural forest. In areas where non-native plantations predominate, prey species such as the collared peccary and the deer are likely to compensate for the reduced availability of species such as white-lipped peccary and coatis.

I chose to discard block 3 from the analysis due to the strong preference exhibited by all species and to allow me to judge utilisation of the remaining blocks with greater precision. If prey species are in fact preferring block 3 it might possibly lead to a higher density of mountain lion in this area; unfortunately this could not be cross-checked.

A more throughout analysis of prey availability adjacent to the main town of Mandaçaia (105 km^2) is warranted although this is separated from the main study area by a wide river. There are records of mountain lion in this area, but the few records of prey animals did not permit me to confidently judge whether this area is as suitable as those that have been considered so far.

Finally, tracks and sightings of prey animals were found to be more frequent in the study area than in parks and reserves elsewhere in southern Brazil, probably because the area receives far more protection than a typical government reserve.

Chapter 5: Density of mountain lions

5.1 Introduction

Investigation of demographic parameters such as population density is fundamental to our understanding of the basic ecological needs of particular species. Few such studies have been attempted on large felids in general or mountain lions in particular in heavily logged or other anthropogenically disturbed areas (Nowell and Jackson 1996). The investigation of large cat population densities at different levels of disturbance is important if we are to predict the likely effects of disturbance prior to such events occuring.

Two main methods of estimating abundance have been used to study the population dynamics of large mammals. *"Open system"* counts are based on methods such as track analysis, faecal counts and sightings. In this method the density of each species is found by counting or estimating the number of individuals occupying an area of known size. *"Closed system"* counts rely on the determination of each animal's home range within a given study area; the sum of the home ranges divided by the number of animals gives the population density.

Open system counts are widely used for assessment of mammalian biomass (Eisenberg and Thorington 1973, Eisenberg 1980, Glanz 1982, Emmons 1984). It is suited to identify ecological relationships between members of the same community, and between areas sampled using the same methodology. However, it should be used with caution when used in comparison with closed system counts because the boundaries for density estimates based on open system counts are usually arbitrarily set. However, the errors are expected to decrease by increasing the area sampled.

Eisenberg and Seidensticker (1976) also emphasised the problem of mixing "ecological" estimates (which they defined as densities achieved by species in appropriate habitat) and "crude" estimates (densities achieved over a wider geographical region). In this chapter the estimated density of mountain lions in the core study area (100 km^2) was extrapolated to the entire 1,255 km^2 property, and is examined in the context of the main finding of Chapter 4 that prey and other resources are equally distributed throughout the property.

In this chapter I investigate the density of mountain lions within a heavily logged area, which still contains a large proportion of natural forest. The density of mountain lions was estimated based on open system methods using tracks and camera traps for discriminating individuals in a 100 km^2 site, the “Park” area where the captive breeding unit and base camp area were located. Tracking has been used mostly as a supplementary technique to estimate activity and density of large felids (e.g. McDougal 1977, Panwar 1979, Schaller and Crawshaw 1980, Rabinowitz 1989, Seindensticker *et al.* 1990, Franklin *et al.* 1999, Smith *et al.* 1999), to detect trends in populations (e.g. Van Dyke *et al.* 1986, Van Sickle and Lindzey 1992, Smallwood 1994, Beier and Cunningham 1996), and also to age and determine the sex ratio of populations (Smirnov and Miquele 1999). Quantitative discrimination of individual mountain lions on the basis of their tracks has previously only been attempted experimentally, when tracks were known to belong to different individuals prior to the analysis. It has been demonstrated that this technique can discriminate individuals with 100% accuracy (Smallwood and Fitzhugh 1993) or may cluster more than one individual in the same group with a 30% likelihood of error (Grigione *et al.* 1999).

The current study is thus among the first to attempt to estimate mountain lion density by track analysis without prior knowledge of the “source” individual. The adequacy of such a density estimate was further evaluated by cross-checking with that obtained by identifying individuals from photographs taken using camera-traps. This technique is also innovative, having been previously applied to evaluate tiger densities in India (Karanth and Nichols 1998). In a critical assessment for detection of four forest carnivores, remote cameras ranked highest in respect to ease of use, effectiveness, and accuracy of identification (Foresman and Pearson 1998). The track discrimination analysis was intended to be fully quantitative, but I had to rely on qualitative analysis in the second half of the study due to small sample size.

5.2 Objectives

The major aim is to provide a population density estimate of mountain lions across the entire property. In addition I investigated the impact of logging and natural forest replacement by non-native forest on the abundance of mountain lions. Because the main study area was restricted to one site, and because not all areas within the whole property had the same proportion of natural and non-native forests as this site, I also investigated whether mountain lions occurred in areas with differing amounts of both types of forest. This would enable me to attempt an extrapolate densities from this site to the whole area.

5.3 Methodology

5.3.1 Camera traps

5.3.1.1 Recording

Three automatically triggered camera systems (Trailmaster, Model TM 1500 Goodson & Associates, Kansas, USA) were used to take photographs of mountain lions as they used the trails. Unlike the "passive" systems which take picture of any moving object that crosses in front the infra-red beams, I used an "active" system in which the height of the beams could be adjusted to take pictures of animals that fell within a particular size range, thus including adults and sub-adults but excluded small juveniles.

The cameras were set in a total of seven different locations during the course of the study; six were within the Park, of which three were located adjacent to the captive breeding area. Photographic records of mountain lions were obtained from five of these sites. One camera was located near the captive breeding centre for the duration of the study, while the others were shifted around mainly within the confines of the Park.

Cameras were set in such a way that would take lateral (Figure 5.2) or frontal-lateral photographs (Figure 5.3) of passing animals. Although frontal-lateral photographs would seem to be useful in distinguishing mountain lions I chose to utilise only lateral photographs, as a comparison based on both types of image was not possible.

Camera traps were set to work mainly at night because of the use of trails and roads by people, and only sporadically were set to function during day-time.

5.3.1.1 Analysis

Since the mountain lion is a plain-coloured animal, error-free quantitative descriptions based on coat patterns to identify particular individuals was not possible. However, a subjective identification of particular individuals was accomplished based on size, colour, marks, shape, and musculature. In some pictures it was possible to identify the sex of the animal. Potential errors in assigning an individual's identity were estimated to be less than 31%, comparable to that based on a track survey conducted by Grigione *et al.* (1999).

A capture-recapture model has recently been proposed for use with camera trap data to estimate tiger densities (Karanth and Nichols 1998). Unlike tigers, mountain lions are not so easily identified on the basis of body markings, and a large number of recaptures at different locations would be necessary to incorporate capture-recapture analysis. The sampling undertaken in the present study was however assumed to be suitable to provide a valuable cross-check on the tracking survey.

5.3.2 Track identification

5.3.2.1 Recording

Well defined tracks (i.e. those with clear contours) were photographed using a camera fitted with either a 35 mm and 300 mm lens, alongside a scale and identifying information. All tracks were photographed in shade to avoid distortion. In the case of poorly defined tracks these were traced onto an acetate sheet.

Care was taken when recording tracks to avoid basic mistakes. For example, during movement the mountain lion usually places the hind foot in front of the fore foot, but occasionally it does the opposite and this can result in track interpretation errors. Also, when recording tracks made on different substrates it is suggested that only the inner outline of deep tracks be recorded due to track spread in deeper soils (Fjelline and Mansfield 1989). Although dogs did not travel the same routes where tracks were recorded, familiarity with differences between dog and mountain lion tracks was acquired prior to field work (see Smallwood and Fitzhugh 1989).

5.3.2.2 Analysis

Analysis of population density of mountain lions based on track sets (defined below) was carried out using a decision matrix (Fitzhugh and Gorenzel 1985), with input derived from both qualitative and quantitative analysis. A *track* is a single paw print (Smallwood and Fitzhugh 1993) and a *track set* is "a line of tracks made continuously by the same mountain lion, as evidenced by physical connection with each other" (Fitzhugh and Gorenzel 1985). Photographed tracks were scanned at 150 dpi resolution, retraced, and scaled to natural size using *Adobe Freehand* (Adobe, San Jose, California) software package. Drawings were overlaid for qualitative comparison in those cases where insufficient data were available for quantitative analysis to be performed. Where sufficient tracks from a set were obtained, nine measurements were taken from each (Figure 5.1).

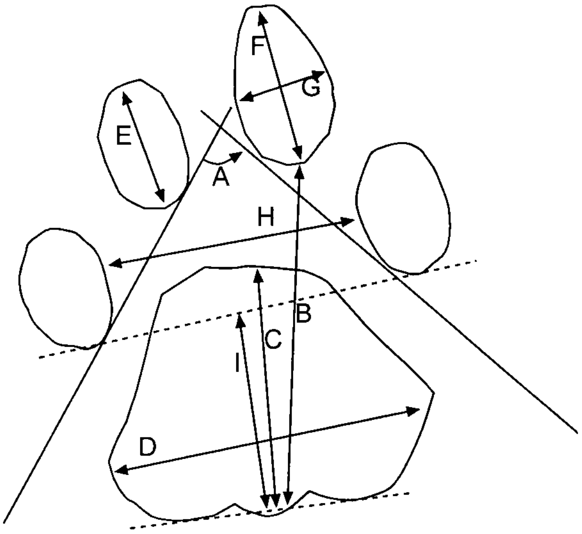
The principle aim of the analysis was to verify how many different individuals produced the recorded tracks. Quantitative differences were verified using Multivariate Discriminant Analysis (also known as Canonical Variation Analysis). The analysis is utilised in those cases when the origin of the populations (or sets) are known (Wiley 1981). Stepwise variable selection was employed to eliminate those variables with little discriminating power, which can destabilise the classification (Williams *et al.* 1990), and to maximise group separation while avoiding high correlation among variables (Smallwood and Fitzhugh 1993).

The analysis was divided temporally in order to avoid cumulative summation of animals during consecutive years, as population fluctuations are likely to occur throughout time. For each temporal period several decision matrices were produced, derived either from quantitative or qualitative analysis, which were then finally combined to produce a matrix including the whole set for that time period.

It is recommended (Smallwood 1993, Grigione *et al.* 1999) that at least three to four different prints of the same paw be measured before discriminant analysis is attempted. It was possible to record sufficient tracks from the first half of the study (March 1998 to July 1999) to perform full quantitative analysis of the four different prints (i.e. left and right hind paws, and left and right front paws). In the second half of the study (from August 1999 to March 2000), however, the number of tracks obtained was insufficient for all track sets, so identification matrices were based mainly on qualitative comparison.

Track measurements of mountain lions were slightly modified after the method of Smallwood and Fitzhugh (1993) (see Figure 5.1), and included the angle between toes (ABT), heel to lead toe length (HLTL), heel length (HL), heel width (HW), third toe length (TTL), lead toe length (LTL), lead toe width (LTW), outer toes spread (OTS), heel to outer toes (HOT).

Figure 5.1. Schematic diagram of the measurements taken of mountain lion tracks, slightly modified after Smallwood and Fitzhugh (1993). A, angle between toes (ABT); B, heel to lead toe length (HLTL); C, heel length (HL); D, heel width (HW); E, third toe length (TTL); F, lead toe length (LTL); G, lead toe width (LTW); H, outer toes spread (OTS); I, heel to outer toes (HOT).



5.4 Results

5.4.1 Camera traps

No photographs of mountain lion were acquired from camera traps in the first few months of the study, even though their tracks indicated that they were crossing within range of the cameras. This was possibly due to the sensitivity at which the system was set, the camera position, or the distance from the camera to the subject. The best results were obtained when the units (transmitter/receiver) were set from 5 to 8 m apart, and the camera unit about 1 to 1.5 m from the ground. However, on some occasions the photograph was not taken even when the animal's tracks indicated that it had actually crossed in front of the camera, as was evident when tracks were apparent but there was no increase in the camera-trap counter. In these cases it was assumed that the mountain lion was probably outside the limit of the infra-red triggering beam.

It is estimated that nine to 13 (31% error) individual mountain lions were photographed from camera traps, including at least two adult males. Adult males were most readily identified because of their larger size, more defined musculature and, in some instances, the scrotum was visible in the photograph (Figure 5.2, 5.3).

Figure 5.2 Lateral photographs of three male mountain lions. The first (collared) is a sub-adult animal, and the juvenile spots are still evident. This individual has a slimmer built than the other two animals photographed, with a somewhat more bushy tail tip. The other two males have distinctive built and coloration, and one shows a scar on the right shoulder.

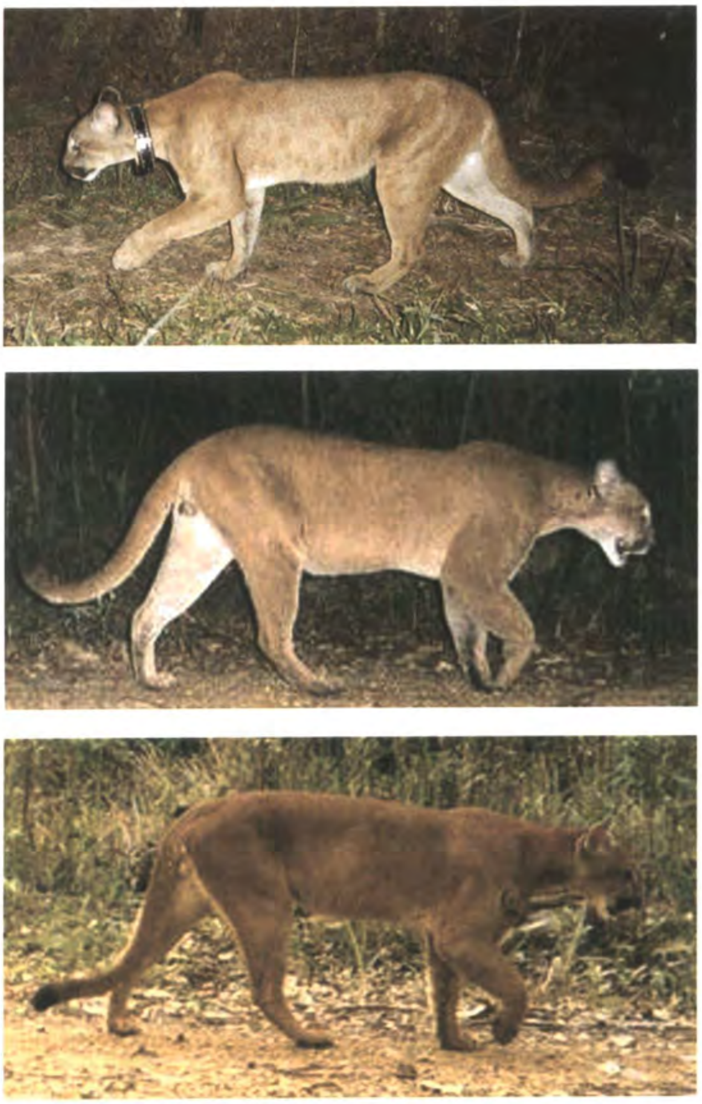


Figure 5.3. Frontal-lateral photographs of two individual mountain lions. Note the heavier buitl and larger head of the first animal, the presence of notches in his left ear, and the scrotum which is only partially evident.

5.4.2 Track matching analysis

The overall results from both the first and second phases of the track survey suggest the presence of six to nine adult and sub-adult mountain lions in the area.

Evidence of the presence of family groups (female and offspring) was also obtained from identification of recurring tracks belonging to the same animals over periods of more than three weeks. During the first period two females were identified as being accompanied by three yearling/sub-adult offspring. During the second time period these offspring had either dispersed or became separated from their mothers, and another female appeared with a sub-adult offspring. It should be mentioned that tracks from young offspring are very difficult to detect, mainly due to their relatively low weight which is insufficient to produce good track prints. Thus by the time their tracks are noticeable they will have already reached a considerable body weight.

Although several different animals used the same roads, under no circumstance were different individuals found to be using the same trail on the same day, except for females and their offspring.

Ageing of mountain lions on the basis of their tracks was conducted with caution since on one occasion small prints, thought to belong to a offspring, were in fact made by the female, as verified when the animals were captured (Chapter 6).

Adults would walk at a steady pace along a road, while offspring would frequently zigzag, perhaps while playing and exploring their environment. I distinguished two main movement patterns from tracks, a *travel mode*, with most distances covered at a walk in a straight line following the road for several kilometres, and a *hunting mode* whereby tracks of the same animal were found encircling a patch of forest or up and down the same road on consecutive days. These behaviours were also evident from camera-trap recaptures and radio-tracking (Chapter 6). On occasions, tracks of a mother and her offspring would split in the trail and re-join each other hundreds of meters ahead on the trail. I assumed from these behaviours that the offspring were almost ready to leave their mother. In fact, by the end of 1999 I was unable to find records of either family groups together.

5.4.2.1 Period I (March 1998 to July 1999)

Track recording was carried out more intensively during the first half of the study, thus allowing for a more quantitative approach than was possible during the second half. Nine mountain lions were estimated to occur in the area during this period based on the final matrix (Table 5.1e).

Discriminant analyses were performed for all four paws. The primary criterion to consider a track set as belonging to a particular mountain lion was that at least 75 % of the tracks from a set should fall within its own group. Sets of tracks were suspected to belong to the same mountain lions when they shared at least 25% of tracks in common when the primary criterion was not met. When none of these criteria was met or when lacking quantitative data, the track sets were analysed qualitatively. In some instances track sets were grouped when analysing one particular paw, but did not group following analysis of another paw, for example, track sets number 7 and 11 grouped under left front and right hind tracks, but not under left hind (see Table 5.1). If sets successfully grouped for at least one paw, it was considered to belong to one mountain lion.

The discriminant analysis derived from hind tracks estimated from four to six individual mountain lions, while front track analysis resulted in an estimate of seven individuals.

The percentage of variance explained by the two main discriminant functions in the four analysis carried out varied from 81.4 % to 100 %. The relative importance of each measurement varied according to the paw, but HLTL and HOT were amongst the most relevant parameters for both hind tracks, and OTS for the front tracks.

Table 5.1. Decision matrices resulting from discriminant analysis, based on data from the first time period (March 1998 to July 1999). Numbers in rows and columns represent track sets in matrix. Each matrix presents the results of quantitative comparison between different sets.

a) right rear track

set	n	1	2	6	7	11	17	18	22	23	24	27
1	6	33%			25%					33%		
2	4		50%						50%			
6	10			50%								
7	8				25%	43%						
11	7					29%						
17	3						100%					
18	5							33%			50%	
22	4								0%			
23	3									67%		
24	6										33%	
27	5											20%

summary

Groups	1	2	3	4
Sets	1, 7, 11, 23	2, 22	17	18, 24

Result: number of mountain lions = 4

b) left rear track

set	n	1	6	7	9	11	12	17	18	24	27
1	6	83%									
6	10		100%								
7	7			86%							
9	5				100%						
11	9					33%					
12	3						67%				
17	3							100%			
18	6								83%		
24	6									50%	
27	6										67%

summary

Groups	1	2	3	4	5	6
Sets	1	6	7	9	17	18

Result: number of mountain lions =6

c) right front track

sets	n	1	6	7	10	11	13	17	18	22	23	24	27
1	7	86%											
6	9		82%										
7	10			60%									
10	3				67%			33%					
11	4					100%							
13	5						40%						
17	5							17%					
18	3								75%				
22	5									67%			25%
23	3										100%		
24	6											67%	25%
27	4												50%

summary

Groups	1	2	3	4	5	6	7
Sets	1	6	10, 17	11	18	23	22, 24, 27

Result: number of mountain lions = 7

d) left front track

set	n	1	3	6	7	11	12	17	22	24	27
1	8	0.62									
3	4		75%								
6	13			100%							
7	4				50%	50%					
11	9					67%					
12	3						100%				
17	3							0%	33%	33%	33%
22	5								80%		
24	6									83%	
27	3										100%

summary

Groups	1	2	3	4	5	6	7
Sets	3	6	7, 11	12	22	24	27

Result: number of mountain lions = 7

e) Final matrix. Shaded areas in the superior half of the matrix result from qualitative track analysis.

set	1	2	3	6	7	9	10	11	12	13	17	18	22	23	24	27
1		=														
2																
3						=				=		=		=		
6																
7																
9										=				=		
10											=					
11									=							
12														=		
13												=		=		
17																
18																
22																
23																
24																
27																

summary

Groups	1	2	3	4	5	6	7	8	9
Sets	1, 2	3, 9, 13, 18, 23	6	7	10, 17	11, 12	22	24	27

Result: number of mountain lions =9

5.4.2.2 Second time period (from August 1999 to March 2000)

Six mountain lions were estimated to occur in the study area during this period. This result excludes one track set (number 46) recorded outside the core study area but which was incorporated in the analysis.

Three groupings (track sets found to belong to the same animal) resulted from qualitative analysis of Matrix 1 (Table 5.2a); these included group 20 (including sets 20, 30, 32, 33, 39, 40, 41), and groups 43 and 45 each represented by only one set.

Matrix 2 (Table 5.2b) originated from discriminant analysis of two matrix subsets, matrix 2.1 from measurements of paw PD (sets 31, 37 and 46) and Matrix 2.2 from measurements of paw PE (sets 35, 36, 37 and 44); both matrix subsets resulted in as many groups as track sets. These matrices were combined into Matrix 2 with any missing cells filled with data from qualitative comparisons; sets 31 and 44 were reassigned to one group (group 31) and the remaining sets entered as separate entities.

The final matrix (Matrix 3) (Table 5.2c) was prepared by concatenating groups from Matrices 1 and 2. Sufficient data were available in reassigned groups 20 (from Matrix 1) and 31 (from Matrix 2) for comparison of paws MD, ME, and PD using discriminant analysis. In addition to groups 20 and 31, the analysis of PD also included groups 37 and 46. No groups were reassigned as a result. Groups 34 (from Matrix 1) and group 35 (from Matrix 2) were combined as the same group (group 34) as a result of qualitative comparison (Table 5.2).

Table 5.2. Decision matrix with data from the second time period (August 1999 to March 2000), number in rows and columns represent track sets in matrix 1 and 2, which are then reassigned to groups representing individual mountain lions in matrix 3 present in the area during the period. Results in shaded cells were derived from qualitative analysis (shape comparison and overlay), unshaded cells are derived from discriminant analysis. The cell with question mark results from the difficulty in defining whether sets 41 and 45 belong to the same animal. Final matrix (c) represents the total number of mountain lions in the period (ranging from 6 to 7), excluding number 46 which is from outside the study area. Cells filled with the sign equal (=) are track sets grouped as same individuals, whether empty cells are different individuals.

a) matrix 1

set	20	30	32	33	34	39	40	41	43	45
20	▨	=	=	=	=	=	=	=		
30	▨	▨	=	=	=	=	=	=		
32	▨	▨	▨	=	=	=	=	=		
33	▨	▨	▨	▨	=	=	=	=		
34	▨	▨	▨	▨	▨					
39	▨	▨	▨	▨	▨	▨	=	=		
40	▨	▨	▨	▨	▨	▨	▨	=		
41	▨	▨	▨	▨	▨	▨	▨	▨		?
43	▨	▨	▨	▨	▨	▨	▨	▨	▨	
45	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨

b) matrix 2

set	31	35	36	37	44
31	▨	?			=
35	▨	▨			
36	▨	▨	▨		
37	▨	▨	▨	▨	
44	▨	▨	▨	▨	▨

c) matrix 3 or final matrix for the period

set	20	31	34	36	37	43	45	46
20	▨							
31	▨	▨	?					
34	▨	▨	▨					
36	▨	▨	▨	▨				
37	▨	▨	▨	▨	▨			
43	▨	▨	▨	▨	▨	▨		
45	▨	▨	▨	▨	▨	▨	▨	
46	▨	▨	▨	▨	▨	▨	▨	▨

Result: number of mountain lions = 6 or 7

5.5 Discussion

This study differs from previous investigations in that it was possible to include sufficient front paw measurements to perform quantitative analysis. Smallwood and Fitzhugh (1993) suggested that front tracks might discriminate better among themselves than would rear tracks, since they seem to have more unique features. One way to evaluate discrimination power between front tracks and rear tracks is to verify the number of variables necessary to distinguish between sets of tracks. If less variables are necessary for full discrimination, it suggests the paws have more unique features and that they are more easily assigned to individuals. However, only two variables were included in the stepwise discriminant analysis for the right hind track, and four variables in all remaining tracks (left hind, left front, and right front tracks). Front tracks nonetheless discriminated more mountain lions in the first time period (n=7) than did hind tracks (4 to 6 individuals).

Comparison between computer drawn and manually traced images and measurements suggested that these could be substituted for one another (Grigione *et al.* 1999), and the increased effort to scan, scale and retrace images in computers may encourage researchers to conduct manual tracing as a more practical approach for track recording.

The number of mountain lions in the 100 km^2 area as estimated from photography was from nine to thirteen. These images were mainly taken during the first half of the study, and yielded a considerably higher density than that estimated from track counts (7 – 9 in period I; 6 in period II). It would appear that discriminant analysis is a conservative technique, and track sets produced by individual mountain lions may either be discriminated completely (Smallwood and Fitzhugh 1993) or may sometimes cluster into a single group (Grigione *et al.* 1999). Overall, a conservative density estimate of adult and sub-adult mountain lions in the study area would range from 6 to 9/100km^2, which is equivalent to 0.06 to 0.09 per km^2. Density estimates of mountain lion where it coexists with jaguar (*Panthera onca*) vary from 0.015 per km^2 (Schaller 1983) to 0.044 per km^2 (Crawshaw and Quigley, in Nowell and Jackson 1996). Presumably mountain lions may reach higher densities where jaguars are absent and habitat suitability is adequate. For example, a protected mountain lion population in Patagonia (Chile) was found to exist at a density of 0.06/km^2 based on radio-tracking, sightings, and tracks combined (Franklin *et al.* 1999). The authors suggested that densities may even reach 0.3 per km^2. In North America densities are lower, ranging from 0.005 to 0.049/km^2 (Anderson 1983), possibly due to the greater size and mobility of the prey.

Predator densities are affected by body size (MacNab 1963) and food abundance (Anderson 1983, Sunquist *et al.* 1999), but a limit is imposed by territoriality (Seidensticker 1973) and probably inter-specific competition. In my study area jaguars were absent which would otherwise prey on peccaries and capybaras, and may, additionally, cause interference competition as mutual avoidance has been previously recorded (Schaller and Crawshaw 1980). Leopard densities are reported to be higher (up to 17-20/100 km^2) in areas where competing predators are absent (Eisenberg 1980, Santiapillai *et al.* 1982).

It has been suggested that large felids will deplete a patch by driving away prey rather than by killing them (Brown *et al.* 1999). If this is correct it is reasonable to assume that movements of large cats between patches will vary according to prey mobility, which could also be reflected in territoriality. Feeding mainly on smaller prey, which are less mobile and easier to catch, may allow predators to stay longer in a given patch, and ultimately result in their achieving a higher density and to experience less inter-specific territorial conflict. The availability of smaller, and presumably easier to catch prey might also allow for the survival of aged animals that are less able to kill larger, faster or stronger prey. This might explain the higher densities of mountain lion recorded in South America, where their diet consists predominantly of smaller prey than that in North America (Iriate *et al.* 1990). Supportive evidence is provided by studies of Rabinowitz and Nottingham (1986), who found in Belize that male jaguar home ranges overlapped considerably. In this case, jaguars occupied small portions of their range for several days before shifting, and this could be due to the large proportion of prey in their diet possessing low mobility (e.g. armadillo comprised 54% of jaguar's diet). This was in contrast to the larger, non-overlapping home range when larger mammals represented the bulk of the diet (Schaller and Crawshaw 1980, Crawshaw and Quigley 1984) and is consistent with the finding that smaller home range sizes were found to be associated with higher concentrations of prey (Crawshaw and Quigley 1991). Low mobility of prey and spatial aggregation may explain the back-tracking behaviour that mountain lions exhibited. Konecny (1989) observed similar behaviour in ocelots (*L. pardalis*).

The population densities of species are known to vary through time, especially in a non-stable system. The present research, however, was conducted over a short period (1.5 years), in order to give a snapshot of density. Thus while I have investigated the variation in spatial density it must be appreciated that only by long term monitoring can a complete understanding of population dynamics be achieved. Greater variation is expected for predators that are largely dependent on a few prey species. A classical example has been the study of the numerical response of lynx to rabbit population fluctuations (Elton and Nicholson 1942). However, the mountain lion has a large selection of prey available, and is expected to show a functional response rather than a numerical response to variations in prey populations. That is to say, it is likely to prey on alternative items when the preferred species have been depleted. Hence, the diversity of prey items available in South America, and in particular in this study area, should be an advantage by increasing system stability for mountain lion.

Different numbers of mountain lions were estimated in the area during the two time periods of the study. This may be explained by dispersal of offspring or by the death of the captured female. Other factors may be involved, including a less intensive data record and larger reliance on qualitative analysis in the second period. Fluctuation in density estimates could also be due to the presence of non-residents among the sampled animals and shifts in spatial aggregation through time (Smallwood 1994).

Track comparison is a new method that can be used to analyse population densities over large areas without being too demanding of resources. In this study area, however, sporadic rain-fall made track collection difficult. During the dry days tracks would not imprint, and during the rainy days the tracks could be washed away.

Another issue concerns the validity of assigning densities when boundaries to study areas are set in a largely arbitrarily manner. However, the concentration of adult and sub-adult animals as well as the presence of resident females with sub-adult offspring attests to the areas suitability as mountain lion habitat. Few large felid populations have been assessed in disturbed habitats (Nowell and Jackson 1996). The presence of intensive logging operations, and the predominance of non-native vegetation does not seem to have compromised the persistence and viability of mountain lions in the area.

Smallwood (1997) has highlighted possible errors that may arise due to extrapolating mountain lion densities across heterogeneous landscapes with associated variations in prey availability. In Chapter 6 the distribution and abundance of the prey species deemed most important to mountain lions seemed not to be greatly affected by differences in the proportion of natural forest throughout the property which varied from 25% to 66%.

Under the assumption that prey is homogeneously distributed within the entire study area (1,255 km^2), the total population of mountain lions would range from 75 to

113 animals. This was not an isolated population since adjacent properties with commercial forest also provide habitat for mountain lions. There was also evidence of mountain lions presence near ranches in the vicinity.

Chapter 6: Movements and habitat utilisation

6.1 Introduction

The mountain lion is a secretive carnivore which is difficult to study in the wild by direct observation. Investigation of mountain lion movements were first performed using capture-recapture methods (e.g. Hornocker 1968, 1970). The advent of radio-telemetry has enabled scientists to follow animal movements remotely and has greatly simplified the study of mountain lions by eliminating the need for frequent recapture (e.g. Seindensticker *et al.* 1973). While live-trapping with cage traps has been successful for many large and medium sized cats such as leopards (Rabinowitz 1989, Norton and Henley 1987, Mitzumi 1993), ocelots (Emmons 1987, Ludlow and Sunquist 1987, Crawshaw and Quigley 1989, Dunstone & O'Sullivan 1996) and jaguar (Rabinowitz and Nottingham 1987), mountain lions have been rarely captured using this method. More typically research on mountain lions has utilised hunting dogs to tree cats which are then sedated with a tranquilliser drug fired from a dart gun. Mountain lions are still difficult to capture compared to other felids, particularly where they inhabit dense forests.

The first investigation of the reaction of mountain lions to environmental disturbance was carried out by Van Dyke *et al.* (1986). Such information remains scanty for felids in general (Nowell and Jackson 1996). The aim of this chapter is to investigate the ranging behaviour of the mountain lion in a commercial timber-growing area in southern Brazil to provide data on home range size and habitat utilisation. Smaller home ranges are to be expected from resource-rich areas, whereas larger home ranges reflect the animal's need to wander further to find the resources it needs. In addition radio-telemetry can also help define which habitat resources are preferred and which are avoided. In this study it was particularly relevant to also investigate the mountain lion's reaction to human disturbances.

6.2 Methodology

6.2.1 Capture, sedation and tagging

A total of eight custom-designed live-traps were available, comprising six fixed location and two moveable traps. Five of the fixed traps were constructed of wooden poles wrapped with chain-link fence, and one was constructed almost entirely of wood poles. Four were of approximate size 5 x 2 x 2 m with the bait located at the far end of the trap. One measured 5 x 4 x 2 m, half of which was occupied by the bait which consisted of several ducks confined within a separate cage. All fixed traps were constructed and set to catch within the Park. Moveable traps were made of iron, and measured 2 x 1 x 0.80 m. They were set at eight different locations over the course of the study; six of these trap sites were within or near the Park area. The traps were surrounded by a strip of plastic "fabric" set 50 cm above the ground to prevent the predator attacking the bait from the outside the trap. Traps were checked every morning either by inspection, or by assessing them remotely with the aid of "trap-site transmitters" (Telonics, Mesa, Arizona) which were usually set at fixed traps.

6.2.2 Radio-tracking technique and data analysis

Radio-collars, antenna and receiver were supplied by Telonics (Mesa, Arizona). Transmitter model MOD-315 were mounted on collars with a total package weight of 105 g, and had a life expectancy of 22 months. Radio-collared mountain lions were located using a model TR2 receiver and a variety of antennae including mobile, fixed site and vehicle-mounted models. Animal locations were plotted with a portable GPS model 12XL (Garmin, Olathe-KS, USA). Occasionally contact was lost during radio-tracking at close range (approx. 800 m), due to the relatively deep creek banks and dense forest cover. Following field work bearings were input into the LOAS software (Ecological Solutions, Sacramento-CA, USA) which generated the location co-ordinates.

Ranging behaviour was analysed using two methods. Minimum convex polygons (Stickel 1954, Harvey & Barbour 1965, White & Garrot 1990) were utilised to estimate home range, and kernel contours (Worton, 1989) to estimate core area. The polygons and core contours were produced in Ranges V (Kenward & Hodder 1996), and exported to ArcView (ESRI, Redlands-CA, USA) where habitat analyses were performed. A digitised map of the study area was provided by the forestry company's GIS department.

6.3 Results

6.3.1 Captures

A female mountain lion and her male offspring were captured on subsequent days (19/20th November 1998) at the same trap, which was located adjacent to the captive breeding area. The trap had been baited with several white ducks. Following capture, the female was encouraged to enter a smaller cage where she was then sedated by hand-administered injection, whereas the offspring was sedated using a dart administered from a blow gun. Both received a mixture of Zoletil at a dose rate of 50 mg/kg (0.6-1 ml), Rompun 0.5 ml, and Atropine 1% (0.3 ml).

The female weighing 20 kg and her larger male offspring 36 kg. On the basis of tooth wear characteristics (Gay and Best 1996), it was estimated that the female was over 15 years old, while her offspring was judged to be over 15 months old.

Both cats were radio-collared and released at the trapping site when fully recovered from the anaesthesia.

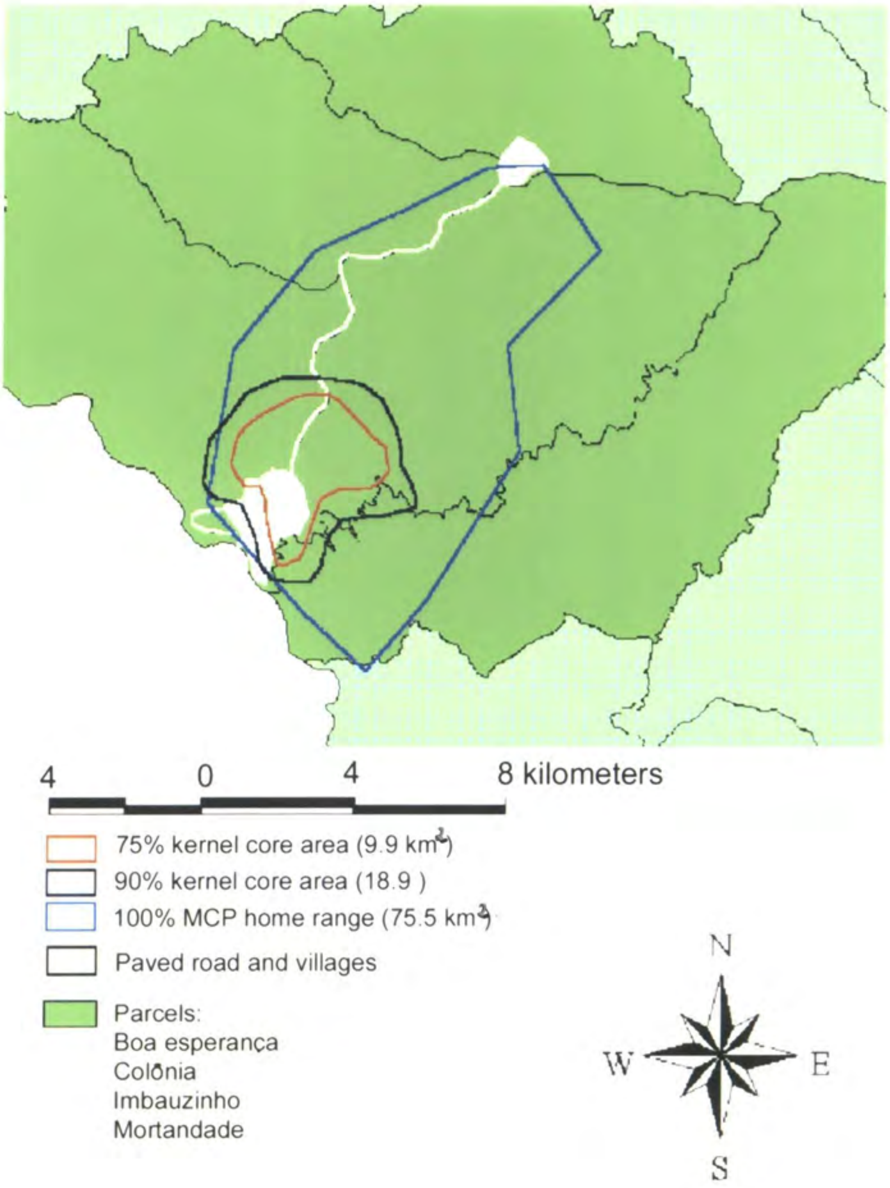
6.3.2 Radio-tracking and home range

The male offspring lost his collar within four days of capture. The collar had been attached loosely attached to avoid choking the animal at a latter date, as the diameter of his neck was believed not to have reached full size. Subsequently, his tracks were usually seen along with his mothers during the study.

Attempts were made to locate her at least once a day. A total of 320 fixes were obtained from the female mountain lion while she was followed for 186 days. She was not located during 43 of these days when she remained out of radio signal reception range.

The size of her home range based on the minimum convex polygon method was 75.5 km^2. For 55% (103 days) of all tracking days the female used a core area of 18.9 km^2, as estimated by the 90% kernel method (Figure 6.1).

Figure 6.1. Home range (MCP) and core areas (based on 90% and 75% kernel isolynes) of the female mountain lion.



6.3.3 Habitat use and activity

The study area was densely irrigated by creeks surrounded by narrow patches of natural vegetation within a matrix of commercially planted forests. This created a very patchy habitat mosaic, in which slight errors of triangulation of radio-fixes were likely to produce biased data on habitat use. Instead of determining the habitat at the time of each location I evaluated habitat use on the basis of the proportion of each vegetation type and other features present within the female's 90% core area using ArcView software. The core area (18.9 km^2) utilised by the female comprised 8.1 km^2 of natural forest and 8.9 km^2 eucalyptus and *Pinus* spp. plantations. The remainder of the core area included a dam (0.63 km^2), and the village of Harmonia (2.1 km^2) (see Figure 6.1). Interestingly, the core area was the most human-disturbed site within the female's home range and within the entire property. The core area also included a rubbish dump, a paved road and was adjacent to the main gas station and to the factory's timber yard, which was constantly busy with trucks and tractor activity.

Of the total number of locations obtained, 7% (n=22) were within 100 m of the paved road, and 15 of these were recorded during day time. Additionally, 51 fixes (16%) were recorded from forest patches located within the village boundary, 21 of which were during day time. Noise from tractors, trucks, and from the factory conveyor belt were audible at several of the sites she frequently used within her core area.

The female mountain lion was recorded crossing the two-lane paved road 38 times during the seven month period of radio-tracking. All recordings were within her core home range area. Seven of these crossings were known to have occurred during the day and eleven at night. On two occasions I was able to record her behaviour during crossing attempts. Once (9:30 on 27/2/99) she headed to the road as if to cross, but stopped and remained on the same side of the road. At 18:15 she was back at the road margin, and although active did not cross. She finally crossed at sometime between 20:25 on 28/2/99 and 04:40 on 01/3/99. In another instance, at 15:45 on 2/4/99 she displayed similar behaviour, approaching the road as if to cross, but turning round and remaining active at the margin. On the following day at 8:30 she again approached the road, crossing it between 16:40 and 19:40. In the interval between 19:40 and 21:20 she crossed back again and at 9:10 on 4/4/99 crossed the road one more time.

Although this female was successful at crossing roads without injury even when accompanied by her offspring, a young adult male mountain lion (46 kg) was hit and killed by a truck while crossing the paved road near the study site.

Her core area incorporated areas of major human disturbances, such as a dump, a village, and a two-lane paved road with dense traffic. Nevertheless activity was detected very near such disturbances during day-time. On one occasion, the female was recorded resting during day-time in a small patch of *Pinus* spp. less than 40 m wide and 100 m long situated approximately 30 m from the paved road and 60 m from the village houses.

Mountain lions also wandered into the relatively open grounds of the breeding centre, where they attempted to prey on the captive animals. On one occasion claw marks were found on a tree trunk which stood in a clearing 40 m distant from the camp house in the breeding centre.

I distinguished whether animals were hunting or travelling on the basis of their speed of movement within and between patches. Average speed of movement within a patch was 156m/h (SD=156). This is certainly an underestimate because it was based on just a few fixes per day. On five of six occasions when it was possible to measure speed of movement between patches this was estimated to be 1,759 m/h (SD=1349).

6.4 Discussion

Mountain lions are very difficult to catch using live-traps, however I was able to catch two animals, and a third entered a trap to recover a fresh kill that had been placed there, but was not caught.

Attempts made to catch mountain lions with dogs were unsuccessful. In secondary vegetation with dense undergrowth it often proved impossible to keep up with the dogs. An account of the difficulties involved in chasing large cats with dogs in dense forest can be found in Rabinowitz (1987).

The population density of solitary-living carnivores is strongly inversely related to the size of the home ranges of adult females (Sandell 1989). Previous studies have shown female mountain lion home ranges to vary from 56.5 km^2 to 237.7 km^2 in the mild climate of southern California (Padley 1997a) and to be as large as 1,717 km^2 in habitats surrounded by desert (McBride 1976) where prey availability is low. In the Patagonian steppe grasslands and *Nothofagus* forests home ranges varied from 24 to 100 km^2 (Franklin *et al.* 1999), whereas in the Atlantic Forests of São Paulo (Brazil) Cullen Jr. (unpubl. manuscr.) recorded a female mountain lion to occupy a range of 90 km^2, which is broadly equivalent to that estimated in the present study (75.5 km^2).

In my study the female mountain lion intensively utilised some very disturbed habitats. Beier (1995) also observed that dispersing mountain lions in the Santa Ana Mountains (California) utilised disturbed corridors, although residents did not. In his study one dispersing mountain lion established a home range which included a corridor incorporating several highly disturbed areas (two golf courses and an equestrian area devoid of understory). The range was intersected by an eight-lane freeway with heavy traffic, which the mountain lion crossed by utilising an underpass and aculvert. Beier (1995) observed other dispersing mountain lions utilising this and other disturbed corridors less frequently. Dispersers came to within 100 m of urban areas and heavily populated parkland for several hours to several weeks, but all travel within corridors and 'habitat peninsulas' occurred at night, and they avoided areas illuminated by artificial light. However, both resident and dispersing mountain lions occasionally rested for the day some 20-100 m from trails heavily used by hikers, cyclists, and equestrians.

In a study of the Florida panther, the location of mountain lion*s* (*panthers*) near highways in Florida did not differ from random (Maehr and Cox 1995). However, these authors believed that this was due to the characteristics of the landscape rather than to the lack of a relationship between animals and the density of roads.

Collision with vehicles on highway accounted for 47% of mortality documented for Florida panthers and was possibly related to the increased traffic associated with tourism at certain times of the year, and to landscape features that influence panther movements (Maehr *et al.* 1991). Beir also noted that four of nine dispersers were killed when crossing roads. Mortality is certainly accentuated due to multi-lane roads. On a two-lane paved road such as that in my study site, accidents were rare, and the resident mountain lion and her offspring were able to frequently cross it without mishap. However, the female seemed reluctant to cross the road in the few attempts that were observed. This certainly interfered in the way she utilised her territory. A solution that can presumably minimise the problem of road crossing is the presence of culverts, particularly in roads with a high density of traffic.

The present results are in contrast to those of Van Dyke *et al.* (1986), who noted that mountain lions in Arizona and Utah tended to avoid logged areas, roads, and human residencies, even though human disturbance was much less than at my site. Only one of their mountain lions resided close to human habitation. The authors concluded that "*concentrated human presence or residence are (areas) essentially lost to (mountain) lion population, even if there is little impact on the habitat itself*".

The differences between the two studies suggest that a re-evaluation of human-cat interactions is warranted and that there is a need for further studies. One possible explanation as to why mountain lions are behaving differently at the two study sites relates to differences in human attitude toward them. Most of the mountain lions in Van Dyke's *et al.* (1986) study area avoided logged areas or areas near human residencies. In these disturbed areas they were more susceptible to poaching/hunting, and two out of three cats that established home ranges here were killed.

In Brazil, hunting of mountain lions is prohibited by law, although poaching remains common place (pers.obs.). At my study site hunting is further discouraged by the fact that it is a private area, with a high level human activity involving company employees, who are encouraged not to become involved in poaching activities and to participate in education programmes concerning environmental issues. It would appear that this has led to a higher than average level of environmental concern amongst them. Furthermore, the company has established it own environmental police force who constantly monitor the area.

Responses of felids to humans vary according to the degree of anthropogenic interference, and their reactions can change over a relatively short period of time. For example, Schaller (1972) recorded that one of his African lions learned to avoid his car after being tagged, and "*required a year of frequent contacts with this animal before he accepted the car as indifferently as he had done prior to tagging*".

Further evidence of large cats becoming habituated to human presence include a study by Franklin *et al.* (1999) who demonstrated that with decreased hunting pressure and harassment by horsemen and their dogs in the Torres del Paine National Park in Chile, that "*remarkable shifts in behaviour occurred in this mountain lion population which have habituated to people and are being observed more often by park visitors*".

Similarly, leopards also can became habituated to humans, and one female at Londolozi Game Reserve in South Africa "*permitted visitors to approach closely, even when she is nursing cubs*" (Norton 1984).

Mountain lions are able to adapt and live in the vicinity of humans when they are not persecuted. The question remains as to what extent habitat disturbances affect mountain lion fitness. This question was addressed in Chapter 5 where the presence of mountain lion's family groups indicated a normal population recruitment. Additional evidence is provided by the relatively high density of mountain lions in the study area, the small home range size of the radio-tracked mountain lion, and her advanced age.

Gittleman (1993) suggests that high survival and longevity of adult females is critical to the continued survival of most carnivore populations. Average age of captive mountain lions has been recorded as 7.5 to 9 years (Young 1946, Spector 1956). The radio-tracked female in this study was estimated to be over 15 years. At this advanced age she was able to breed and raise young into adulthood, despite the fact that her core area of activity enclosed the highest level of disturbance in the entire property. Although this concerns only one animal it provides additional evidence of the high adaptability of mountain lions to modified environments. Similar or better fitness is expected in areas within the property where disturbances are less conspicuous

Part II: Ecology of the Kodkod

Chapter 7: Density and habitat utilisation

7.1 Introduction

The little information available on the habitat requirements of the kodkod (*Oncifelis guigna*) seem to be conflicting when examined. Nowell and Jackson (1996) suggest that the kodkod has a strong habitat association with Valdivian and Araucaria forests because its distribution coincides with these forest types in Chile. Other authors (Redford and Eisenberg 1992, J.Rottmann *in litt.* 1993) consider it to be a resilient species and to do well in altered habitats such as deforested and non-native pine and eucalyptus plantations in the Valparaiso area of Chile (C.Weber *in litt.* 1993, J.Rottmann pers.comm. in Melquist 1984) where is thought to be common (Green 1991). It has also been stated to be commonly found near human habitation (Greer 1965). Sanderson and Melquist (unpubl. manuscr.) have pointed out that kodkods, particularly females, prefer to use forested areas and Green (1991) has suggested semi-open country with few trees and shrubs, but not grasslands and desert are utilised.

The Patagonian Ice Sheet is the third largest in the world and in Aisén Region XI of Chile is an inhospitable area of 17,000 km^2 running parallel to the Pacific coast from about 46° to 50° S. Kodkods are not generally recorded above the timberline (Redford and Eisenberg 1992), and, hence, the higher altitudes often with extensive ice caps and open grass-lands which characterise this part of the Andes may impose a barrier to their dispersal. I approached the investigation of habitat utilisation by analysing movements of kodkod within diversified vegetation and slope gradients. The utilisation of habitat on an individual scale may hopefully prove relevant to understand the factors affecting distribution at a larger scale.

Density of kodkod was estimated also as a means to scale their densities to it's the geographical distribution of the species, in such a way to help to illustrate the vulnerability status of the species based on demographic parameters. While the usefulness of the density estimates based on carefully collected information is essential, studies in a particular areas cannot be extrapolated without some compensation to allow for variation in habitat quality. In this study the habitat requirements of kodkods were investigated using an approach slightly adapted from Miquele *et al.* (1999) after Johnson (1980). These authors suggest that habitat selection may occur at three different spatial scales, first order selection describing the range of habitats within the geographical distribution of a species, second order selection concerns the habitat composition within the home ranges of individuals, while third order selection identifies the selection of habitats by an individual within its home range. This third order selection is essentially at the level of habitat choice or "preference/avoidance" (Neu *et al.* 1974).

The kodkod is believed to be at risk because there is a paucity of knowledge on it's biological requirements , the extent of existing threats, and its restricted distribution. The kodkod has one of the smallest distributions amongst wild felids; its geographical range is restricted to a narrow strip within Chile and Argentina from latitudes 30° to 50° S and longitudes 70° to 75°, encompassing approximately 160,000 km^2 (Nowell and Jackson 1996). It is currently listed on the Appendix II of CITES, and has been ranked “Category 2” in a comparison of vulnerability among felids on a global scale (Nowell and Jackson 1996). Under the same criteria, it is listed in “Category 1” in South America (Nowell and Jackson 1996) and is thus considered more vulnerable than the Andean mountain cat *Oreailurus jacobitus* and the jaguar *Panthera onca* both of which are listed in CITES Appendix I. Regions within the kodkod’s distribution have been subject to habitat loss, especially by deforestation as a result of deliberate burning for agricultural development (Veblen & Ashton 1978, Meserve *et al.* 1991). This may have resulted in population reduction in the north of the kodkod’s range (Nowell & Jackson 1996).

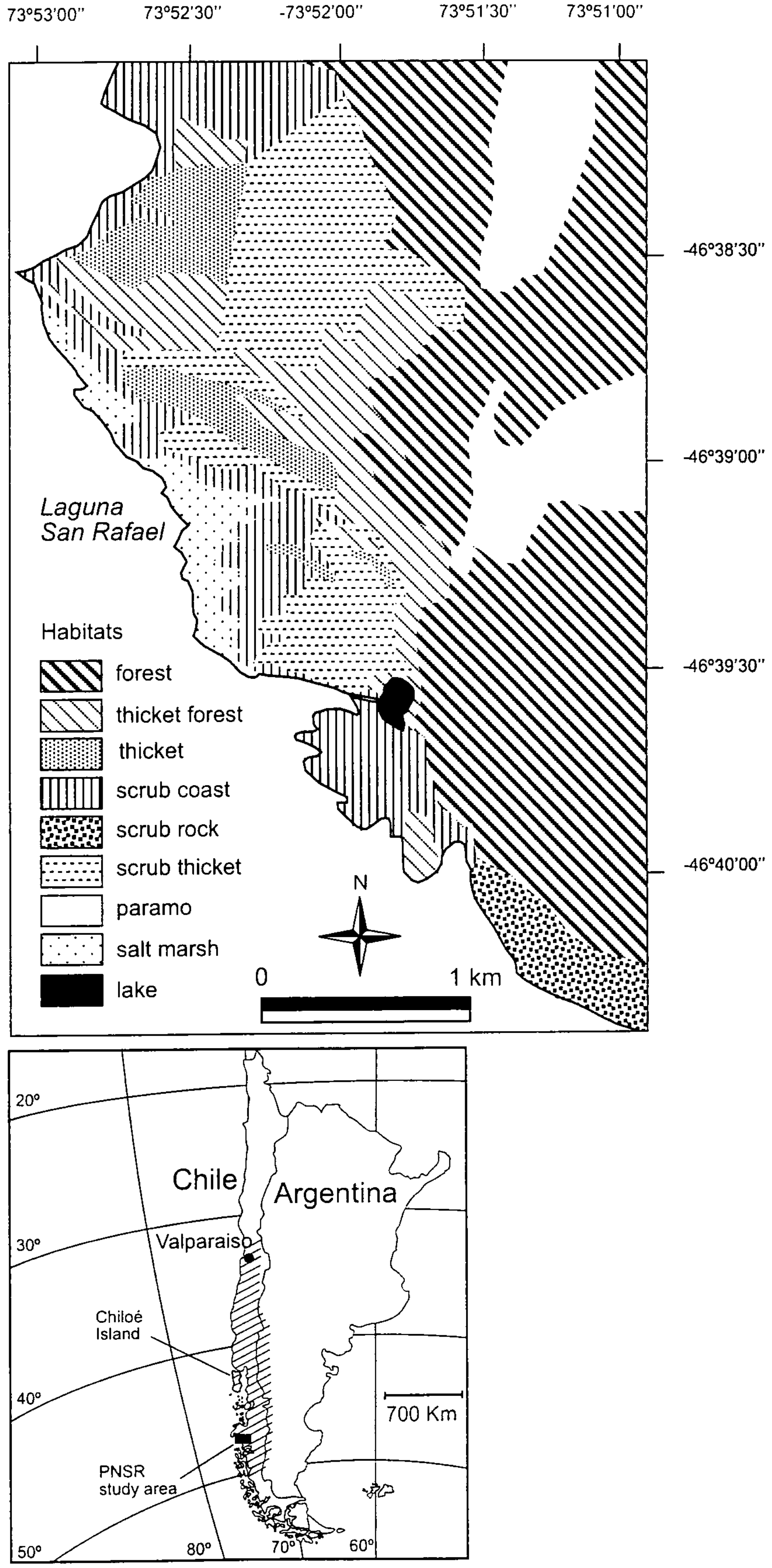
7.2 The kodkod study area

The study area is located in the Parque Nacional Laguna San Rafael (PNLSR), near the Taitao Peninsula and *Golfo de Penas*, from 73° 51'E to 73° 53'W and from 46° 38' to 46° 40' 30''S, and adjacent to the San Rafael Glacier (45 km long and about 3 km wide), which is the fastest moving glacier in the world. The study area is surrounded by mountains up to 2,000 m high to the east, by the Patagonia Ice Sheet and a glacial lagoon to the west. Laguna San Rafael National Park (PNLSR) was created in 1959, with a total area of 1,750,000 ha. At the northern limit, rises the Monte San Valentín (4,058 m), the highest peak at the Patagonian mountain range.

The vegetation is considered transitional between the northern Patagonian and the Magellanic Evergreen Temperate Forests (Pisano 1981). Some of the Valdivian species reach the southern limit of their distribution here, and the majority of the vascular flora belongs to the Austral Chilean-Argentinean element, which is rich in endemics (Pisano 1981). Mean temperature and annual precipitation at two zones near the PNLSR varies from 8.3 to 9.0° C and 1,979 to 3,463 mm respectively (Zamora and Santana 1979).

The PNLSR study site encompasses regions of temperate rainforest, paramo (high-altitude grasslands), scrubland, thicket, saltmarsh (sedge and reed communities), beach communities, a rocky outcrop ('scrub-rock' in the analysis) and a glacial laguna. *Nothofagus nitida* is the characteristic species of the Evergreen Western North Patagonian Forest of coastal and riparian sites up to an altitude of 200-250m, and predominates within the forest of PNLSR where it is found in association with *Nothofagus betuloides, Laureliopsis philippiana* and *Drimys winteri.*

Figure 7.1. Map of Parque Nacional Laguna San Rafael (PNLSR) with different habitats.



7.3 Methodology

The fieldwork component analysed in this Chapter is based on on-going studies conducted by researchers other than myself (see acknowledgement).

7.3.1 Habitat mapping and analysis

In the absence of accurate topographical maps of the area, aerial photography of PNLSR was commissioned in order to map vegetation boundaries and features of the terrain, including a trail system that facilitated access to the site. Such features were also surveyed on the ground using a GPS (Garmin 45) and by taking compass bearings and measuring distances between points.

This information was used to categorise the habitat patches in the aerial photographic map, which was digitised in ArcInfo (ESRI, Redlands-CA, USA). Aerial photographs were taken from 10.000 feet and joined with Photoshop (Adobe, San Jose, California). The raster image was then georeferenced in ArcInfo with UTM (datum Clarke 1866) GPS locations. This was a multi-step process, beginning with the conversion of the TIF (Tagged Information File) generated by Photoshop into a format suitable for input into ArcInfo This was achieved using the XV Unix software package (John Bradley, Grasp Lab., Univ. Pennsylvania USA) running on Solaris (Sun Microsystems, San Antonio, Palo Alto, CA USA). A separate coverage was created (using the command "Generate") with the known UTM locations to accomplish the georeferencing (known as "ticks"). The next step was to issue the command Register within the ArcInfo window (see appendix 2).

The rectified image was then imported into ArcView (ESRI, Redlands-CA, USA) where polygons were drawn around different habitat types. Individual Minimum Concave Polygon home range contours generated in RangesV were superimposed on the image within ArcView and the proportion of habitats within the home range each kodkod was quantified.

The availability of habitat within each individual range was utilised to generate an expected number of radio-locations within that habitat type. The expected number of locations was tested against the observed numbers using χ^2 statistics and Bonferroni intervals of confidence.

Second and third order selection of habitats was investigated using two habitat classifications for each order, one determined by categories of vegetation cover and one determined by slope. Due to their continuous nature the habitat classifications '*scrub*', '*thicket*' and '*forest*', as defined by vegetation cover and species composition were partially pooled. The habitat categories used in the analyses were therefore: (1) *Salt marsh*; (2) *Coastal scrub*; (3) *Scrub-thicket*; short and medium height (<1.5m) vegetation; (4) *Scrub-rock*; (5) *Thicket*; (6) *Thicket-forest,* mixed stands of thicket and trees; (7) *Forest* and (8) *Paramo.* The slope parameter was based on availability and utilisation of habitats at or near sea-level habitat compared to those at higher altitudes (>50 m) and on mountain slopes.

While under anaesthetic the cats were weighed, measured, radio-collared, and tissue samples for DNA analysis were collected. A uniquely coded PIT tag was implanted sub-cutaneously for identification purposes. Following handling, animals were returned to the traps and given water and food. They were released when alert and co-ordinated, usually some 2-3 hours later, at the site of capture.

7.3.2 Radio-tracking

Field work was conducted during four 10-week periods (October to December 1997, January to March 1998, October to December 1998, January to March 1999) totalling 175 days at PNLSR. Detailed information on capture and handling of kodkods can be found in Dunstone *et al.* (in submission) Activity patterns, range size, spacing pattern and habitat use were derived from radio-tracking data. Kodkod were fitted with transmitters (CONF 1A *Telonics Mesa, Arizona*) on a collar of butyl construction incorporating a whip-antennae. The transmitter package (weight 22 g) had an operational battery life of 4.3 months and a potential line of sight range of 4 km;

although within the forest a 500m range was more typical. The transmitters were fitted with activity sensors (S6B) that produced a change in signal when the animal was inactive. Animals were tracked using receivers (model TR4, *Telonics*, *Mesa, Arizona*) with hand-held 3-element Yagi antennae. The locations of kodkods were estimated by triangulating from three or more radio-fix bearings or direct sightings, then plotted onto field maps. A 24 h period was covered by dividing it into four, 6-h shifts. During a given day a complete 24 h coverage of focal cats was aimed for, or alternatively track individuals for 12 hours and then cover the neglected period the following day. As it was possible to locate most of the radio-collared cats at any time of the day or night within the study area it was thought unlikely that the data-set were biased by sampling.

Radio-locations ('fixes') were usually taken systematically at 30 minute intervals. The timing of the tracking shifts and intervals between fixes were pre-determined and therefore not influenced by the behaviour of the animal. While taking fixes, the signal was recorded as either (i) moving, (ii) stationary but active, (iii) stationary but inactive or (iv) 'indeterminate', based on diagnostic patterns in signal strength and pulse frequency (sensor switch). Only clearly defined cases were used in the analyses. Because the likelihood of incorrect activity classification can be great (Janis *et al.* 1999) activity was also characterised by recording changes in speed. Weather conditions were recorded at the time of each fix as were the presence and location of other collared animals if they were in the vicinity of the target animal. Radio-tracking data was analysed using Ranges V package (Kenward & Hodder 1996) and the home range polygons exported to a GIS (*ArcView*) incorporating habitat classification derived from aerial photography. Core areas were calculated utilising kernel analysis whereby the aggregation of fixes are treated separately as in cluster analysis (Kenward 1987). I did not attempt to reduce auto-correlation within the radio-tracking data-set since broadly equivalent sampling effort was applied to radio-tracking in all habitats. Furthermore, the mean day range area was estimated to be similar to the size of most forest patches, thus individual kodkods were potentially able to move easily between habitat types. In addition auto-correlation based on area use was high for most animals. To reduce this would require the assignment of fixes at intervals of greater than two days, which would then result in under-sampling the data-set.

7.4 Results

7.4.1 Study animals

Ten kodkods were captured using nine traps, of which six were fitted with radio-collars. Weights ranged from 1.3 to 1.5 kg for adult females (n= 3) and 1.4 to 1.5 kg for sub-adult or young adult males (n=2). All adult males weighted 1.9 kg (n=3), and a juvenile male weighted 0.9 kg when first captured (Table 7.1). Age class was based on body weight, tooth wear, and subsequently confirmed on the basis of their observed territorial behaviour.

Animals were located on 38 to 66% of total tracking days (Table 7.2).

Table 7.1. Basic description of the kodkods captured at Parque Nacional Laguna San Rafael (PNLSR). Weights are in kg and measurements in cm, sex are M (males) and F (females) in the ID column.

Name	ID	Status/Age	Colour	Weight (kg)	Total length (cm)	Tail length (cm)
Shakey	M1	Subad. male	spotted	1.4	62.5	21.2
Christian	M2	Subad. male	spotted	1.5	64.3	23.2
Oscar	M3	Adult male	black	1.9	64.0	21.3
Lana	F4	Adult. female	spotted	1.5	59.8	21.1
Laura	F5	Adult. female	spotted	1.4	59.8	21.0
Tibbles	M6	Juv.male	black	0.9	48.0	17.2
Victor	M7	Adult male	black	1.9	59.0	19.5
Juliet	F8	Adult female	spotted	1.3	60.0	20.3
DeeDee	F9	Juv. female	black	0.9	51.5	17.0
Rafael	M10	Adult male	spotted	1.9	66.5	23.0

Table 7.2. Summary of locational data obtained at PLSR for six kodkods

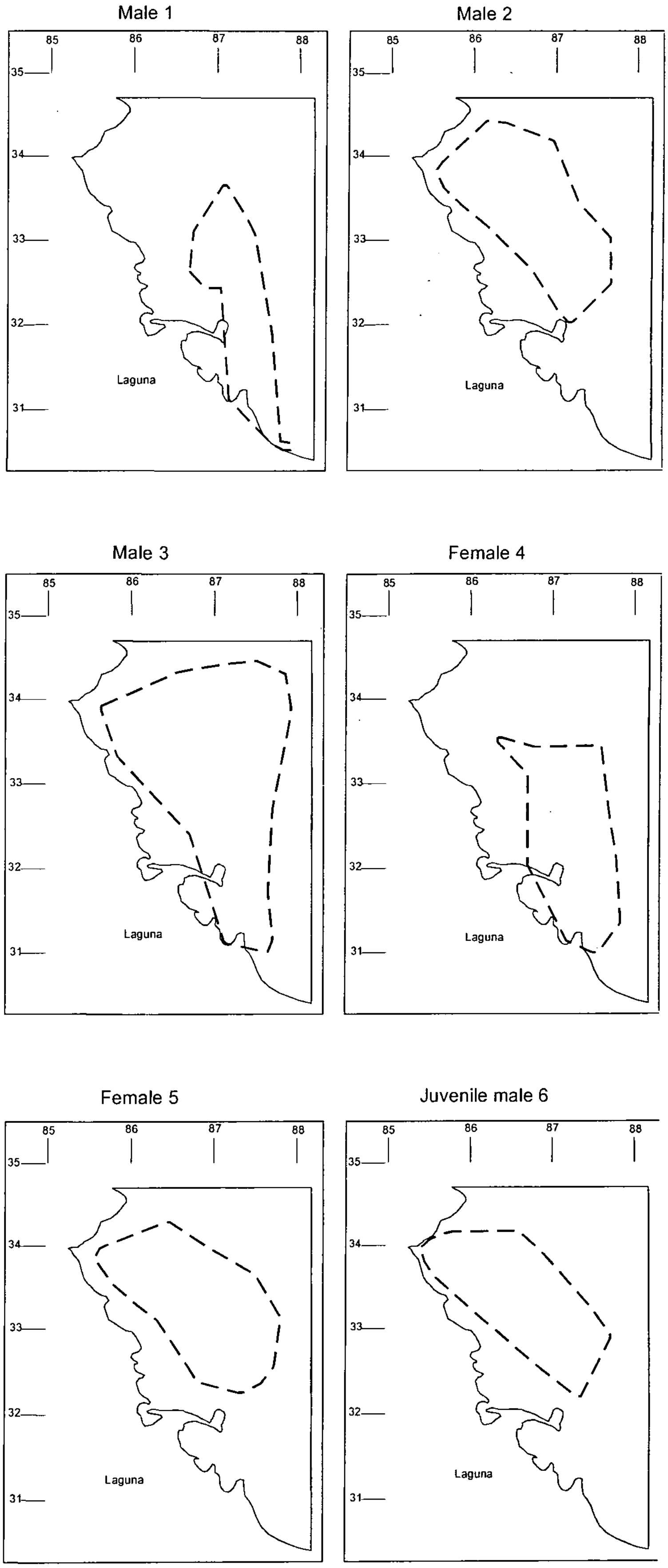
Animal	Total tracking days	number of days contacted	percent of days contacted
M1	80	53	66
M2	74	38	51
M3	94	36	38
F4	67	35	52
F5	74	45	61
M6	85	35	41

7.4.2 Home range sizes

A total of 3,826 fixes were obtained over the course of the study averaging 21.8 fixes/day, ($\overline{X}$=513, SD=175 per animal) plus an additional 135 habitat utilization plots and 566 activity pulse and weather recordings.

Two measures of calculating home range size were employed, minimum concave polygons (MCP) (Stickel, 1954; Harvey & Barbour, 1965; White & Garrot, 1990) and kernel analysis (Worton, 1989). Minimum concave polygon method was chosen as opposed to minimum convex polygon because this method excluded un-utilised areas such as the lagoon and the marsh plains. Concave polygons derived from the home range analysis were overlaid on a 1 km^2 grid UTM map of the study area (Figure 7.2). The total area occupied by the home ranges of radio-tracked individuals (1 adult male, 2 sub-adult males, 2 adult females, and 1 offspring) was 5.14 km^2.

Figure 7.2. Kodkod home ranges (MCP). Dotted lines are kodkod home ranges. Co-ordinates are in UTM (i.e., each grid a $1km^2$).



Male 1

Male 2

Male 3

Female 4

Female 5

Juvenile male 6

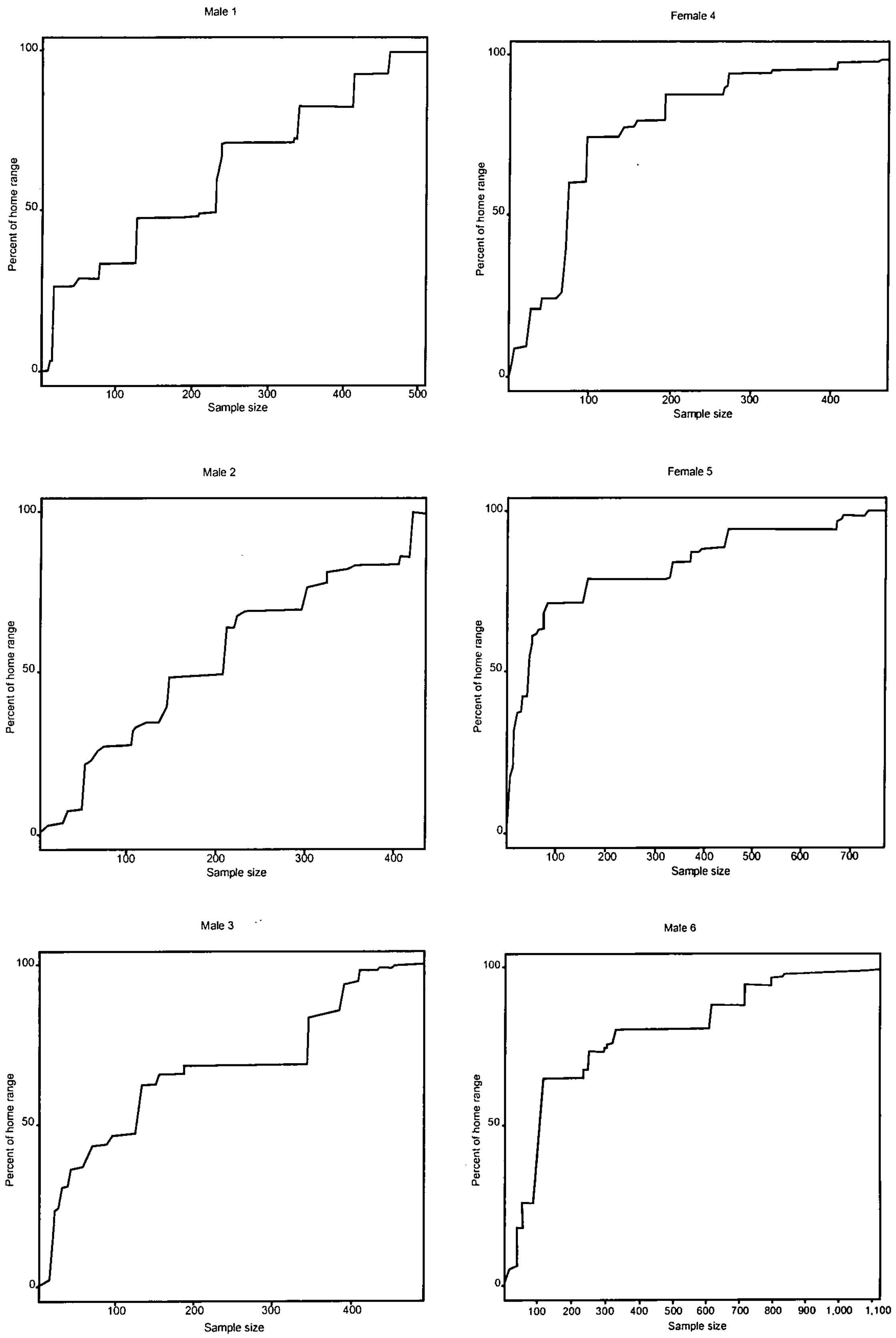
On this basis the density of the adults and sub-adults combined is 0.97 individuals/km^2. However, two additional animals were captured within this area, but not radio-tracked. Thus it was impossible to determine if they were residents or transient animals. If they are assumed to be residents, the density of kodkod in the area would be 1.56 individuals/km^2. Average home range size estimated using MCP was 2.6 km^2 and fixed kernel analysis based on 90% inclusion was 1.2 km^2 (Table 7.3).

Table 7.3. Home range of kodkods (in km^2), estimated using the method of Minimum Concave Polygons with 50 m grid cells and Fixed Kernel (90%) analysis.

Animal	Number of fixes	Concave polygon	Fixed Kernel
M1	512	1.7	0.8
M2	434	2.6	1.1
M3	497	4.4	2.2
F4	476	2.3	0.9
F5	779	2.6	0.9
M6	1121	2.3	1.2

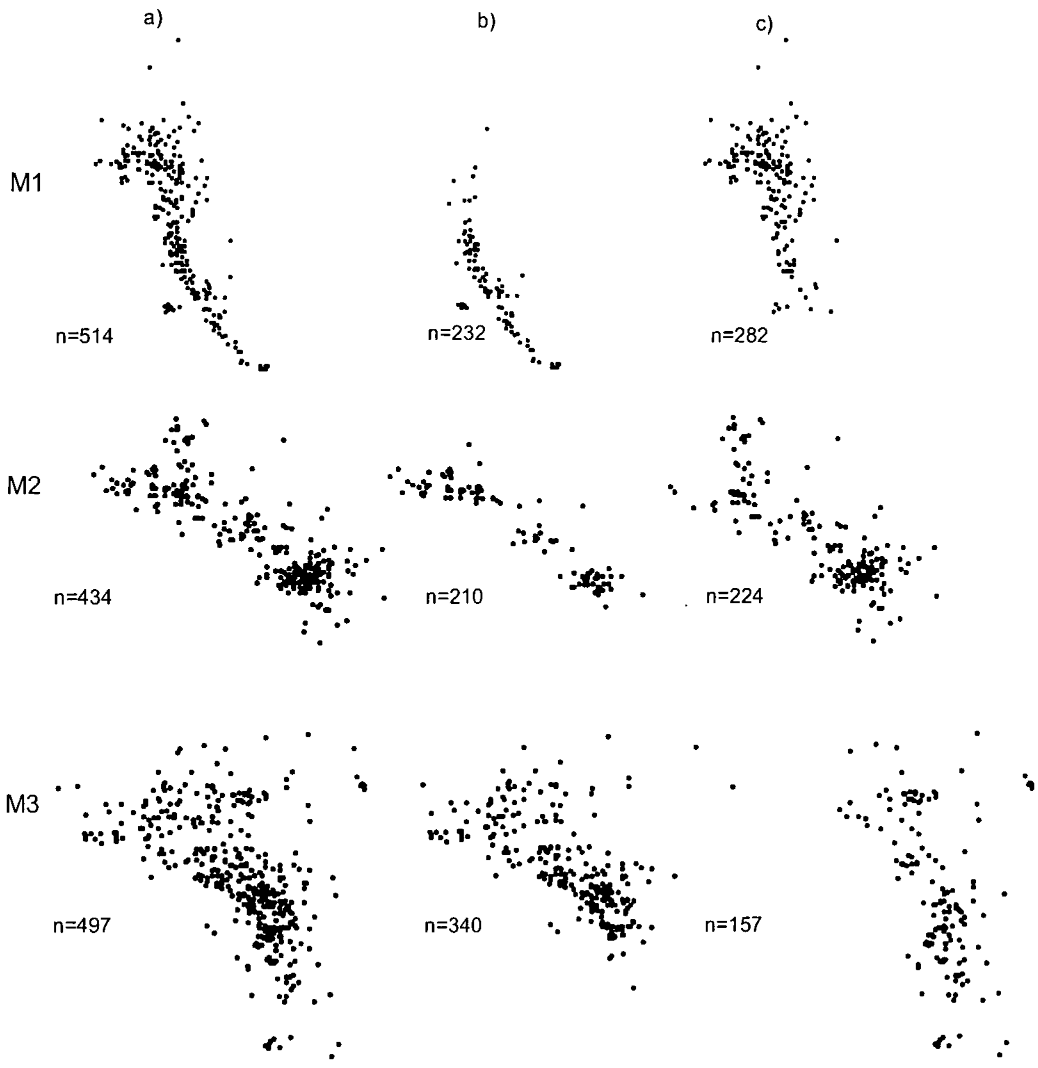
Figure 7.3 illustrates how the estimated home range area (calculated using MCP) (area curve, Odum and Kuenzler 1955) increases as a function of cumulative radio-tracking effort. While the home ranges of the two females and a juvenile seem to reach an asymptote, those of males appear not to have stabilised.

Figure 7.3. Area curves for the six individual kodkods.



Males 1 and 3 used different areas of their range during the study by expanding northward and southward, respectively, while male 3 also extended his range by utilising the outermost areas. The criteria utilised to display first and second set of plots was based on noticeable range expansion (Figure 7.4).

Figure 7.4. Utilisation of home ranges by three individual male kodkods, a) total plots b) and c) first and second set of plots.



7.4.3 Range Overlap

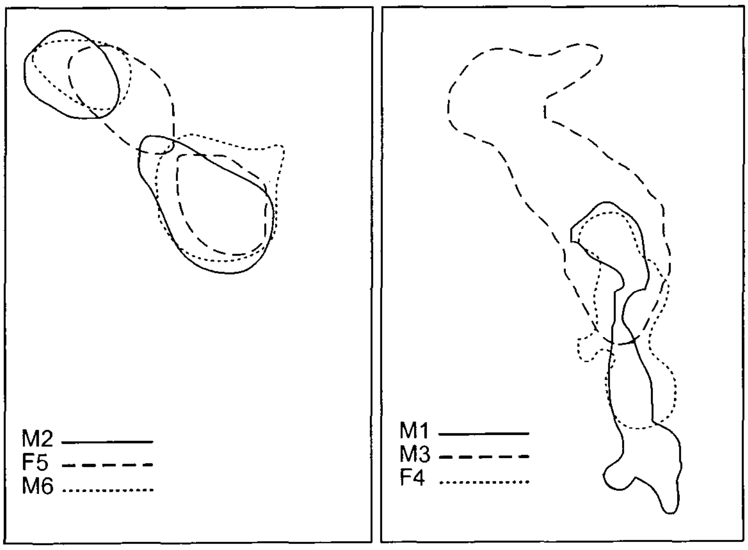
Fixed kernel core areas based on 75% utilisation isolynes were generated for each kodkod in RangesV. The software automatically overlaid core areas and output range overlaps (Table 7.4). For instance male 3 had the largest core area, encompassing 93% of F5, 78% of M6 and 77% of M2 core areas; but no part of the ranges of other animal's encompassed more than 50% of his core area. Animals that displayed a more even overlap included M2 and M6 with above 70% overlap each, and over 50% overlap was found between M6 and F5, M2 and F5, M1 and F4.

Animals M2, F5 and M6 possessed two distinct core areas, while the others had only one (Figure 7.5).

Table 7.4. Overlap of core areas (based on 75% inclusion of fixes in fixed kernel analysis) expressed as percent of home range. Home range of individuals in rows are encompassed by home ranges of individuals in columns.

	M1	M2	M3	F4	F5	M6
M1	100	27	41	57	21	24
M2	19	100	77	14	55	78
M3	17	45	100	23	45	46
F4	55	19	54	100	15	16
F5	17	66	93	13	100	72
M6	17	77	78	12	59	100

Figure 7.5. Overlay of core area contours (75% fixed Kernel) for six kodkods.



7.4.4 Habitat utilisation

The PNLSR study area (see Figure 7.1) encompassed approximately 9 km^2 with maximum dimensions of 2.9 km by 4.6 km. The approximate areas of the major habitat types within the site, as determined from aerial photography are given in Table 7.5. The predominant habitat is dense scrub-thicket and forest, which is bounded by coastal scrub, scrub-rock and saltmarsh. Inland the terrain rises steeply through densely forested slopes to areas of open paramo.

Table 7.5. The approximate size of the seven major habitats within the PNLSR study site.

Habitat type	Area km^2
Forest	3.63
Scrub thicket	1.57
Paramo	0.92
Thicket forest	0.90
Scrub coast	0.86
Thicket	0.49
Salt marsh	0.31
Scrub rock	0.29

7.4.4.1 Proportion of habitats within the kodkod's home ranges (2nd order selection)

The areas of the different habitat types available within the home range of each radio-tracked kodkod in this study are shown in Table 7.6. Forest, thicket forest, and scrub-thicket habitats predominate, whereas thicket and open areas (scrub-rock, coastal scrub and paramo) were less likely to be included within the ranges.

The more varied habitats found at lower elevations (<50 m) predominated within kodkod ranges ($\overline{X}$=72%, SD=14) compared to the more homogeneous forests intermingled with paramo at higher altitudes.

7.4.4.2 Habitat preference/avoidance (3rd scale selection)

A comparison of the observed habitat utilisation and that expected on the basis of availability is shown in Table 7.6 and Figure 7.6. Some individual variation was apparent, all the habitat types available, with the exception of paramo and thicket, were utilised more frequently than expected by at least one of the kodkods. This probably facilitated extensive home range overlap while still maintaining a degree of spatial separation. Habitat preference/avoidance was tested using χ^2 Goodness-of-Fit with

Bonferroni intervals of confidence. These analyses (Table 7.6) indicated that kodkods at PNLSR exhibit a consistent preference for thicket-forest.

Four main patches of thicket-forest were identified; the largest was 0.52 km^2 in size and elongated along the north-south axis. Two patches were located to the north of the site and were 0.06 and 0.23 km^2 in area. The patch to the south was 0.05 km^2 in area and comprised an 'island' that was regularly isolated from the mainland by the high tide. Kodkods would transverse 100 m of open beach from the nearest forest patch to reach this thicket forested island. However, they did not traverse the full length of thicket (520 m) or of scrub-thicket (900 m) to reach an isolated patch (0.06 km^2) of thicket-forest in the north. No individuals encompassed areas of saltmarsh within their home range. Paramo and coastal scrub habitats were also avoided. Of the six kodkods radio-tracked, only two utilised sea level habitats and slope areas in a similar proportion to their availability within their respective ranges, while the remaining four animals preferred lower elevations (Table 7.7). The juvenile kodkod (M6) was frequently found (11% of 1072 fixes) located in a woodshed 15 m from the ranger station.

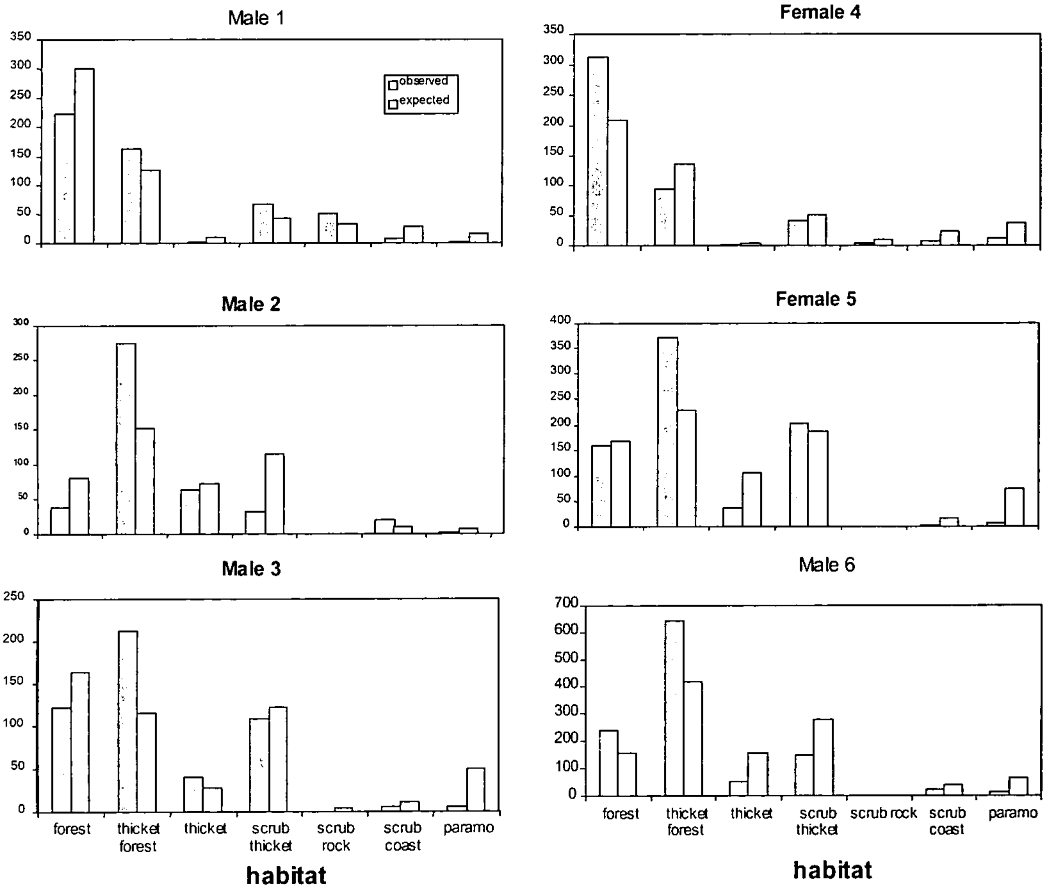
Table 7.6. Statistics of habitat use, using χ^2 and Bonferroni ($\alpha=0.10$) intervals of confidence. The proportion of available area (pi_0) is compared with the theoretical proportion of occurrence (pi) to determine if the hypothesis is accepted or rejected, i.e., $pi=pi_0$. If $pi_0>pi$ the animal is using the habitat (k) less than expected, if $pi_0<pi$ it is using more than expected.

Animal	Habitat (k)	Proportion of available area (pi_0)	Number of fixes observed	Number of fixes expected	χ^2	Proportion observed in each area (pi)	Confidence interval on proportion of occurrence (pi)	Habitat selection
Male 1	forest	0.50	223	302	21	0.43	$0.38 \le p_1 \le 0.49$	-
$Z_{0.993}=2.45$	thicket forest	0.21	163	127	10	0.32	$0.27 \le p_2 \le 0.37$	+
	thicket	0.02	2	9	6	0.00	$0.00 \le p_3 \le 0.01$	-
	scrub thicket	0.07	67	42	14	0.13	$0.09 \le p_4 \le 0.17$	+
	scrub rock	0.05	51	33	10	0.10	$0.07 \le p_5 \le 0.13$	+
	scrub coast	0.05	7	28	16	0.01	$0.00 \le p_6 \le 0.03$	-
	paramo	0.11	1	15	13	0.00	$0.00 \le p_7 \le 0.01$	-
Male 2	forest	0.19	39	81	22	0.09	$0.06 \le p_8 \le 0.12$	-
$Z_{0.982}=2.10$	thicket forest	0.35	274	152	97	0.63	$0.58 \le p_9 \le 0.68$	+
	thicket	0.17	65	73	1	0.15	$0.11 \le p_{10} \le 0.19$	=
	scrub thicket	0.27	32	116	61	0.07	$0.05 \le p_{11} \le 0.10$	-
	scrub coast	0.02	21	11	10	0.05	$0.03 \le p_{12} \le 0.07$	+
	paramo	0.01	2	6	3	0.00	$0.00 \le p_{13} \le 0.01$	=
Male 3	forest	0.33	122	165	11	0.25	$0.20 \le p_{14} \le 0.29$	-
$Z_{0.9927}=2.44$	thicket forest	0.23	212	116	79	0.43	$0.37 \le p_{15} \le 0.48$	+
	thicket	0.06	41	28	6	0.08	$0.05 \le p_{16} \le 0.11$	=
	scrub thicket	0.25	109	122	1	0.22	$0.17 \le p_{17} \le 0.26$	=
	scrub rock	0.01	1	4	2	0.00	$0.00 \le p_{18} \le 0.01$	=
	scrub coast	0.03	6	12	3	0.01	$0.00 \le p_{19} \le 0.02$	-
	paramo	0.10	6	50	39	0.01	$0.00 \le p_{20} \le 0.02$	-
Female 4	forest	0.44	312	209	50	0.66	$0.60 \le p_{21} \le 0.71$	+
$Z_{0.9928}=2.44$	thicket forest	0.29	95	136	12	0.20	$0.15 \le p_{22} \le 0.24$	-
	thicket	0.01	2	5	2	0.00	$0.00 \le p_{23} \le 0.01$	=
	scrub thicket	0.11	42	52	2	0.09	$0.06 \le p_{24} \le 0.12$	=
	scrub rock	0.02	5	11	3	0.01	$0.00 \le p_{25} \le 0.02$	=
	scrub coast	0.05	8	24	11	0.02	$0.00 \le p_{26} \le 0.03$	-
	paramo	0.08	12	38	18	0.03	$0.01 \le p_{27} \le 0.04$	-
Female 5	forest	0.22	160	168	0	0.21	$0.17 \le p_{28} \le 0.24$	=
$Z_{0.9916}=2.39$	thicket forest	0.29	371	228	90	0.48	$0.43 \le p_{29} \le 0.52$	+
	thicket	0.14	36	105	46	0.05	$0.03 \le p_{30} \le 0.06$	-
	scrub thicket	0.24	203	186	2	0.26	$0.22 \le p_{31} \le 0.30$	=
	scrub coast	0.02	2	18	14	0.00	$0.00 \le p_{32} \le 0.01$	-
	paramo	0.09	7	74	60	0.01	$0.00 \le p_{33} \le 0.02$	-
Male 6	forest	0.14	238	155	41	0.21	$0.19 \le p_{34} \le 0.24$	+
$Z_{0.9916}=2.39$	thicket forest	0.37	645	415	120	0.58	$0.55 \le p_{35} \le 0.62$	+
	thicket	0.14	55	155	67	0.05	$0.03 \le p_{36} \le 0.07$	-
	scrub thicket	0.25	148	275	61	0.13	$0.11 \le p_{37} \le 0.16$	-
	scrub coast	0.04	23	41	9	0.02	$0.01 \le p_{38} \le 0.03$	-
	paramo	0.06	15	67	42	0.01	$0.01 \le p_{39} \le 0.02$	-

Table 7.7. Statistics of slope use, using χ^2 and Bonferroni ($Z_{0.975}=1.96$, $\alpha=0.10$) intervals of confidence. The proportion of available area (pi_0) is compared with the theoretical proportion of occurrence (pi) to determine if the hypothesis is accepted or rejected, i.e., $pi=pi_0$. If $pi_0>pi$ the animals is using the slope (k) less than expected, if $pi_0<pi$ it is using more than expected.

Animal	Slope (k)	Proportion of available area (pi_0)	Number of fixes observed	Number of fixes expected	χ^2	Proportion observed in each area (pi)	Confidence interval on proportion of occurrence (pi)	Habitat selection
Male 1	Plains	0.63	316	321	0	—	—	=
	Hill	0.37	196	191	0	—	—	=
Male 2	Plains	0.86	421	374	6	0.97	$0.95 \leq p_1 \leq 0.99$	+
	Hill	0.14	13	60	37	0.03	$0.01 \leq p_2 \leq 0.05$	-
Male 3	Plains	0.70	419	349	14	0.84	$0.81 \leq p_3 \leq 0.88$	+
	Hill	0.30	78	148	33	0.16	$0.12 \leq p_4 \leq 0.19$	-
Female 4	Plains	0.49	214	232	1.3	0.45	$0.40 \leq p_5 \leq 0.49$	=
	Hill	0.51	262	244	1.3	0.55	$0.51 \leq p_6 \leq 0.60$	=
Female 5	Plains	0.79	742	616	26	0.95	$0.94 \leq p_7 \leq 0.97$	+
	Hill	0.21	37	163	97	0.05	$0.03 \leq p_8 \leq 0.06$	-
Male 6	Plains	0.87	1021	980	1.8	0.91	$0.89 \leq p_9 \leq 0.92$	+
	Hill	0.13	104	146	12	0.09	$0.08 \leq p_{10} \leq 0.11$	-

Figure 7.6. Observed and expected utilisation of seven available habitat types by kodkods at PNLSR.



7.4.4.3 Activity and movement patterns

Activity was monitored in two independent ways; either by interpreting the activity pulses from the radio collar or by calculating the distance moved between consecutive fixes. For most of their time individual kodkods were active within a small area or patch, interspersed with movements (or dislocations) between patches that were accompanied by an increase in speed. Change in patch use and speed of movement between patches was determined by *visualising* kodkod movements when toggling between successive fixes within the Ranges V analysis software. The movements between fixes were then compared with the speeds estimated by calculating the distance between consecutive fixes and then dividing it by the time elapsed. Within patch movements, which I refer to as *hunting*, took place at slower speeds (<500 m/h) than movements between patches (*travelling*).

The pattern of activity based on movements between successive fixes was generally similar for all radio-tracked kodkods. Individuals were recorded *hunting* between 60 to 80% of their time (see Table 7.8). The exception to this general pattern was M1 who was active for only 48 % of his time. This could be due to the larger areas of forest in his range (Figure 7.6) and/or a lesser degree of home range overlap with other kodkods. Subtle circular movements within a patch are unlikely to be detected by radio-tracking, but with the help of the activity sensor it was possible to determine that animals were active (i.e. not resting) between 19 and 29% of all stationary radio-fixes.

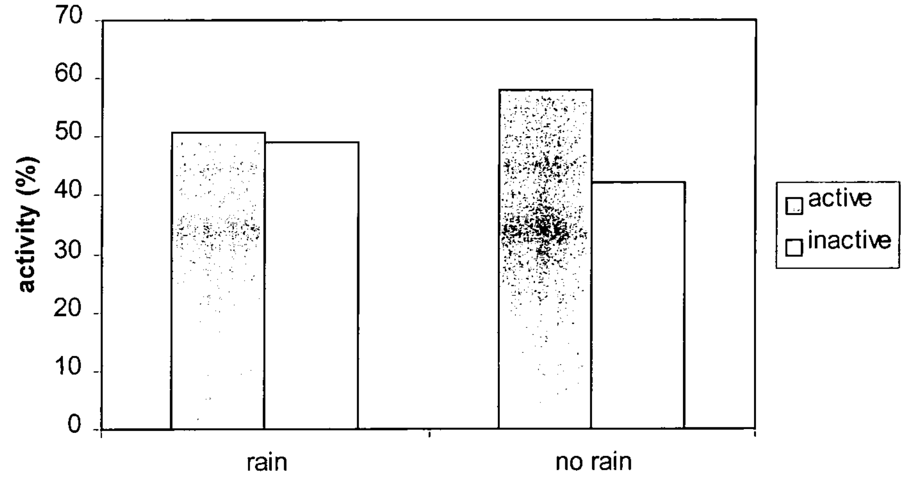
Table 7.8. The proportion of observations spent in different activities. *Hunting* and *travelling* are percentages derived from *moving*.

Animal	n (fixes)	Moving (%)	Hunting (%)	Travelling (%)
M1	518	48	82	18
M2	418	60	91	9
M3	480	77	81	19
F4	459	81	82	18
F5	764	80	87	13
M6	1108	63	88	12

No significant changes in speed was found during periods of rainfall (ANOVA, *F*=0.74, *df*=3561, *p*>0.05) or between movements occurring by night or by day (ANOVA, *F*=0.07, *df*=3707, *p*>0.05).

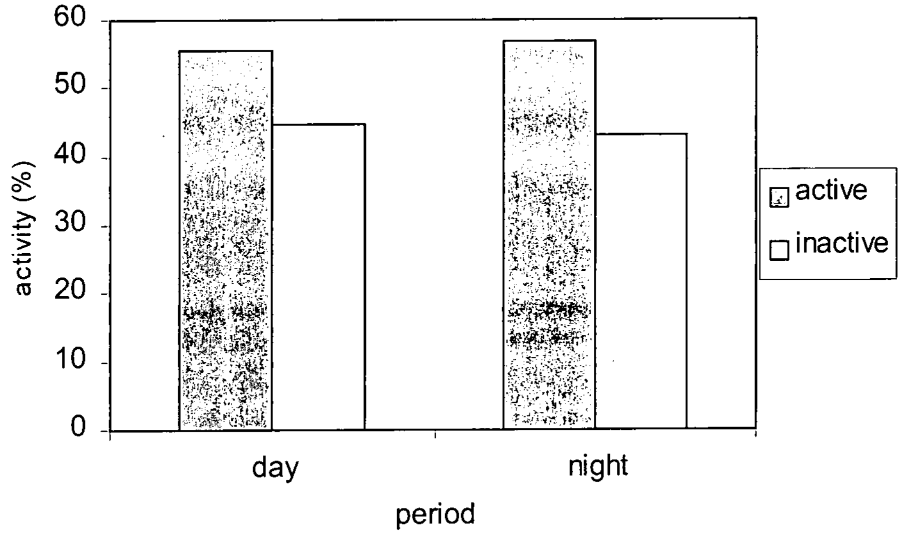
No apparent changes in activity was detected during periods of rainfall (Figure 7.7)

Figure 7.7. Comparison of activity of kodkod under different weather conditions.



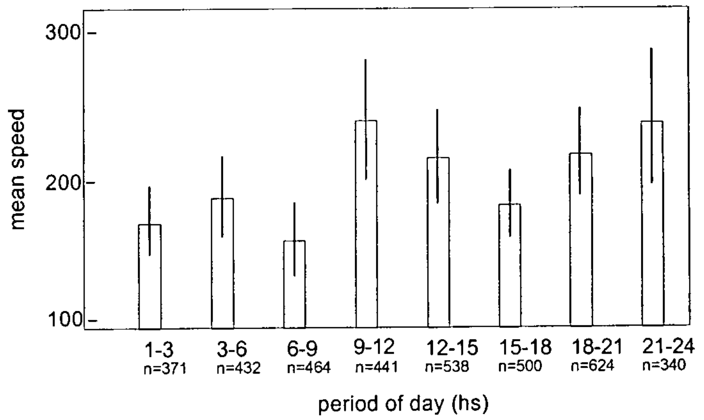
Levels of activity during night and day based on activity pulses (Figure 7.8) were similar to those obtained in speed recordings.

Figure 7.8. Comparison of active of kodkod during day and night periods based on activity pulses.



Significant difference in the frequency of movements were found between different periods of the day (ANOVA, *F*=5.3, *df*=3708, $p<0.05$) (Figure 7.9). Movements were of slower speed between 06:00 and 09:00, and higher between 09:00 and 12:00 and between 21:00 and 24:00. Kodkods moved significantly slower at dawn ($\overline{X}$=146, SE=14) than at dusk ($\overline{X}$=233, SE=17) and other periods ($\overline{X}$=206, SE=6) (ANOVA, *F*=5.5, *df*=3705, $p<0.05$).

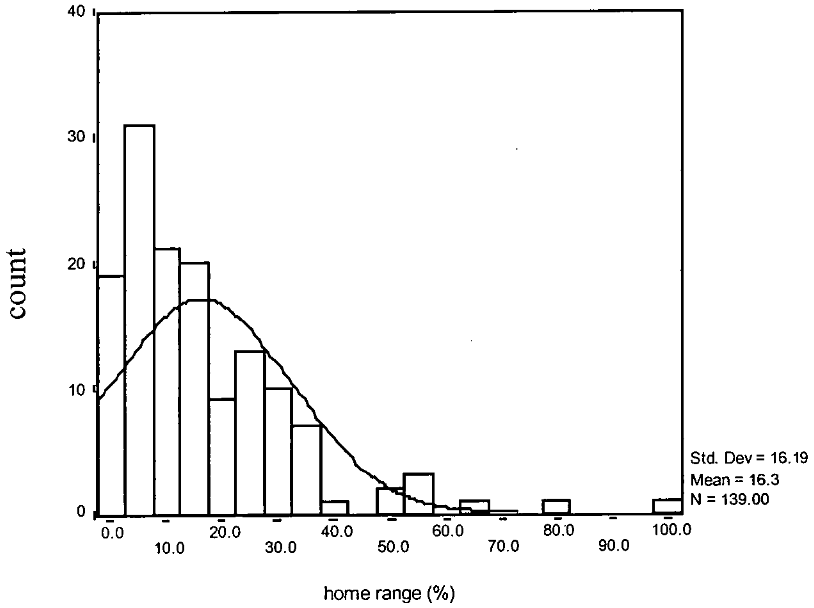
Figure 7.9. Activity pattern of kodkods based on mean speed of movement during different hours of the day and night. Bar indicate means, and lines are SE.



7.4.4.4 Day ranges

In order to verify what proportion of its total range each cat used on a daily basis, I calculated 100% Minimum Convex Polygons of 139 daily home ranges using the software Ranges V. The results are presented as a histogram in Figure 7.10. An average of 16.3 of the kodkods' home range was utilised daily (SD=16.9).

Figure 7.10. Frequency distribution of day range areas (in percent) for the six kodkods. Statistics are Standard Deviation, Mean and number of day range areas.



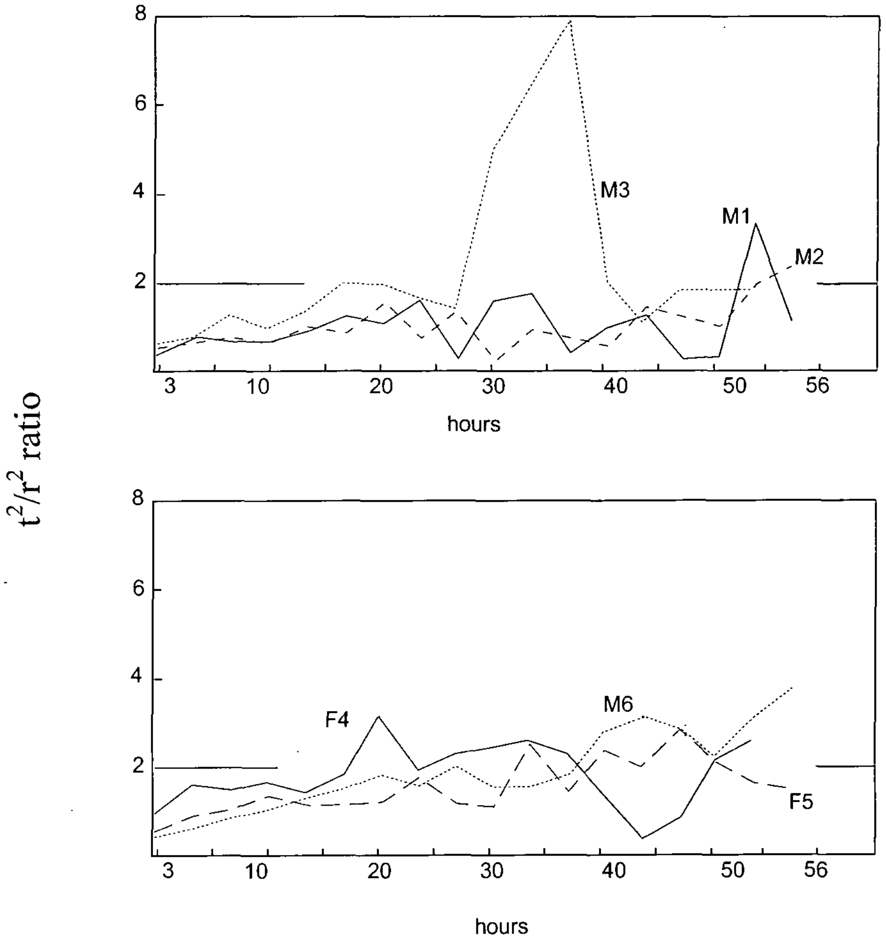
The geometric centre of each day range was determined and the distance between the range centres on consecutive days was calculated. These were found to be smaller than the largest axis of the range, suggesting circular movements within the range (Table 7.9).

Table 7.9. Average distance between range centres on consecutive days and average range span along its largest axis.

Animal	n days	Distance from centres ($\overline{X}$)	Range Span ($\overline{X}$)
M1	18	588	868
M2	17	436	746
M3	18	460	946
F4	12	398	881
F5	28	294	902
M6	26	402	870

A strong correlation was found in range use even after two days. Figure 7.11 plots the increasing sampling intervals in hours on the x-axis and Schoner's index (see Swihart and Slade 1985, Kenward and Hodder 1995) on the y-axis. If the value of the index is low, this indicates a high correlation between distance and time, e.g., because during short sampling intervals the animal did not have time to move far before it was next located. Swihart and Slade (1985) proposed that the sampling interval at which 3 consecutive values on the y axis are higher than 1.96 represents the time at which distances between fixes no longer depend appreciably on time. A line is drawn across the graph at this level.

Figure 7.11. Autocorrelation graphs of kodkod home range utilisation. (t^2 is the mean squared distance between successive fixes, and r^2 is the mean squared distance of observation from the core areas).



7.5 Discussion

The relative ease with which kodkods could be trapped increases their potential for scientific study. Males M1 and M2 were probably young animals at date of first capture since they were well below the weight of adult males. Body weights of adults were similar to those reported on Chiloé (Sanderson & Sunquist unpubl.manuscr.). Weight differences between individual cats were considerably greater than differences in body length, however, none of the cats appeared to be undernourished, or in ill health. A higher incidence of melanism (40%) is reported here than on Chiloé (14%) (Sanderson and Sunquist unpubl. manuscr.).

7.5.1 Home range and density

The mean home range sizes (based on minimum concave polygons) of sub-adult males and a juvenile male was 2.2 km^2, whereas two adult females averaged 2.5 km^2, and one adult male had a range size of 4.4 km^2.

In a human-fragmented landscape in Chiloé, Sanderson and Sunquist (unpubl.manuscr.) reported the ranges of two adult males and two adult females to average 3.6 km^2 and 1.26 km^2 respectively (MCP $n>100$). The same authors found ranges of two adult male to be smaller (1.7 and 1.8 km^2) in continuous forests.

However at PNLSR the similarity of home range sizes between females 4 and 5 suggests that differences in the composition of their habitats did not influence range size. While forest predominated in the home range of female number 4, thicket-forest and scrub-thicket predominated in that of female number 5.

There is a two-fold difference in home range size of females from PNLSR and Chiloé. These could be attributable to the relative differences in abundance of resources at the two sites. The high degree of home range overlap or relatively lower prey availability at PNLSR may force females to hunt over larger areas.

The kodkods at PNLSR lack inter-specific interference and/or competition from other mammalian carnivores, which are present on Chiloé and which could theoretically result in larger home range sizes due to a lowered prey base. Several species of raptor, however, were known to be present at PNLSR, and are thus potential competitors for the mammalian prey base. The only mammalian predator known to be present within the study area was *Galictis cuja*. Foxes do not inhabit this part of the PNLSR. Rangers reported that puma occasionally pass through the study area in winter. A relatively high degree of spatial overlap between core areas within the ranges of individual kodkods was found (Figure 7.5), but concomitantly, some differential use of habitats by individual kodkods appears to allow use of resources at different spatial and temporal scales (Figure 7.6). The exception to this concerned female (F5) and her partially-dependent offspring (M6) who showed maximal range overlap probably indicating some dependency of the juvenile on the female. Such flexibility in resource use and mutual avoidance, at least in the temporal domain, may help explain why kodkod can sustain a high degree of overlap of core areas, and thus reach high densities. This high degree of adaptability may well be relevant to the long term survival of this species in an ever increasingly anthropogenically modified environment.

7.5.2 Habitat utilisation

Kodkods included in their range more forest, thicket-forest and scrub-thicket than other habitat types (2nd order selection) and selected for thicket-forest, and against paramo and coastal scrub at the 3rd order level of selection. A preference for habitats near or at sea level rather than on slopes was noted (Table 7.7); the former are associated with mixed scrub-thickets and thicket-forests and the early succession stages of *Nothofagus* forests. It is likely that this habitat preference is associated with availability of prey, since these younger stages of succession may harbour greater populations of prey than are found in forests at later stages of development. This has previously been shown for Patagonian forests by Pearson and Pearson (1982), and recently demonstrated for temperate forests in the northern hemisphere (Fernandez, Evans & Dunstone 1994, 1996; Fernandez, Dunstone & Evans 1999).

The rather compartmentalised home range utilisation by the kodkod (Figure 7.4, 7.11) is presumably linked to the spatial distribution of its prey. Foraging theory predicts that consumers will feed in the patch with the highest density of prey. Once the prey density in that patch equals that of the next richest patch consumers will feed on both patches. As the process continues consumers will gradually be feeding in an increasing range of patches (Royama 1971). While depletion of food resources is the "basic" process underlying habitat use for many species, for territorial species, intra and inter-specific interference may cause differential habitat use. However, intra-specific avoidance does not seem to be a major problem faced by kodkods in this study area as shown by the extensive range and core area overlaps. Inter-specific competition which may also lead to interference does not seem occur in the study area, since potential competitors like the fox and other predators are absent.

The restricted mobility of the kodkod's prey and the apparently low level or lack of intra and inter-specific interference, may have resulted in a home range utilisation that resembles an ideal free distribution (Fretwell and Lucas 1970); that is, individuals go to the patch where the rewards are highest and are not constrained by restricted dispersal.

In a preliminary survey of the small mammal fauna at PNLSR it was found that *Akodon olivaceous* was the most abundant rodent species (Scott *et al.* 1999). This species is known to occur at high densities ranging from 25 to 100 animals per ha, and to favour grass and brush areas (Robson and Redford 1992) although they may also range into semi-arid shrub-land with as much as 46% bare ground (Pearson 1983). This species has also been shown to be the most frequently occurring species in the kodkod's diet at this site, followed by *Irenomys tarsalis* and *Auliscomys micropus,* and the marsupial *Dromiciops australis*. Together these species of small mammals comprised 48% occurrence of the kodkod's diet (Dunstone *et al.* in submission). With the possible exception of *I. tarsalis*, these small mammals favour the early stages of forest succession (Pearson and Pearson 1982), and can achieve high densities in these habitats. Patterson *et al.* (1989) demonstrated that *D. australis* and *A. micropus* were more common at higher altitudes, however, they did not sample at altitudes below 425 m.

The status of kodkods immediately outside the study area at PNLSR is unknown although attempts have been made to capture kodkods at the fringes of the study area, with little success (two sightings and one capture). The kodkod population at PNLSR may well be geographically isolated by the presence of the Andes which present a formidable barrier to the dispersal of kodkods to the east, as do the ice-fields to the south and ocean to the west. Kodkods have been previously recorded up to the tree line at 1900 - 2500 m (Miller and Rottmann, 1976, Melquist 1984), though towards the southern limit of their distribution (PNLSR) the tree line can be as low as 500 m (Hueck and Seibert 1981).

The geographical range of the kodkod includes substantial areas that are inhospitable to mammalian life. Permanent ice caps and mountainous areas reduce the area of habitat available to cats. It is thus important to distinguish between "ecological" population density by which I imply the number of cats present in suitable habitat rather than their "crude" density calculated over the entire range, estimated at 160,000 km^2 (Nowell and Jackson 1996). The Patagonian Ice Sheet, the third largest in the world, encompasses an inhospitable area of 17,000 km^2. It runs parallel to the Pacific coast preventing range expansion of the kodkod to the east. The eastern edge of the ice sheet is located just 2.5 km to the west of the PNLSR study area and extends throughout Region XI from about 46° S to 50°S. Given this extreme environment it is not surprising that approximately 90% of the kodkod's geographical range is largely free from human occupation and other human mediated disturbance. In other parts of their range, e.g. Chiloé, they are able to live in human fragmented landscapes where they are acknowledged to be predators of poultry near households (Sanderson & Melquist in press), which can often result in persecution (Nowell and Jackson 1996).

Kodkods also appear to tolerate some human disturbance in PNLSR. Some core areas within PNLSR encompassed the only human habitation – the ranger's station – where sightings of cats were common and where activity was concentrated, perhaps as a result of rubbish tipping. They also did not seem adverse to traversing distances >100 m across open beach to reach an isolated patch of thicket-forest during the day or night.

Although there seems to be an strong habitat association of the kodkod with Valdivian and *Araucaria* forests at 1st order habitat selection (Redford and Eisenberg 1992, J.Rottmann *in litt.* 1993), the results found in the current study suggests a more flexible habitat association at 2nd and 3rd order levels. This flexibility may enable this species to utilise resources in a variety of habitats in a manner such as to allow extensive home range overlap and thus achieve high densities. It may be that a mosaic of different habitats is necessary for the long-term survival of kodkod populations, as various prey (and other resources) become available at different times of the year.

Chapter 8: General discussion

Several approaches have been used towards the conservation of wildlife and habitats. These include conservation of threatened species, hotspots, community based conservation, tourism, wildlife exploitation, etc. These approaches usually require knowledge of the species inhabiting them. The conservation of hotspots has been suggested (Myers 1988, 1991) as a more beneficial and cost effective strategy than the conservation of individual threatened species.

There are many reasons to continue species conservation programs (Bright and Morris 2000, Muruthi *et al.* 2000), although deciding which species the conservation effort should be directed to is more complicated. Those considered to be vulnerable, *keystone* or *umbrella* species are usually believed to be the most important (Paine 1966, Howe 1984, Terborgh 1986, Cox *et al.* 1991, Primack 1993, Heywood 1995, Meffe and Carrol 1997, Simberloff 1998, Abrams 1999).

Vulnerability can be assessed in a number of different ways (e.g. IUCN 1994, Nowell and Jackson 1996, Weaver *et al.* 1996). Usually this is a difficult task due to the lack of basic information, such as relative abundance throughout the species' geographic range. For example, five species of Neotropical cats are considered "*indeterminate*" or "*insufficient known* "under the IUCN (1994) criteria due to the lack of demographic data. Nowell and Jackson (1996) developed a broad approach which enabled the ranking of vulnerability status among felids. As these authors have noted, further research is needed on species' biology, particularly in the Neotropics. Demographic and meta-population parameters are required to provide an accurate indication of current trends in their populations.

Berlow *et al.* (1999) has suggested that most species have only a weak or no detectable effect on the abundance of other species, while a few have strong effects. Top predators are usually considered important in maintaining biodiversity in general (Willis 1974, Jansen 1978, Greene 1988, Terborgh 1990, Redford 1992, Palomares *et al.*1995, Terborgh *et al.* 1997, Soulé and Terborgh 1999), and can thus be considered as *keystone* species. Predators which utilise large areas as territory are referred to as *umbrella* species. Such species are more likely to incorporate a greater diversity of organisms in their territories when areas are located in high diversity habitats such as tropical forests.

The mountain lion and the kodkod may be considered as both *keystone* and *umbrella* species. Although the kodkod is small in size it inhabits a region with high degree of endemism (Osgood 1943), thus suggesting its role as an *umbrella* for endemic species. The role of mountain lion as a *keystone* species can be best understood in a high diversity *hotspot* area such as the Atlantic forest in Brazil (Myers 1988, 1991).

There is a paucity of information on basic demographic parameters such as relative abundance, and habitat utilisation behaviour for the kodkod (Nowell and Jackson 1996) and for the mountain lion in the Neotropics (Anderson 1983).

The study of habitat utilisation and tolerance of disturbance is relevant to the prediction of which habitats wild felids are likely to survive in, given the occurrence of environmental perturbations. With this knowledge, recommendations can be then be implemented *a priori* in commercial systems (e.g. forestry operations) in such a manner as to ensure at least a minimum habitat quality to ensure survival of their populations.

Environmental disturbances may hinder the persistence of wild felids through fragmentation of their populations and modification to their prey base (density and/or diversity). Habitat impoverishment may increase distances between and/or reduce the size of patch fragments. Although, in general, the effect of landscape on the movement patterns of animals has yet to receive detailed attention (Wiens 1997), considerable knowledge has been gained in some aspects of habitat utilisation by mountain lions living in sub-optimal habitats. This information is relevant to their survivorship in human-modified landscapes. However, for the kodkod no such data are available, and information on habitat utilisation is somewhat preliminary.

Wild felids are usually tolerant of a variety of disturbances to their habitat, but the resulting fragmentation of landscapes may result in isolation of their populations.

For example 61% of all identified "Tiger Conservation Units" are comprised of habitat fragments between which there is no connectivity (Wikramanayake 1999).

Connectivity is best considered as the maintenance of forested corridors, although this is not often possible. Species differ in their tolerance of habitat modification, and thus in the manner in which they utilise corridors at different levels of disturbance. There has been much debate on whether corridors act to increase the rate of animal movement between fragments (e.g. Haddad 1999). Some species of felids, including the mountain lion (Beier 1995) and the ocelot (Ludlow and Sunquist 1987), have been observed using forested corridors for dispersal. Corridors have also been recommended as a conservation management tool for other felid species (e.g. jaguar, Quigley and Crawshaw 1992, Leite *et al.* unpubl.manuscr., Weber and Rabinowitz 1996; ocelot, Tewes and Miller 1987, Young and Tewes 1994).

Fragmentation of habitats may have a greater impact on the community structure of the prey of large cats living in forested areas, including most of the Neotropics, than in areas where a patchy environment is part of the natural landscape. In East Africa for example, ungulates feed largely on grass, while in the Neotropics they forage on a variety of food sources (e.g. fruit) that are generally less available (see Eisenberg 1980).

Human persecution is another important source of mountain lion mortality (Currier 1983, Weaver *et al.* 1996), but they have shown resilience to intensive exploitation in western North America (Smith 1989). This is probably due to a combination of mountain lion characteristics, such as their potential for dispersal, population recruitment and use of cryptic habits. Their ability to forage over vast areas for widely scattered prey is demonstrated by female large home range sizes (e.g. 1,717 km^2) in open areas such as deserts (McBride 1976). In this case the cost/benefit ratio of foraging is likely to be equivalent to that attainable when foraging in widely dispersed high quality patches. In good quality habitats, average home range size of female mountain lions may be as small as 111 km^2 (e.g. Padley 1997a).

One question that had not been previously addressed concerns the foraging costs to large felids that are associated with subsisting in a mosaic of native and planted non-native forests in the Neotropics. In this context it is also desirable to evaluate the minimum patch size threshold required to maintain a viable range area for an individual mountain lion.

The current research has partially addressed these questions by demonstrating that the core area of the radio-tracked female mountain lion was composed of an approximately equal extent of natural forest and planted non-native forest. The female spent at least 55% of tracking days utilising a core area of 18.9 km^2, which represented 25 % of her total home range (75.5 km^2). Although the patch size of natural forest cover in the core area was small (8.1 km^2) it was connected by means of an extensive network of riverine forest which facilitated prey population immigration. Other landscape features such as the presence of steep banks in riverine forests provide additional protection for den sites for important mountain lion prey species such as the armadillo.

In addition, densities of mountain lion based on camera-trap and tracking data were comparable to estimates made in high density sites elsewhere (see Anderson 1983). Comparison of tracks seemed to yield a more conservative estimate, ranging from 0.06 to 0.09 individuals/km^2, whereas photographic comparison resulted in an estimate of 0.09 to 0.12 mountain lions/km^2.

The question still remains as to whether an even lower proportion (i.e. <50%) of natural forest could still provide adequate mountain lion habitat. This question was partially addressed by investigating the distribution of prey resources across areas which varied in the proportions of natural forest they contained. Although the relative density of prey species changes according to habitat type this does not appear to affect overall prey availability. For example, the observed reduction of coatis in non-native planted forest is substituted for by the availability of alternative prey such as deer and collared peccaries.

Mountain lion populations thus seem able to live in areas with different proportions of native forest interspersed with fragments of forest plantation. It is also well established that mountain lions are able to inhabit areas dominated by open habitats such as deserts (Anderson 1983). However, these findings conflict with that of habitat preference by the Florida Panther; Maehr and Cox (1995) recorded on ly 25% of panther radio-locations in patches smaller than 500 ha. However they did not report the precise size of patches available but suggested that the association of panthers with larger patches was possibly linked with the availability of their main prey.

Little is known concerning the degree of tolerance of the mountain lion to human presence, and which man-made disturbances other than clearings (e.g. roads, villages, timber extraction) are likely to disrupt their movement patterns.

Beier (1995) found that mountain lions in the Santa Ana mountains of California traversed narrow corridors with a high level of human disturbance. There were also a number of households in the area, but none of the adult resident mountain lions made use of nearby areas. One dispersing mountain lion established a home range which required it to cross an eight-lane highway, accomplished by using a vehicle underpass and culvert. In another study, Van Dyke *et al.* (1986) concluded that mountain lions tended to avoid logged areas, roads, and human residencies.

These patterns were not wholly supported by the findings of the present study. Here an adult female mountain lion was found to make extensive use of disturbed areas near households and close to car traffic. The fifteen year-old radio-tracked female was recorded crossing a two-lane paved road with heavy traffic 38 times during seven months, including seven known occurrences during the night and eleven times during the day. Track records indicated that she was frequently accompanied by her sub-adult offspring. Her core area also encompassed a rubbish dump, and a village (2.1 km^2 in area), within which she made extensive use of forested patches.

This behavioural difference between resident mountain lion in this study and the ones studied in North American sites (Van Dyke *et al.* 1986, Beier 1995) is likely to be attributable to differences in the extent of human persecution. Avoidance reactions are a form of defensive behaviour by means of which animals minimise their exposure to situations that appear to be dangerous (McFarland 1999). While mountain lions were hunted in the study sites of Van Dyke *et al.* (1986) and Beier (1995), in my study site they enjoyed complete protection which certainly minimised their avoidance reaction to human beings. Mountain lions that established home ranges encompassing villages and households were not culled, as was the case in North America. This level of protection of wildlife populations is exceptional in South America. A more common pattern involves extensive persecution of both mountain lions and their prey base even within the boundaries of government reserves and despite protective legislation.

Unlike the mountain lion, information on kodkod behaviour and ecology is essentially anecdotal. It is believed to feed largely on small mammals, particularly small rodents which humans do not generally persecute in the Neotropics. Habitat disturbance and fragmentation are known to cause substantial modification to the diversity and composition of small mammal communities (Fernandez, Evans & Dunstone 1994, 1996; Fernandez, Dunstone & Evans 1999), and will either reduce species diversity (Meserve *et al.* 1991), or increase it (Gascon *et al.* 1999), depending on the nature and the intensity of the disturbance. In the *Nothofagus* dominated forests of Patagonia, Pearson and Pearson (1982) noted that the number of individuals and the biomass of small mammals did not positively correlate with structural complexity of the forest. Habitat disturbances are thus unlikely to compromise the stability of populations of small felids if the biomass and productivity of alternative prey is maintained. This plasticity of felid foraging behaviour is reflected in their ability to adapt to alternative prey (Pearson 1964, 1966, Rudani 1974, Beasom and Moore 1977, Bergerud 1983, Liberg 1984, Leopold and Krausman 1986). They are also able to synchronise activity to the various circadian rhythms of their different prey (Schaller and Crawshaw 1980, Rabinowitz 1986), and to modify search modes and/or hunting strategy according to its density (e.g. Saunders 1963, Pearson 1964, Nellis and Keith 1968, Elliot *et al.* 1977). This adaptive behaviour is facilitated by the high productivity of the small mammal community. Small mammals may, at any one time, provide a low standing crop biomass, but over the annual cycle contribute significantly in terms of secondary productivity (Eisenberg 1979, Emmons 1987), for example, rabbits (*Oryctolagus cuniculis*) have been reported to support predation by cats of up to 4.5 times their standing biomass (Fitzgerald 1978).

The investigation of the habitat utilisation by kodkod presented here has revealed that individuals can make use of secondary vegetation (e.g. scrub-thicket, thicket-forest), although avoidance of open habitats was noted. Kodkod preferred habitat fragments at or near sea-level rather than the older, more structured, homogeneous forests characteristic of slopes. It has also been suggested that they can live in disturbed habitats including forest plantations (C.Weber *in litt.* 1993, J.Rottmann pers.comm. in Melquist 1984) and in areas which have been deforested except for small remnant patches (Weber *in litt.* 1993 cited in Nowell and Jackson 1996). Intensive use of secondary growth has also been recorded for other cat species that are commonly associated with forest, including the margay *Leopardus wiedii*, ocelot and the jaguarundi *Herpailurus yaguagurundi* (e.g. Konecny 1989, Azevedo 1996).

The availability of rodent prey does not seem to be a major obstacle to kodkod survival in fragmented habitats. The rodent species (*D. australis, A. olivaceous, A. micropus*) which are known to comprise the bulk of the mammalian prey component (Dunstone *et al.* in submission) inhabit secondary growth or even open habitats (Pearson and Pearson 1982, Robinson and Redford 1992.). Direct monitoring of habitat preferences of radio-telemetered kodkods demonstrated that although open areas such as scrub coast, scrub rock, and paramo habitats were only occasionally utilised they seemed to show no reluctance to cross them.

In one case, a small habitat fragment (0.06 km^2) of preferred vegetation cover (thicket-cover) was not utilised possibly because of the distance from the two nearest forest-thicket patches (500 and 900 m). Because kodkods did traverse the intervening areas it is likely that this behaviour was related to the low benefit/cost ratio of associated with foraging in this particular patch rather than a reluctance to cross 'hostile' land. Kokods may not be willing to traverse large tracts of unfavourable ground to locate new foraging opportunities in the manner that a mountain lion does. This pattern of foraging however cannot be scaled to long distance movements such as those associated with dispersion.

Sanderson and Sunquist (unpubl.manuscr.) found that only the ranges of males included human-disturbed landscapes, such as potato fields, pastures, logged forests and other cleared areas. These authors suggested that such disturbed areas were not frequently utilised or crossed, even though two of the kodkods in their study area were killed, one of them in a hen house.

Thus, in general, it seems that open areas are not appropriate foraging grounds for kodkods and that small patches of preferred vegetation cover may not foraged if they are too distant from larger patches. Nevertheless, kodkods will occasionally overcome the relatively high risks and associated foraging costs to raid poultry houses for their prolific prey.

The nature of habitat utilisation by the kodkod suggest that they are likely to occur at low densities in open habitats such as páramo and scrub rock, and are more common in secondary forests at lower elevations. I suggest that kodkods are likely to occur at an uneven density throughout their geographic range. It is to be hoped that continuing investigation will provide a clearer picture of the accurate densities of kodkod in the many differently structured habitats that occur within their range.

8.1 Vulnerability issues

The geographic range of the kodkod is very restricted, but the viability of its populations may be safeguarded by the facts that it feeds on relatively common rodent species and its populations can reach high densities locally.

From radio-tracking data I estimate an ecological density of 0.97 kodkod/km^2. If extrapolated to the entire geographical range of the kodkod, this yields a total population size of 155,000 individuals. The presence of hostile terrain e.g. glaciers and open ground, which may exceed half of its geographic distribution, must be taken into account, in which case the population may be as low as 77,500 individuals. This estimate should at best be regarded as an approximation. In order to place these estimates into perspective, it should be noted that to be listed at the lowest category of risk (*vulnerable* in the IUCN Red List categories (1994) the total population number should not exceed 10,000 mature individuals..

Although apparently capable of inhabiting forest of variable structure and composition, the kodkod may prove to be particularly vulnerable to population isolation resulting from habitat fragmentation due to its presumed low dispersal capability which is limited by its small body size, landscape features, and habitat association. It is not known over what distances kodkods are able to disperse. Landscape features within its geographic range are likely to have been a major factor in restricting dispersal of this species. The Pacific Ocean to the west and the Andes to the east are a barrier to the dispersal of small mammal species in southern Chile, with the only connection to the north. Meserve *et al.* 1991 argues that since southern Chile is isolated from the eastern slopes of Andes, small mammal immigration has had to occur primarily from north to south along the western flanks of the Andes. They further suggest that extirpation and widespread burning of forests and site impoverishment associated with human colonisation and exploitation of extant forests to the south (41° S) may have led to dramatic effects on the diversity of faunal assemblages at some sites at lower latitudes.

On the other hand, the rodent prey of the kodkod appear to be able to survive in modified environments although they may be subject to changes in diversity or density at different stages of environmental impoverishment (Meserve *et al.* 1991) and succession occurring during subsequent recolonisation.

Mountain lions inhabit a broad range of different ecosystems and, as they are of larger body size, do not suffer the same dispersal limitations as do kodkod. However, a consequence of their large body size is that each individual requires a substantial home range to provide adequate energy for maintenance activities. Thus vulnerability of the mountain lion stems from the fact that a viable population will require to occupy an area of considerable size.

Mountain lion density at my study site in southern Brazil was found to be relatively high compared to other estimates from North America (see Anderson 1993). High densities were also found in Parque Nacional Torres del Paine in Chile, in a study area where the concentration of guanacos *Lama guanicoe* was highest (Franklin *et al.* 1999).

Crude estimates of mountain lion population are available from state-wide surveys of several North American States (see Smith 1989, Padley 1997b) but not for Latin America. For the purposes of comparison with kodkod estimates, I summed the maximum values of the available *crude* estimates and divided them by the total area surveyed. Although the reports were eight years apart and did not encompass the same area, values of 0.0057 and 0.0061 mountain lions/km^2, respectively were obtained. If this density estimates are applied to the geographical range of the mountain lion (17,120,000 km^2, Nowell and Jackson 1996) a rough estimate of the maximum population would range from 97,907 to 105,200 mountain lions. It is thus interesting to note that on this basis, the total population of mountain lions is largely equivalent to that previously estimated for the kodkod.

The implications of such a comparison illustrate the contrasting difference between the vulnerability factors affecting the two species. On a geographical scale mountain lions dispersal may be hampered because their populations are very far apart, although their ability to disperse and adapt to changing environments may compensate for this disadvantage.

Other factors that affect mountain lion persistence include the vulnerability of their larger prey. In this respect larger cats usually face a greater threat than do smaller species, since their potential prey are commonly hunted by man for food (Ojasti 1991, Redford and Robinson 1991, Vickers 1991, FitzGibbon *et al.* 1996, Hofer *et al.* 1996, Peres 1996, Cullen Jr. *et al.* 2000) or because of the damage they cause to agricultural crops (Seindesticker *et al.* 1990, Van Tassel *et al.* 1999).

Of the prey items that are commonly taken by mountain lions in southern Brazil, the most persecuted by humans are deer *Mazama* sp. (Cullen Jr. *et al.* 2000) and the armadillo *Dasypus novemcinctus* (Cullen Jr. *et al.* 2000, Leite *et al.* unpubl.manuscr.). The white-lipped peccary, which may also be an important dietary constituent when available, is believed to have suffered local extinction in several Amazonian reserves due to over-hunting (see Peres 1996) and is less common than the collared peccary in areas of southern Brazil where hunting takes place (pers.comm.).

Mountain lions are also directly persecuted as a result of livestock depredation incidents throughout its geographical range (e.g. Miller 1980, Yáñez *et al.* 1986, Iriarte *et al.* 1991, Cunningham *et al.* 1995; Franklin 1991, 1999), and in southern Brazil this is also the case (Mazzolli 1992, Mazzolli *et al.* 1997, submitted). Possibly as a result of this persecution and lack of available prey within more disturbed sites, mountain lions in this area are mainly confined to remnant primary vegetation above 800 m (Ihering 1853, Mazzolli 1993).

Capturing prey appears to be a more complicated procedure for larger cats that frequently perform elaborate stalking strategies than for smaller felids that rely on rushing and/or ambushing their prey (Beckoff *et al.* 1984). Large cats (mountain lions, lions, tigers, and jaguars) occasionally sustain injuries or may be killed during attempted prey capture (Perry 1970, Schaller 1972, Seindesticker *et al.* 1973, Sunquist 1981). In addition, Robinson and Redford (1989) have suggested that the diet and body mass of particular species affects their ability to persist in circumscribed areas. According to these authors, large bodied species occur at lower densities and exhibit greater spatial variation in density than do smaller species, which thus increases their susceptibility to localised extinction.

In the Neotropics, and particularly in Brazil, the effect of scarcity is further exacerbated by their greater association with forested habitats. Although in the Neotropics, compared to north America, mountain lions have a wider range of prey items available, these prey are more often associated with forests which are being cleared at a fast rate. Forest clearings may become hostile terrain for prey, thus compromising the mountain lion's foraging efficiency.

Prey density is an important component in determining the population density of cats, but prey diversity is also a significant factor for the stability of their populations. Behavioural plasticity in food acquisition refers to the capacity of individuals to substitute one resource for another in the face of environmental disturbance, thereby ameliorating fluxes in food availability (Weaver *et al.* 1996). On the other hand, the absence of alternative prey is thought to be responsible for the fluctuation in density and decline in recruitment in lynx populations (Elton and Nicholson 1942, Saunders 1963, Nellis and Keith 1968, Brand *et al.* 1976, Beason and Moore 1977).

Prey availability and human persecution seem to be the major determinants of mountain lion survival (or resilience). When their populations are not persecuted and an adequate prey base is available they seem to be able to coexist with man even in highly modified environments.

8.2 A habitat approach to conservation

For many species protecting adequate blocks of connected habitat will be the single most important way to ensure their long-term survival (MacKinnon 2000). However, less than 10% of the world's terrestrial ecosystems lie within protected areas (Groombridge 1992) and the majority of countries have inadequate resources to ensure their legal protection, particularly in the tropics, where they are often understaffed or exist only on paper (Peres 1995). To achieve the goal of habitat conservation, WWF, other NGOs and the World Bank have sought to establish new reserves, ensure the protection of existing ones, and attempted to increase the proportion of the world's productive forest managed under independently certified sustainable protocols (McKinnon 2000).

Under these protocols productive commercial forests should maintain within their boundaries intact patches of native forest which act as refugia for some species, allowing them to be managed as population sources (Pulliam and Danielson 1991). Refugia may occur at several spatial scales. Habitat patches can act as refugia within a mosaic comprised of partially and even some completely inadequate habitats. If the species is able to forage across this mosaic of habitats, the mosaic itself can act as a refugia. Furthermore, this mosaic can be envisaged to be embedded in a complex of mosaics on a greater spatial scale.

Such patterns of habitat disturbance with a multitude of combinations of patch distribution and sizes are often found in privately-owned land, commercially managed for productivity. Although the suitability of such private lands for wild cats is a subject of considerable debate (Nowell and Jackson 1996), their potential as refugia should not be under-estimated. The ideal situation is to transform traditional sink areas into source areas. Outside government reserves it is desirable that strategies that aim to reconcile human needs with conservation interests be pursued (Primack 1993).

In order to emphasise the potential importance of private areas to conservation on a global scale, 20 million hectares of forests have been certified under the Forest Stewardship Council (FSC) (WWF 1996). Under a program called Forest Conservation and Sustainable Use involving WWF and the World Bank there is a projected goal to reach 200 million hectares of such certified systems by 2005.

On a local scale, the private area (1,255 km^2) certified by the FSC where the present mountain lion study was conducted is equivalent in size to 21.3 % of the total government reserves in the State of Paraná (5,892 km^2, SOS Mata Atlântica 1993). The entire area owned by Klabin timber company alone amounts to 2,240 km^2 which is equivalent to 38 % of the total area set aside for government reserves. Private lands are also an important habitat component for mountain lions in Florida (Belden 1988, Maehr 1990). Other examples include the Pantanal in Brazil, 95% of which is privately owned (Quigley and Crawshaw 1992). However, private lands are infrequently managed to maintain wildlife populations because of conflict with commercial agro-forestry operations. Nonetheless, there is a world-wide trend to implement sustainable managed productive systems which are not completely exclusive of wildlife survival, including forestry, wildlife management, and eco-tourism (Prance 1992, Child 1995, Taylor & Dunstone 1996, Evans 1999). The role of these managed areas is best described as complementary to the existing network of protected reserves (Frankel 1983). Of all managed systems, environmental-friendly forestry has gained momentum as the demand of consumer markets for wood supplied from "*green*" sources have been established in the form of "buyers group". This consumer market has been encouraged by the WWF's Global Forest and Trade Network programme (WWF 1996, ECE/FAO 2000).

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Appendix I –

List of parcels with their respective size, rank value (according to percentage of native forest), proportion of native forest and proportion of Araucaria stands

Parcels	ranking	total size (km^2)	% native	% Araucaria
Mandaçaia	–	105.5	?	5.12
Mortandade	1	72.37	66.09	4.30
Restingão	1	63.65	60.79	9.07
Bom Retiro	1	48.78	60.50	33.54
Jaguatirica	2	86.03	59.25	2.12
Trinita	2	82.71	57.88	5.15
Invernadinha	2	52.76	57.15	6.92
Imbauzinho	2	69.06	56.38	22.69
Palmas	2	31.71	53.98	10.86
Socimbra	3	57.42	48.69	0.61
Faz Velha	3	74.10	47.51	0.32
Pinhal Bonito	3	52.08	47.02	18.64
Vila Preta	3	62.94	45.07	0.12
Anta Brava	3	49.37	44.24	9.31
Boa esperança	3	56.20	42.24	9.73
Cerradinho	3	97.13	41.28	3.66
Recanto	4	43.99	38.59	4.31
Mirandinha	4	75.58	34.63	1.64
Faisqueira	4	63.57	29.94	1.66
Agronomia	4	74.10	27.63	0.08
Colonia	4	42.18	23.98	1.28

Appendix II – commands to register and rectify images in Arc/Info

```
Register {name of the image} {name of the coverage} 2 # # # # point.
```

The Register command opened three windows, two with the aerial image and one with the tick points. The tick points had to be encompassed by a square, and by doing so the larger image window displayed the tick points overlaying the image. Each location in the image to be assigned a tick point was (left) clicked with the mouse first and subsequently the tick point related to it. After this was accomplished for all tick points, Register push button was pressed followed by Save.

A new command was issued afterwards, Rectify, as follows:

```
Rectify {name of the image} {name of the new image – or output} nearest
```