The effect of group composition on maternal reproductive success in cooperatively breeding golden lion tamarins (Leontopithecus rosalia) and Goeldi's monkeys (Callimico goeldii) in European zoos.

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The effect of group composition on maternal reproductive success in cooperatively breeding golden lion tamarins (*Leontopithecus rosalia*) and Goeldi's monkeys (*Callimico goeldii*) in European zoos.

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The effect of group composition on maternal reproductive success in cooperatively breeding golden lion tamarins (*Leontopithecus rosalia*) and Goeldi's monkeys (*Callimico goeldii*) in European zoos.

Katharine Flach

Abstract

In cooperatively breeding callitrichids, non-maternal investment in infants is thought to increase maternal fitness. This increase in maternal fitness may occur through an increase in offspring survival or maternal reproductive output and is likely to be affected by the group composition since the levels of investment undertaken by non-maternal group members vary with age and sex. To investigate the effects of group composition on female reproductive success in a captive environment, I used historical records of golden lion tamarins (*Leontopithecus rosalia*) and Goeldi's monkeys (*Callimico goeldii*) in European zoos. In this large, multi-group data set, I found that the number of adult males and non-mother adult females present at birth positively affects offspring survival in golden lion tamarins, depending on the litter size. However, this association might not be caused by helpers' investment levels as most deaths occurred neonatally, and the number of adult males present did not significantly increase offspring survival measured after 1 day. I found no evidence for an association between group composition and inter-birth interval or litter size in golden lion tamarins. In Goeldi's monkeys, offspring survival and inter-birth intervals did not vary with the number of adult males or adult females. The number of non-littermate young present in Goeldi's monkey groups was positively associated with offspring survival and negatively with inter-birth interval, which I suggest is related to local environmental factors, or female condition, rather than the helping behaviours of young individuals.

The effect of group composition on maternal reproductive success in cooperatively breeding golden lion tamarins (*Leontopithecus rosalia*) and Goeldi's monkeys (*Callimico goeldii*) in European zoos.

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1 Introduction

1.1 Life history strategies

Organisms need energy to grow, maintain their condition, and reproduce. As the energy available to an organism in any environment is finite, investment in one component of fitness reduces the ability to invest in other components of fitness (Fisher 1930). To maximise inclusive fitness, trade-offs between traits that affect current and future fitness affect an organism's investment in growth and development, fecundity, and parental care, and influence the timings of events such as the age of weaning, maturation and senescence (Roff 1992; Stearns 1992, 2000). The individual pattern of developmental and reproductive events that constitute an organism's life is known as its life history strategy.

An organism's optimum life history strategy varies with the ecological environment and survival probability. Environments with a low survival probability select for rapid development with an early onset of reproduction, as genes which are correlated with a fast life history are more likely to be passed on (Read & Harvey 1989; Gaillard, Pontier, Allainé, *et al.* 1989; Promislow & Harvey 1990; Stearns 1992; Fisher, Owens & Johnson 2001). The low probability of future reproduction and low offspring survival also selects for a large number of offspring born in a small number of reproductive events (Charnov & Schaffer 1973; Gaillard, Pontier, Allainé, *et al.* 1989; Promislow & Harvey 1990). In environments where lifespan is longer and more predictable, the first reproductive event is later, and more energy is invested in maintaining condition for future reproduction (Read & Harvey 1989; Gotthard, Nylin & Nylin 1995; Promislow & Harvey 1990; Fisher, Owens & Johnson 2001). These environments are also associated with a slow reproductive rate and high parental investment as the genetic contributions to future generations are maximised by investment in high-quality offspring (Promislow & Harvey 1990).

One life history trade-off is that between investment in the quality and quantity of offspring. Post-natal investment increases an infant's survival probability and fitness through protection, energetic input and the opportunity to learn, but the costs of investment in multiple offspring lead to lower investment per offspring, or reduce the future investment potential of the parent (Williams 1966; Trivers 1972; Clutton-Brock 1991; Royle, Smiseth & Kölliker 2012). Slow reproductive rates and high parental investment levels evolve in environments where producing high-quality offspring is associated with the greatest reproductive success (review in Clutton-Brock 1991). If the costs of parental investment limit a breeder's reproductive success then investment in offspring by non-maternal helpers, either the sire or by non-parents (allocare/allocarers), can increase the breeder's reproductive success (Hatchwell 1999). However, a female's willingness to allow non-maternal contact with her dependant offspring depends on the probability of mishandling and infanticide. For example, infanticide by unrelated males is selected for in species with longer gestation than lactation, and post-partum amenorrhea (van Schaik 2000; Schaik & Janson 2000). Where the costs of non-maternal contact are outweighed by the fitness benefits of additional investment, allocare is selected for, and breeders may follow two strategies. First, they may maintain their level of parental care, such that allocare increases the overall investment in an offspring and thus the parent's reproductive success through increased offspring survival and fitness (additive care). Second, they may reduce their parental investment such that allocare maintains overall offspring investment and enables breeders to increase their fecundity or reproductive lifespan (load-lightening) (Hatchwell 1999; Balshine, Leach, Neat, *et al.* 2001; Russell, Langmore, Gardner, *et al.* 2008).

A high level of allocare is found in cooperatively breeding species. Cooperative breeding is a breeding system in which both the parents and non-parental group members care for infants (Wilson 1975). Allocarers are often independent offspring that delay natal dispersal and reproduction due to a low probability of reproductive success and high dispersal costs (Emlen 1982a; Stacey & Ligon 1991). This philopatry is associated with direct benefits to the helpers. Larger groups are associated with lower predation risk and higher foraging and hunting success, and the additional developmental period before first reproduction increases a helper's future ability to compete for resources or mates (reviewed in Ekman, Dickinson, Hatchwell, *et al.* 2004; Clutton-Brock 2006). Indirect fitness benefits may have led to the evolution of allocare in some species, since allocarers are often related to the breeders (Hamilton 1963, 1964; reviewed in Dickinson & Hatchwell 2004). However, allocaring also confers direct fitness benefits to helpers. Allocaring may increase a helper's group tenure or increase group size, extending or increasing the direct benefits a helper receives from group living (Gaston 1978; Emlen 1982b; Kokko, Johnstone & Clutton-Brock 2001; Clutton-Brock 2002; Dickinson & Hatchwell 2004). Allocaring may also increase a helper's reproductive success through an increase in social prestige, reproductive opportunity, or parental experience (Davies & Hatchwell 1992; Zahavi 1995; Clutton-Brock 2002; Dickinson & Hatchwell 2004). These direct benefits led to the evolution of cooperative breeding in species where allocarers are not closely related to breeders, and are also evolutionarily important in some cooperatively breeding species with high intragroup relatedness (Clutton-Brock, Brotherton, O'Riain, *et al.* 2000; Clutton-Brock 2002; Dickinson & Hatchwell 2004).

The net inclusive fitness advantages of allocaring, and therefore a helper's willingness to invest, vary with individual differences in environmental and social conditions, sex, age, experience, relatedness, and condition (review in Clutton-Brock 2006). In most species, the costs of helping are higher in immatures than in fully-grown individuals, and the extent of allocare undertaken increases with helper age to adulthood (Clutton-Brock 2006; Erb & Porter 2017). There are often sex differences in the level or type of allocare (Stacey & Koenig 1990; Cockburn 1998; Clutton-Brock, Brotherton, O'Riain, *et al.* 2001). Sex biased allocaring behaviours are frequently attributed to dispersal patterns; the philopatric sex invests more than the dispersing sex prior to dispersal as it receives greater direct fitness benefits from group augmentation, social prestige or local territory enhancement (Owens & Owens 1984; Emlen, Merritt Emlen & Levin 1986; Legge 2000; Clutton-Brock 2002; Clutton-Brock, Russell, Sharpe, *et al.* 2002). The variation in the fitness benefits of allocare should be considered to understand the evolution and maintenance of allocare and cooperative breeding in different taxonomic groups, and the reasons for variation between individuals of the same species.

1.2 Allocare in primates

Primates have slow life histories for their size, and a high frequency and extent of allocare compared to other mammals (Charnov & Berrigan 1993; Zimmermann & Radespiel 2013; Tecot & Baden 2015). Primates' long lifespans, in addition to ecological constraints of territory and mate availability, lead to a low turnover of breeding opportunities in many species which increases the inclusive fitness benefits of philopatry and allocare (Emlen 1982a; Wild & Korb 2017). However, the evolution and maintenance of allocare is limited by female tolerance of non-maternal contact with dependant offspring (Maestripieri 1994). In many primate species, late weaning and post-partum amenorrhea lead to a high probability of male infanticide (van Schaik 2000). In these species male allocare is unlikely to evolve as female tolerance of male allocare interactions with offspring will be selected against due to the high costs of infanticide (Maestripieri 1994; Mitani & Watts 1997; Ross & MacLarnon 2000).

Where there are net fitness benefits of allocare, female primates may undertake additive care, maintaining their investment levels with additional allocare. This increase in overall offspring investment increases maternal reproductive success through offspring survival or quality (Pereira, Klepper & Simons 1987; Bardi, Petto & Lee-Parritz 2001; Charpentier, Van Horn, Altmann, *et al.* 2008). Alternatively, they may undertake a load-lightening strategy, maintaining offspring investment levels by reducing maternal investment levels with increasing allocare. This reduction in maternal investment facilitates an increase in female lifetime reproductive output through shorter inter-birth intervals, larger litters, increased maternal survival, or longer maternal reproductive tenure (Fairbanks 1990; Mitani & Watts 1997; Ross 1998; Ross & MacLarnon 2000). The maternal strategy employed depends on the maximisation of reproductive success and varies both between and within species with the socio-ecological conditions (Ross & MacLarnon 2000; Bales, French & Dietz 2002).

1.3 The callitrichids

Within primates, some of the highest levels of non-maternal care are found in the Neotropical primates (Huck & Fernandez-Duque 2012). However, even in owl monkeys (*Aotus spp.*) and titi monkeys (*Callicebus spp.*), where parental care is substantial and fathers are frequently the primary caregivers, non-parental care is rarely observed (Dixson & Fleming 1981; Fragaszy, Schwarz & Shimosaka 1982; Wolovich, Perea-Rodriguez & Fernandez-Duque 2007). In contrast, all species in the callitrichid family breed cooperatively, and group members undertake extensive allocare (review in Díaz-Muñoz 2016). The callitrichid family is comprised of marmosets (*Cebuella, Micro, Callibella, Callithrix*), tamarins (*Saguinus, Leontopithecus*) and Goeldi's monkeys (*Callimico goeldii*), although the precise phylogeny remains unclear (Rylands, Heymann, Lynch Alfaro, *et al.* 2016; Garbino & Martins-Junior 2018).

Callitrichid groups range in size from 2 to over 30 individuals (Digby & Saltzman 2009). Groups are often made up of one breeding pair and offspring, but unrelated subordinate adults may also be present (Koenig 1995; Baker & Dietz 1996; Ferrari & Digby 1996). The ecological constraints of saturated habitats and the low probability of successful independent breeding have selected for philopatry and offspring of both sexes remain in the natal group for several years after reaching sexual maturity (Goldizen & Terborgh 1989; Díaz-Muñoz & Ribeiro 2014). Callitrichid mating systems vary with the social and ecological conditions (Sussman & Garber 1987; Goldizen, Mendelson, van Vlaardingen, *et al.* 1996; Goldizen 2003; Arruda, Araújo, Sousa, *et al.* 2005; Garber, Porter, Spross, *et al.* 2016). There is generally a dominant male, who sires most offspring born in the group, although females may mate with multiple males and can produce litters of mixed paternity (Sussman & Garber 1987; Baker, Dietz & Kleiman 1993; Huck, Löttker, Böhle, *et al.* 2005; Bales, French, McWilliams, *et al.* 2006; Díaz-Muñoz 2011; Garber, Porter, Spross, *et al.* 2016). Callitrichid groups are consistently reported to have one behaviourally and reproductively dominant female, but the extent of reproductive monopolisation varies between species (French 1997). In some species, subordinate female ovulation is suppressed and the dominant female monopolises reproduction (review in Saltzman 2003). In other species, subordinate females have normal cycling patterns and two breeding females may be present (plural breeding) (reviews in French 1997; Digby & Saltzman 2009). Plural breeding can be costly to the dominant female and they may inhibit subordinate females from breeding through aggression, eviction, or, where subordinate females give birth, infanticide (Dietz & Baker 1993; French 1997). Consequently, subordinate females' pregnancy success and offspring survival is consistently lower than dominant females' (Digby 1995; Saltzman 2003; French, Bales, Baker, *et al.* 2003; Henry, Hankerson, Siani, *et al.* 2013). Despite their low reproductive success, subordinate male and female callitrichids may achieve higher inclusive fitness by remaining in the natal group than by dispersing and searching for a breeding vacancy (Dietz & Baker 1993; Baker, Dietz & Kleiman 1993).

1.3.1 Reproductive output in callitrichids

An increase in reproductive output has been selected for in callitrichids since the last common ancestor with other Neotropical primates (Martin 2012). Some callitrichid species are able to produce two litters which develop during the wet season when resources are abundant, although this occurs more regularly in captivity than in the wild (Dietz, Baker & Miglioretti 1994; Digby, Ferrari & Saltzman 2007). The short inter-birth intervals are made possible in callitrichids by the absence of post-partum amenorrhea and high levels of postpartum conception success (McNeilly, Abbott, Lunn, *et al.* 1981; Ziegler, Bridson, Snowdon, *et al.* 1987; Jurke, Pryce, Döbeli, *et al.* 1994; Digby, Ferrari & Saltzman 2007). The costs of the resulting simultaneous pregnancy and lactation are reduced through extending the period of gestation before the major growth of the embryo. This delays the additional energy expenditure of pregnancy until the previous infant is weaned (Windle, Baker, Ridley, *et al.* 1999; Martin 2012).

The number of infants produced per reproductive event also affects callitrichids' reproductive success. Female callitrichids have the physiological adaptations for single births (for example a single uterus) but multiple births have evolved secondarily (Martin 2012). The average litter size varies slightly between species, but the predominant litter size is two, with litters of up to three reported in the wild and up to six in captivity (Sousa, Silva & Vidal 1999; Savage, Soto, Medina, *et al.* 2009; Tardif, Ross & Smucny 2013; Boulton & Fletcher 2015). A notable exception is Goeldi's monkeys, which have evolved from litter-producing ancestors to produce singletons. There are two major hypotheses to explain the ultimate function of increased litter size in callitrichids. One links the selection for multiple births to callitrichids' small size (Leutenegger 1973, 1979). The callitrichid family have undergone an evolutionary reduction in size and extant callitrichid species have an average adult body mass of 0.3-0.6 kg, (except pygmy marmosets (*Cebuella pygmaea*), which are around 0.1 kg) (Smith & Jungers 1997). Their small size and subsequent high neonatal to adult body mass ratio may have led to a high frequency of issues with parturition (Leutenegger 1973, 1979). The costs of neonatal or female loss at parturition could have selected for a reduction in individual neonate mass via twinning

(Leutenegger 1973, 1979). The high post-natal costs of producing twins would lead to increases in the maternal and helper benefits of allocare, and select for allocare (Leutenegger 1973, 1980; Tardif 1997). The alternative hypothesis suggests that allocare and reduced neonatal size evolved prior to, or at the same time as, the increase in reproductive output (Ross 1991; Martin 1992; Ah-King & Tullberg 2000; Stockley & Hobson 2016). The inclusive fitness benefits of allocare to both breeders and helpers may have been sufficient for its evolution. With additional investment from allocarers, breeding females may have been able to increase reproductive success through additive or load-lightening investment behaviours (Ah-King & Tullberg 2000; Stockley & Hobson 2016).

While the order in which these traits evolved is unclear, their maintenance requires an evolutionary advantage to some, or all, of the individuals involved. The following sections address the costs and benefits of allocare first to helpers and then to breeding females in order to understand the evolution and maintenance of cooperative breeding in callitrichids.

1.3.2 Allocare in callitrichids

Callitrichid allocaring behaviours are costly to helpers. The main infant caring behaviours in callitrichids are infant carrying and food provisioning (Heymann 1990; Ferrari 1992; Rothe, Koenig & Darms 1993; Santos, French & Otta 1997). Infant carrying imposes costs of reduced feeding time and social interactions, as well as reduced leaping distances and travelling speed, and higher predation pressure (Price 1992a; Schradin & Anzenberger 2001a; Caperos, Morcillo, Peláez, *et al.* 2012). Helpers nutritionally provisioning infants incur the time and energetic costs of obtaining this food (de Moura, Nunes & Langguth 2010). The combined costs of these allocaring behaviours decreases helpers' body mass during the period of infant dependency (Sánchez, Peláez, Gil-Bürmann, *et al.* 1999; Achenbach & Snowdon 2002). The costs of allocare to helpers must be balanced by inclusive fitness benefits to be maintained. Callitrichid helpers are frequently assumed to receive a high level of indirect fitness benefits due to the high degree of intergroup relatedness associated with philopatry in both sexes (Löttker, Huck & Heymann 2004). However, callitrichid kin relationships are complicated by the possibility of multiple-sire litters and the fact that foetuses share chimeric tissue (Huck, Löttker, Böhle, *et al.* 2005; Ross, French & Ortí 2007; Díaz-Muñoz 2011; Sweeney, Curran, Westmoreland, *et al.* 2012). This genetic chimerism may obscure the degree of relatedness between individuals and affect allocare incentives, with preliminary research suggesting that males are more likely to invest in chimeric than non-chimeric young (Ross, French & Ortí 2007). The complexity of relatedness in callitrichids, and the absence of data on the association between allocare behaviours and genetically determined relatedness, makes the importance of indirect fitness benefits to the evolution and maintenance of allocare unclear.

Helpers also receive direct benefits from allocare. Primiparous females benefit from allocare experience, because it improves their own subsequent reproductive success (Pryce 1993; French 1996). Subordinates of both sexes benefit from remaining in the group, however subordinate females pay fitness costs of aggression and possible eviction due to the costs of plural breeding to the dominant female (Dietz & Baker 1993; Saltzman 2003; Saltzman, Digby & Abbott 2009). Allocare by subordinate females may therefore act as 'rent payment', with subordinate females receiving direct benefits of reduced aggression and delayed eviction (Gaston 1978; Emlen 1982b; Pryce 1993; Sánchez, Peláez & Gil-Bürmann 2002). The costs of both philopatry and dispersal are lower in subordinate males than females; there is a low degree of male intra-sexual aggression or enforced eviction and males are more likely to be accepted as a subordinate immigrant in a group than a female (French & Inglett 1989; Baker & Dietz 1996; Yamamoto, Araujo, Arruda, *et al.* 2014). The reproductive benefits of inheriting the breeding position may explain male philopatry, but do not explain allocare in subordinate males (Yamamoto, Araujo, Arruda, *et al.* 2014). Male allocare would be selected for if it increased reproductive success, but an association between investment effort in males and reproductive success has not been found in callitrichids (Tardif & Bales 1997). Although the direct benefits of allocare to subordinate males are unclear, the sex differences in the direct benefits received have led to a sex bias in allocare across callitrichids. Males have been found to help more than females in several studies and the number of male (but not female) helpers correlates with infant growth and survival in several studies (Cleveland & Snowdon 1984; Sussman & Garber 1987; Heymann 1990; Sánchez, Peláez, Gil-Bürmann, *et al.* 1999; Zahed, Kurian & Snowdon 2010; but see Tardif, Carson & Gangaware 1992; Santos, French & Otta 1997; Yamamoto, Box, Albuquerque, *et al.* 1996; Schradin & Anzenberger 2001b).

The net fitness benefits, and therefore allocaring effort, also differ with a helper's age. Juvenile callitrichids undertake allocaring behaviours but are consistently found to have lower investment levels than older individuals, and both sexes increase allocaring effort to adulthood as an increase in body size and experience decreases the costs of allocare (Tardif, Carson & Gangaware 1992; Yamamoto, Box, Albuquerque, *et al.* 1996; Santos, French & Otta 1997; Zahed, Kurian & Snowdon 2010). However, immature females help more than immature males as young female helpers receive greater direct benefits from allocaring experience than similarly aged males (Price 1992b; Pryce 1993). The benefits of allocare then decrease with female experience but remain constant with male age, leading to higher levels of allocare in adult males than females (Zahed, Kurian & Snowdon 2010; Burkart 2015).

1.3.3 Maternal reproductive strategies in callitrichids

The evolution and maintenance of allocare requires maternal tolerance of helpers' contact with offspring. This suggests that breeding females receive net fitness benefits, or at least do not pay net fitness costs, from allocare (Ross & MacLarnon 2000). The potential costs of allocare are lower in callitrichid females than other primates, as postpartum oestrus leads to a low risk of male infanticide (McNeilly, Abbott, Lunn, *et al.* 1981; Digby 1995; Digby & Saltzman 2009). At the same time, the potential maternal fitness benefits from allocare are high. Infant carrying and provisioning behaviours are costly to undertake, but increase offspring success. Infant carrying reduces predation and infanticide risks, and may also be an anti-parasitic strategy, and food sharing provides infants with nutritional and informational benefits, cushioning them from physical and experience-based limitations to foraging and accelerating growth (Feistner & Price 1990; Price & Feistner 1993, 2001; Ross 2001; Rapaport & Ruiz-Miranda 2002; Brown, Almond & Van Bergen 2004; Rapaport 2006, 2011).

An increase in the levels of allocaring behaviours can increase maternal reproductive success through an increase in offspring success or an increase in maternal reproductive output, depending on the maternal strategy. If female callitrichids undertake additive care strategies, an increase in allocare would be associated with maintained maternal investment, and therefore an increase in overall offspring investment. In support of this hypothesis, infants in larger groups are carried and provisioned more than those in smaller groups, and the level of maternal contributions is maintained with changes in the number of helpers (Price 1992a; Santos, French & Otta 1997; Bales, Dietz, Baker, *et al.* 2000). This increased investment in individual infants with increasing helper numbers correlates with higher infant survival (Johnson, Petto & Sehgal 1991; Rapaport, Kloc & Warneke 2013; Watsa, Erkenswick & Robakis 2017 but see Rothe, Koenig & Darms 1993; Jaquish, Tardif & Cheverud 1997; Savage, Soto, Medina, *et al.* 2009). Alternatively, if female callitrichids undertake load-lightening strategies, this would predict a decrease in investment effort with an increase in allocare (Bales, French & Dietz 2002; Fite, Patera, French, *et al.* 2005; Savage, Soto, Medina, *et al.* 2009 but see Price 1992; Santos, French & Otta 1997; Bales, Dietz, Baker, *et al.* 2000; Zahed, Kurian & Snowdon 2010). The reduction in maternal energetic expenditure on post-natal investment would then lead to an increase in reproductive output (Mitani & Watts 1997; but see Bales, O'Herron, Baker, *et al.* 2001; Boulton & Fletcher 2015).

The overall group size or number of helpers present are inaccurate proxies for the amount of allocare received, as the fitness benefits to each sex and the amount of allocare undertaken are affected differently by the ecological and social conditions (Price 1992a; Bales, Dietz, Baker, *et* *al.* 2000). Investigation of the effect of allocare on maternal reproductive success should thus consider the number of each sex of adult helper separately. The presence and number of non-littermate dependent young should also be taken into account. The amount of helping effort that immature individuals receive is expected to be greater than the allocaring effort they undertake, decreasing the total investment in the current litter. The litter size should also be considered, as it will influence the amount of pre-natal and post-natal investment per offspring. Individuals from larger litters have lower neonatal survival, which may relate to the lower body mass at birth associated with an increase in litter size (Jaquish, Gage & Tardif 1991; Jaquish, Tardif & Cheverud 1997; Leong, Terrell & Savage 2004; Ward, Buslov & Vallender 2014). Maternal and allocarer post-natal investment levels increase with litter size, but carrying and nursing time per offspring is lower in larger litters than smaller litters (Price 1992a; Tardif, Layne & Smucny 2002). The effect of allocaring behaviours on maternal success would therefore be expected to vary with the size of the litter receiving care.

The reproductive strategy a female undertakes with additional allocare may vary with individual condition and other local environmental factors. Female condition, body mass, and energy availability are associated with ovulation number, the rate of prenatal litter size reduction, litter size at birth, and inter-birth intervals (Kirkwood 1983; Tardif & Jaquish 1997; Tardif, Power, Oftedal, *et al.* 2001; Tardif, Ziegler, Power, *et al.* 2005). Senescence-related reductions in fertility have been observed in older females in captivity (Tardif 1985; Tardif & Ziegler 1992), but generally maternal age has not been found to correlate with fertility and is positively associated with pre-natal growth and infant survival (Jaquish, Gage & Tardif 1991; Tardif & Bales 2004; but see Smucny, Abbott, Mansfield, *et al.* 2004).

1.3.4 Callitrichid reproduction in captivity

In captivity, callitrichids are predominantly kept as a breeding pair and their offspring (Anzenberger & Falk 2012). While this does not directly mimic wild conditions of flexible group size and mating system, it prevents the aggressive breakdown of groups and enables closer control of reproduction and therefore inbreeding avoidance. Female callitrichids have a higher reproductive output in captivity, with more frequent biannual births and larger average litter sizes than reported in wild females (Dietz, Baker & Miglioretti 1994; Jaquish, Cheverud, Tardif, *et al.* 1996; Jaquish, Tardif & Cheverud 1997; French 1996; Leong, Terrell & Savage 2004; Savage, Soto, Medina, *et al.* 2009). The higher reproductive output has been linked to higher female body mass in captivity as a consequence of diet and lower activity levels (Kirkwood 1983; Tardif & Jaquish 1997; Araújo, Arruda, Alencar, *et al.* 2000; O'Connell, Moore, Price, *et al.* 2001). There are no clear differences in allocaring behaviours between wild and captive callitrichid populations, although the evidence is limited. Infants were carried for the same amount of time and maternal contributions did not differ between wild and captive common marmosets, and offspring of re-introduced golden lion tamarins were provisioned more than offspring of wild-born parents but transfers were similar in character (Yamamoto, Box, Albuquerque, *et al.* 1996; Ruiz-Miranda, Kleiman, Dietz, *et al.* 1999). The evident environmental differences between wild and captive callitrichid groups means than female success cannot be directly compared between them. However, the environmental similarities between captive groups enable the effects of allocare on female success to be explored while controlling for the effect of the physical environment, and the extensive records maintained by captive programmes provide accurate data sets of a size which are not feasible from wild populations.

1.4 Aim and study species

I aim to investigate the effect of group composition on female reproductive success in captive callitrichids. While all species of callitrichids breed cooperatively, variation in investment behaviours and reproductive strategies across species means that it is important to examine each species individually to understand the factors influencing reproductive strategies (Santos, French & Otta 1997; Goldizen 2003; Díaz-Muñoz 2016).

I initially intended to investigate seven callitrichid species (white-fronted marmosets (*Callithrix geoffroyi*), common marmoset (*C. jacchus*), pied tamarins (*Saguinus bicolor*), cotton-topped tamarins (*S. oedipus*), golden-headed lion tamarins (*Leontopithecus chrysomelas*), golden lion tamarin (*L. rosalia*), and Goeldi's monkeys (*Callimico goeldii*). I selected genera which represent the range of reproductive strategies present in the callitrichid family to compare the influence of group composition on reproductive success across the family (Goldizen 2003; Burkart 2015; Díaz-Muñoz 2016). Except for common marmosets, the species are also all part of European Endangered Species Programmes, which manage the conservation and genetic diversity of many endangered species in European zoos (The European Association of Zoos and Aquaria 2016). Their reproduction is therefore closely monitored and recorded, and any resulting findings are of considerable interest to institutions. I gained support from the Callitrichid Taxon Advisory Group of the European Association of Zoos and Aquaria (EAZA) for the use of data from all seven requested callitrichid species. However, despite efforts to obtain more, I only acquired the studbook data for two species: golden lion tamarins and Goeldi's monkeys.

Golden lion tamarins and Goeldi's monkeys have similar development and post-natal strategies. In both species, allocare starts around 1 month after birth (later than most callitrichid species), there is no clear sex bias in helping behaviours, and infants reach adulthood shortly after 1 year of age (Hoage 1982; French, Inglett & Dethlefs 1989; Dettling & Pryce 1999; Santos, French & Otta 1997; Schradin & Anzenberger 2001b, 2003). However, the species differ in maternal reproductive output: breeding females in golden lion tamarins generally give birth to twins annually, while in Goeldi's monkeys breeding females give birth to singletons biannually (reviewed in Díaz-Muñoz 2016). It is therefore interesting to explore maternal reproductive success and plasticity in maternal strategy with variation in group composition in these two species with similar allocaring behaviours but different reproductive strategies.

1.4.1 Golden lion tamarins

Golden lion tamarins are found in primary, secondary and successional forests on the Atlantic coast in the state of Rio de Janeiro, Brazil (Rylands 1996; Dietz, Peres & Pinder 1997; Kierulff & Rylands 2003). They are fauni-frugivores, eating principally ripe fruit and nectar but also small animals (Dietz, Peres & Pinder 1997).

Golden lion tamarins live in groups of two to 11 individuals (Dietz & Baker 1993; Kierulff & Rylands 2003). Immigration is mostly restricted to breeder replacement and is highly male biased, with high levels of aggression towards potential female immigrants (Baker & Dietz 1996). Subordinate females are not hormonally suppressed and have a greater success attempting to breed in their natal group than dispersing (French, Inglett & Dethlefs 1989; Dietz & Baker 1993). However a dominant breeding skew in both sexes is maintained though monopolisation of mating during the fertile period by the dominant male and a high level of pregnancy loss and neonatal abandonment in subdominant female (Baker, Dietz & Kleiman 1993; Henry, Hankerson, Siani, *et al.* 2013).

Golden lion tamarins infants are carried exclusively by the mother until they are about one month old, later than most callitrichid species (Santos, French & Otta 1997). Infants are then mainly carried by helpers until they are capable of independent locomotion, which increases in frequency during the second and third months of life (Hoage 1982; Santos, French & Otta 1997). Weaning begins around 1 month after birth, although infants mainly acquire their food through provisioning rather than independent foraging until approximately 4 months old, with provisioning gradually decreasing until they are around 1 year of age (Hoage 1982; Rapaport 2011). As expected from sex differences in the direct fitness benefits of helping in other callitrichids, juvenile females commence infant carrying earlier than males and helper contributions are higher in adults than juveniles (Hoage 1982).

1.4.2 Goeldi's monkeys

Goeldi's monkeys are found in north-eastern South America. Most of their range is in Peru, extending into south Columbia, west Brazil and north Bolivia (Christen 1999; Ferrari, Iwanaga, Ramos, *et al.* 1999). Although Goeldi's monkeys occur across a large range, they live at a low density: groups of up to 12 individuals live in home ranges of over 100 ha and neighbouring groups' home ranges may not share a boundary (Porter 2001; Porter, Sterr & Garber 2007). The home range may cover that of several tamarin groups and they frequently form mixed-species groups with sympatric tamarin species (Pook & Pook 1982; Porter, Sterr & Garber 2007). Goeldi's monkeys spend most of their time in the dense undergrowth of primary forest, but also use secondary and bamboo forests (Pook & Pook 1982; Porter, Sterr & Garber 2007). Their preference for dense vegetation, large home ranges and subsequent low population densities relate to the high dependency of fungi in the diet, but Goeldi's monkeys also eat fruit and insects (Pook & Pook 1982; Porter, Sterr & Garber 2007).

In Goeldi's monkeys, subordinate females are not hormonally suppressed, and there may be more than one breeding female per group (Dietz & Baker 1993; Dettling & Pryce 1999). Unlike all other callitrichid species, the predominant litter size is one, with twins infrequently reported (Altmann, Warneke & Ramer 1988). Biannual births are regular in captivity, but not consistent in the wild (Altmann, Warneke & Ramer 1988; Porter 2001; Porter, Sterr & Garber 2007). Offspring are carried uniquely by the mother for a mean of 27.5 days in captivity (Schradin & Anzenberger 2003), and maternal carrying investment decreases rapidly after the first transfer to allocarers (Heltne, Turner & Wolhandl 1973; Masataka 1981). Infants are infrequently off carriers before 6 weeks of age but from 10 weeks of age they locomote independently more than half of the time (Heltne, Turner & Wolhandl 1973; Schradin & Anzenberger 2001b). The onset of weaning is around 4 weeks of age but parental-infant conflict is associated with a decline in carrying rather than weaning, perhaps due to provisioning from allocarers (Masataka 1981; Jurke & Pryce 1994; Porter 2001; Ross, Porter, Power, *et al.* 2010). Female Goeldi's monkeys reach sexual maturity at a median of 57 weeks in captivity and males reach adult body mass at 60 weeks old, and have been reported to sire young from 13 months in captivity (Beck, Anderson, Ogden, *et al.* 1982; Dettling & Pryce 1999; Dettling 2003).

1.5 Hypotheses

Assuming that investment levels are associated with offspring survival, and that allocare is positively correlated with overall investment, I hypothesise that:

Hypothesis 1: Male allocare increases offspring survival.
Prediction: The probability of infant survival will correlate positively with the number of male helpers per offspring.

Hypothesis 2: Female allocare increases offspring survival.
Prediction: The probability of offspring survival will correlate positively with the number of female helpers per offspring.

Hypothesis 3: The presence of non-littermate young (all individuals less than 1 year of age present in the group, excluding the current litter) decreases offspring survival.
Prediction: The probability of offspring survival will correlate negatively with the number of non-littermate young per offspring.

Assuming that litter size and inter-birth interval are limited by the costs of maternal investment, and that allocare is negatively correlated with maternal costs:

Hypothesis 4: Male allocare decreases inter-birth intervals.
Prediction: The inter-birth interval will correlate negatively with the number of male helpers per offspring.

Hypothesis 5: Female allocare decreases inter-birth intervals.
Prediction: The inter-birth interval will correlate negatively with the number of female helpers per offspring.

Hypothesis 6: The presence of non-littermate young increases inter-birth intervals.
Prediction: The inter-birth interval will correlate positively with the number of non-littermate young per offspring.

Hypothesis 7: Male allocare increases litter size.
Prediction: The size of the subsequent litter will correlate positively with the number of male helpers per offspring.

Hypothesis 8: Female allocare increases litter size.
Prediction: The size of the subsequent litter will correlate positively with the number of female helpers per offspring.

Hypothesis 9: The presence of non-littermate young decreases litter size at birth.
Prediction: The size of the subsequent litter will correlate negatively with the number of non-littermate young per offspring.

2 Methods

2.1 Data collection

Zoos record the life history, husbandry and veterinary procedures of animals within their collections. The predominant animal-management software currently used by zoos is the Zoological Information Management System (ZIMS). ZIMS is operated by Species360 and allows for real-time management within an institution and as a method of sharing information with other organisations (Species360 2018). With the end of wild capture for zoos, captive populations are required to be genetically self-sufficient. Grouping captive individuals into regional or worldwide studbooks maintains genetic diversity without the need for new genes. These species-specific records, or Studbooks, are registers of the genetic and location history of all individuals held in member institutions (either international or regional) and are used for *ex situ* population management (WAZA: World Association of Zoos and Aquariums n.d.). Institutions report the data to the species' studbook keeper, who updates the studbook, collates a periodical studbook report, and makes location and breeding recommendations.

I used historical records of golden lion tamarins and Goeldi's monkeys held in institutions accredited by EAZA collected from Studbook reports and ZIMS. The golden lion tamarin and Goeldi's monkey's studbook keepers sent me studbook reports and I was granted access to shared ZIMS records as a researcher associated with the Zoological Society of London. I gathered data on all infants born in EAZA-associated zoos between 1st January 2000 and 14th July 2017, inclusive. I restricted the data set to births starting from the year 2000 to reduce the confounding effects of husbandry changes over time and inaccuracies in the data from the transfer from paper to digital records. There were 110 institutions with breeding groups of the study species during the study period (Appendix A). Of these, 26 had breeding groups of both species. For each offspring born, I collected the birth and death dates, dam and sire ID, sex, and lifetime institution movements (locations and dates) from studbook reports, then used ZIMS to cross-reference, check discrepancies and missing data. From these data, I created variables for litter size, inter-birth interval, dam age, group composition at the date of each birth, and age at death/end of the study (Appendix B). If the studbook and ZIMS record differed and I could not determine the correct information from the records of other individuals, I used the life history information from ZIMS, as recommended by the golden lion tamarin European studbook keeper (N. Lindsay, personal communication). Sample sizes in analyses differ due to missing data.

2.2 Variables

2.2.1 Offspring survival

To investigate the effects of group composition on offspring survival, I measured offspring survival to 1 year after birth, correct to 1 day. This included animals that were still alive or of unknown status at the end of the study. The preferred variable for the analysis of offspring survival is survival measured from the date of birth. However neonates are first identified several hours after birth as callitrichids, including golden lion tamarins and Goeldi's monkeys, commonly give birth at night (Price, Payne & Wormell 2016). It is therefore frequently unclear whether a neonate first observed dead was a late-term abortion, stillborn or live-born that died subsequently. Aborted and stillborn neonates represent maternal pre-natal investment effort however the inclusion of neonates which were not live-born would skew analysis of the investment effort on post-natal survival. Since these individuals could not be accurately removed from the data set, and to understand the potential impact of the inclusion of potential stillbirths on the results of previous studies I analysed the survival of infants from birth to 1 year and from 1 day to 1 year separately, as suggested by Jaquish et al. (1991). I selected 1 year as a proxy for offspring maturation and the end of helper investment based on the ages of sexual maturation and the reduction in investment received in golden lion tamarins and Goeldi's monkeys (Hoage 1982; French, Inglett & Dethlefs 1989; Dettling & Pryce 1999; Dettling 2003).

2.2.2 Litter size

I measured litter size at birth as the number of individuals born to the same female on the same day. This included recorded or potential stillbirths or late-term abortions. The term 'next litter size' refers to the size of the following litter from the same female and is used to analyse the effects of group composition on the next reproductive event. Where the mother of a litter was unknown, I considered the next litter size for all potential mothers in the group as unknown.

2.2.3 Location and group composition

Member institutions of EAZA are required to undergo inspections to ensure they to reach EAZA's codes and standards, and follow husbandry and dietary recommendations from the EAZA Callitrichid Taxon Advisory Group (The European Association of Zoos and Aquaria 2017, 2019). The enclosures and husbandry practices are therefore similar across locations. As I did not have access to in-depth husbandry information or individual health records, I used the location as a proxy for the effects of local conditions on female reproductive success. I obtained this information from the ZIMS record of the movement of an individual in or out of an institution.

I used the ZIMS records of individuals' movements and the group composition data from the studbook reports to establish the group composition at each birth. Breeding groups of golden lion tamarins and Goeldi's monkeys in EAZA institutions are established from a breeding pair recommended by the studbook keeper. Subsequent offspring remain as helpers until they are removed or the group is split. On the recommendation of the golden lion tamarin European studbook keeper, I assumed that any unrelated non-breeders present at the institution at the time of a birth were in a separate enclosure (N. Lindsay, personal communication). I could not always date the movement of a related individual into a different enclosure within an institution, or the splitting up of a breeding group. Where I could not confirm the precise group composition at the time of a birth, I did not include the group composition information in the data.

I defined 'adults' as individuals in the group greater than 1 year of age when an infant was born, in line with sexual maturation and allocaring behaviours in these species, and considered all adults as potential helpers (Hoage 1982; Beck, Anderson, Ogden, *et al.* 1982; Dettling & Pryce 1999; Dettling 2003). The number of adult males includes the father (where present), and the number of adult females excludes the mother. I defined 'young' as individuals less than 1 year of age and excluded littermates from the number of young individuals in a group. The 'young' individuals included offspring of any breeding females present and could therefore include older siblings of the current litter and non-sibling age-mates from other breeding females present.

2.2.4 Breeding female, maternal age and inter-birth interval

The mother of an individual or litter was either reported in the original data or could be assumed based on the group composition. From this information, I calculated maternal age as the age of the breeding female at each birth event. The term 'inter-birth interval' refers to the amount of time from the current birth to the following birth of the same female, both correct to 1 day. It is used for analysis of the effects of group composition on the next reproductive event. I removed inter-birth intervals where breeding was impossible, generally due to the absence of a potential breeding male. Where the mother of a litter was unknown, I considered the inter-birth interval for all potential mothers as unknown.

I did not include the sex of the offspring in the models because previous studies have shown that offspring sex does not predict offspring survival in the first year in golden lion tamarins or the first 18 months in captive golden lion tamarins and Goeldi's monkeys (French 1996; Rapaport, Kloc & Warneke 2013).

2.3 Ethical statement

I used data from historical records and the study was not intrusive to zoo regimes or live individuals. The Durham University Anthropology Department Research Ethics Committee granted ethical clearance, and the European Association of Zoos and Aquaria Callitrichid Taxon Advisory Committee endorsed the study.

2.4 Data analysis

I investigated the effects of group composition on four response variables: offspring survival from birth to 1 year and from 1 day to 1 year, inter-birth interval, and size of subsequent litter (golden lion tamarins only). For offspring survival and inter-birth interval, I used Cox proportional hazards models in R 3.4.3 using the coxme package, and for litter size I used a Poisson generalised linear mixed model (GLMM) in R 3.4.3 using the lme4 package (Bates, Maechler, Bolker, *et al.* 2015; RStudioTeam 2016; RCoreTeam 2017; Therneau 2018) (Appendix C).

For each model, I included the numbers of adult males, adult females, and young as covariates. I also included maternal age as a covariate to account for the effect of age on female reproductive success. I fitted each model with a random intercept per location and breeding female to account for within-location and within-female variation. To analyse the golden lion tamarin data set I also fitted litter size as a covariate and included interactions between the number of adult males and litter size at birth, the number of adult females and litter size at birth, and the number of young and litter size at birth to investigate the influence of helper number relative to the number of offspring being cared for simultaneously. I present the results of full models.

3 Results

3.1 Descriptive statistics

3.1.1 Golden lion tamarins

The 71 female golden lion tamarins gave birth to 297 litters and 550 offspring. The females had a mean of 4.1 litters (sd = 2.96, range = 1-15) and 7.7 offspring each (sd = 5.76, range = 1-31). The mean golden lion tamarin litter size was 1.9 (sd=1.86, range =1-3). Twins were most common (65%), then singletons (25%), and triplets (10%). The mean maternal age at birth was 7.22 years (sd = 3.28, range = 1.79-16.09) and the mean inter-birth interval was 0.77 years (sd = 0.33, range 0.21-2.60; median 0.73 years). In the golden lion tamarin data set 233 (42%) of the offspring died before 1 year. Of these individuals, 143 died on or before the first day (61% of deaths <1 year, 26% of total offspring).

The golden lion tamarin breeding groups were located in 41 different institutions. There was a mean of 1.8 adult males present at a birth (sd = 1.78, range 0-7), a mean of 0.6 non-maternal adult females present (sd = 1.08, range = 0-5), and a mean of 0.7 non-littermate young (sd = 0.90, range = 0-4).

3.1.2 Goeldi's monkeys

The 177 female Goeldi's monkeys gave birth to 881 litters and had a mean of 5.0 litters each (sd = 4.22, range = 1-22) each. There were three cases of Goeldi's monkey twins (<1%) from different breeding females and locations. The mean maternal age at a birth event was 7.78 years (sd = 3.33, range = 1.30-18.84), and the mean inter-birth interval was 0.64 years (sd = 0.42, range = 0.31-5.51; median 0.50 years). In the Goeldi's monkey data set 298 (34%) of offspring died within the first year. Of these individuals, 141 died on or before the first day (47% of deaths <1 year, 16% of total offspring).

The Goeldi's monkey breeding groups were from 95 locations. In Goeldi's monkey groups there were a mean of 1.9 adult males present at a birth (sd = 1.21, range = 0-9), a mean of 1.0 adult females (sd = 1.37, range = 0-7), and a mean of 0.8 other young (sd = 0.81, range = 0-5).

3.2 Offspring survival

Golden lion tamarin offspring had significantly lower survival in the first year of life than Goeldi's monkeys (Cox proportional hazards test: coef = -0.35, Z= -4.02, N= 1434, P<0.001). The hazard ratio of 0.70 (95% confidence intervals = 0.59-0.84) corresponds to a 41% higher chance of death before 1 year in golden lion tamarins than Goeldi's monkeys, with the major difference in mortality occurring in early life (Figure 1). Analysis of survival after the first day of life, however, showed that the difference between the species was not significant (Cox proportional hazards test: coef = -0.12, Z= -0.89, N= 1150, P = 0.37).

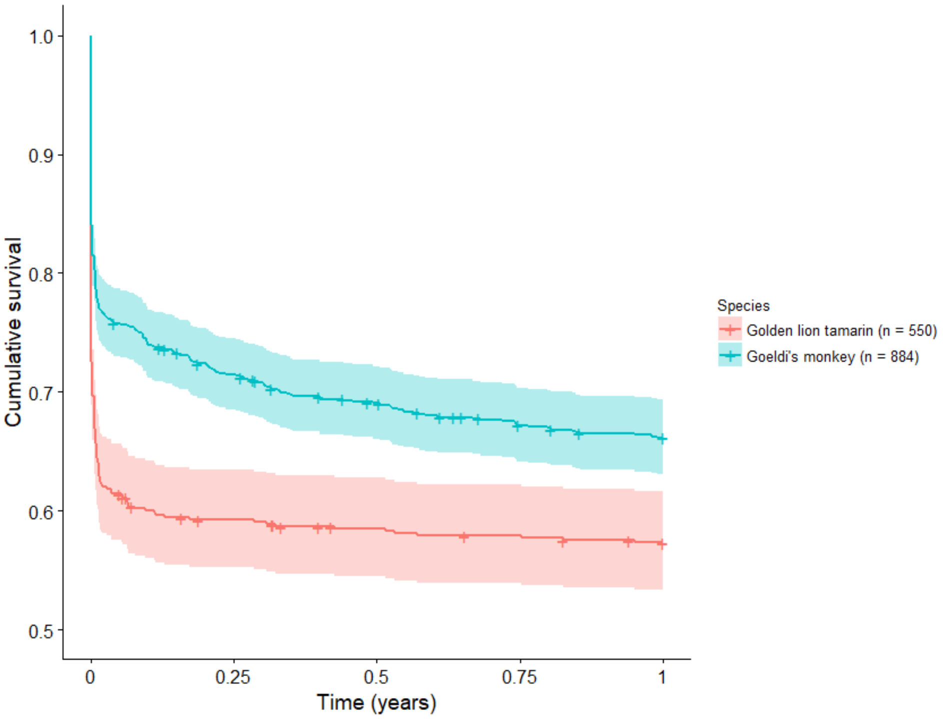


Figure 1. Cumulative survivals from birth to 1 year for golden lion tamarin and Goeldi's monkey offspring. Crosses denote censored cases and shading indicates 95% confidence intervals.

3.2.1 Golden lion tamarin survival

The interaction between the number of adult males and the litter size predicted survival from birth to 1 year for golden lion tamarins (Table 1). For each litter size offspring survival was higher when a larger number of adult males was present, although for triplets survival was similar with one or two adult males present (Figure 2). The association between survival and adult male number for each litter size was predominantly seen neonatally (Figure 2), and analysis of survival after the first day showed no significant interaction between the number of adult males and the litter size, and no significant influence of the number of adult males or the litter size on offspring survival to 1 year (Table 2).

The interaction between the number of adult females and litter size was also associated with offspring survival to 1 year, both in analysis from birth and from 1 day (Table 1 & 2). For singletons, survival was higher with one adult female helper present than with no adult females present, and higher again with two or more present (Figure 3). Offspring survival was highest in the presence of two adult females, but the small sample size for larger numbers of females restricts the interpretation of this pattern. The survival of twins was initially similar in groups with one or more adult female present, but offspring with two adult females were more likely to die during the first 6 months, leading to lower offspring survival to 1 year in groups with two adult females than groups with other non-zero numbers of adult females (Figure 3). For triplets, offspring with no adult females present had the highest mortality but those with two or more adult females present survived only slightly better (Figure 3).

The interaction between the number of young present in the group and litter size was not associated with survival during the first year for golden lion tamarins (Tables 1 & 2). There was no significant effect of maternal age on offspring survival from birth to 1 year, but there was a significant effect of maternal age after the first day to 1 year (Tables 1 & 2). Offspring of older mothers were less likely to survive between 1 day and 1 year than offspring of younger mothers (Figure 4). Holding the other covariates constant, an additional year on maternal age decreased offspring survival probability by a factor of 0.14 or 86% between 1 day and 1 year (Table 2).

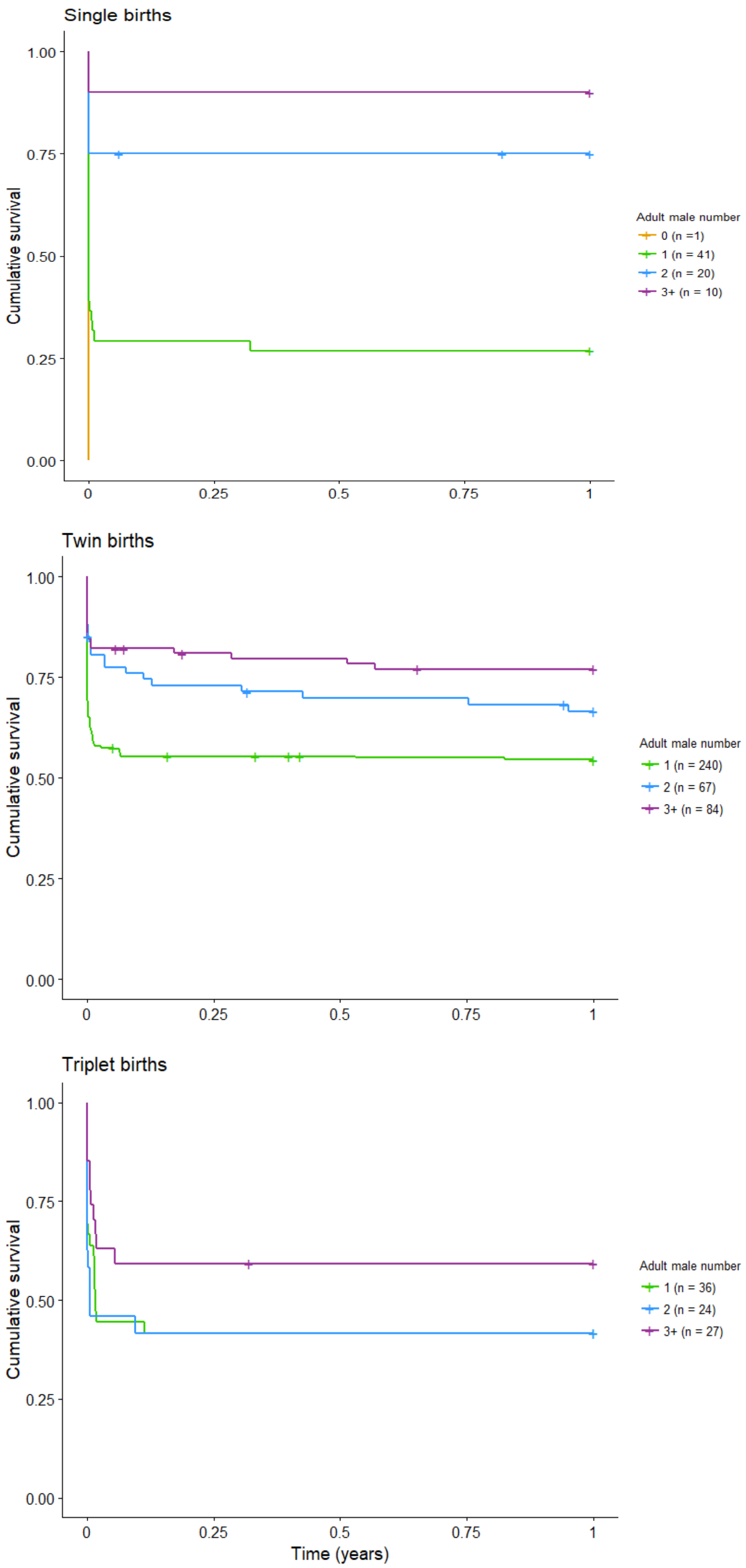
Due to the difference between the factors associated with offspring survival when I measured survival from birth or from 1 day, I used a post-hoc GLMM to investigate which factors were significantly associated with the probability of survival to 1 day. I used a Poisson generalized linear mixed model (GLMM) in R 3.4.3 using the lme4 package (Bates, Maechler, Bolker, *et al.* 2015; RStudioTeam 2016; RCoreTeam 2017). I included the numbers of adult males, adult females, and young, and maternal age and litter size as covariates, and included interactions between the number of adult males and litter size at birth, the number of adult females and litter size at birth, and the number of young and litter size at birth. I fitted the model with a random intercept per location and breeding female. I found that no measures of group composition were associated with offspring survival to 1 day, but an increase in litter size was associated with an increase in survival to 1 day (Table 3) (Figure 5).

Table 1. Results of a Cox's proportional hazards model investigating the effects of group composition on offspring survival in golden lion tamarins. Bold indicates significant results.

	coef	Exp(coef)	SE(coef)	Z value	P
Adult males	**-1.11**	**0.33**	**0.37**	**-3.06**	**<0.005**
Adult males*litter size	**0.42**	**1.52**	**0.15**	**2.72**	**0.01**
Adult females	**-0.92**	**0.40**	**0.32**	**-2.61**	**0.01**
Adult females*litter size	**0.37**	**1.44**	**0.14**	**2.61**	**0.01**
Young	-0.59	0.56	0.41	-1.43	0.15
Young*litter size	0.13	1.14	0.18	0.74	0.46
Litter size	**-0.80**	**0.45**	**0.24**	**-3.30**	**<0.001**
Maternal age	0.04	1.04	0.03	1.40	0.16
Random effects	Variance	SD			
Location	$3.97e^{-4}$	0.02			
Female	0.40	0.63			

Table 2. Results of a Cox's proportional hazards model investigating the effects of group composition on offspring survival after the first day in golden lion tamarins. Bold indicates significant results.

	coef	Exp(coef)	SE(coef)	Z value	P
Adult males	-0.84	0.43	0.59	-1.43	0.15
Adult males*litter size	0.40	1.49	0.25	1.61	0.11
Adult females	**-1.29**	**0.27**	**0.61**	**-2.13**	**0.03**
Adult females*litter size	**0.52**	**1.69**	**0.24**	**2.18**	**0.03**
Young	-0.22	0.80	0.73	-0.30	0.76
Young*litter size	-0.14	0.85	0.32	-0.49	0.62
Litter size	-0.16	0.85	0.41	-0.39	0.70
Maternal age	**0.14**	**1.15**	**0.05**	**2.87**	**<0.005**
Random effects	Variance	SD			
Location	0.76	0.87			
Female	0.21	0.46			


Single births

Twin births

Triplet births

Figure 2. Cumulative survival to 1 year of golden lion tamarin offspring with different numbers of adult males present in the group, split by litter size. Crosses denote censored cases.

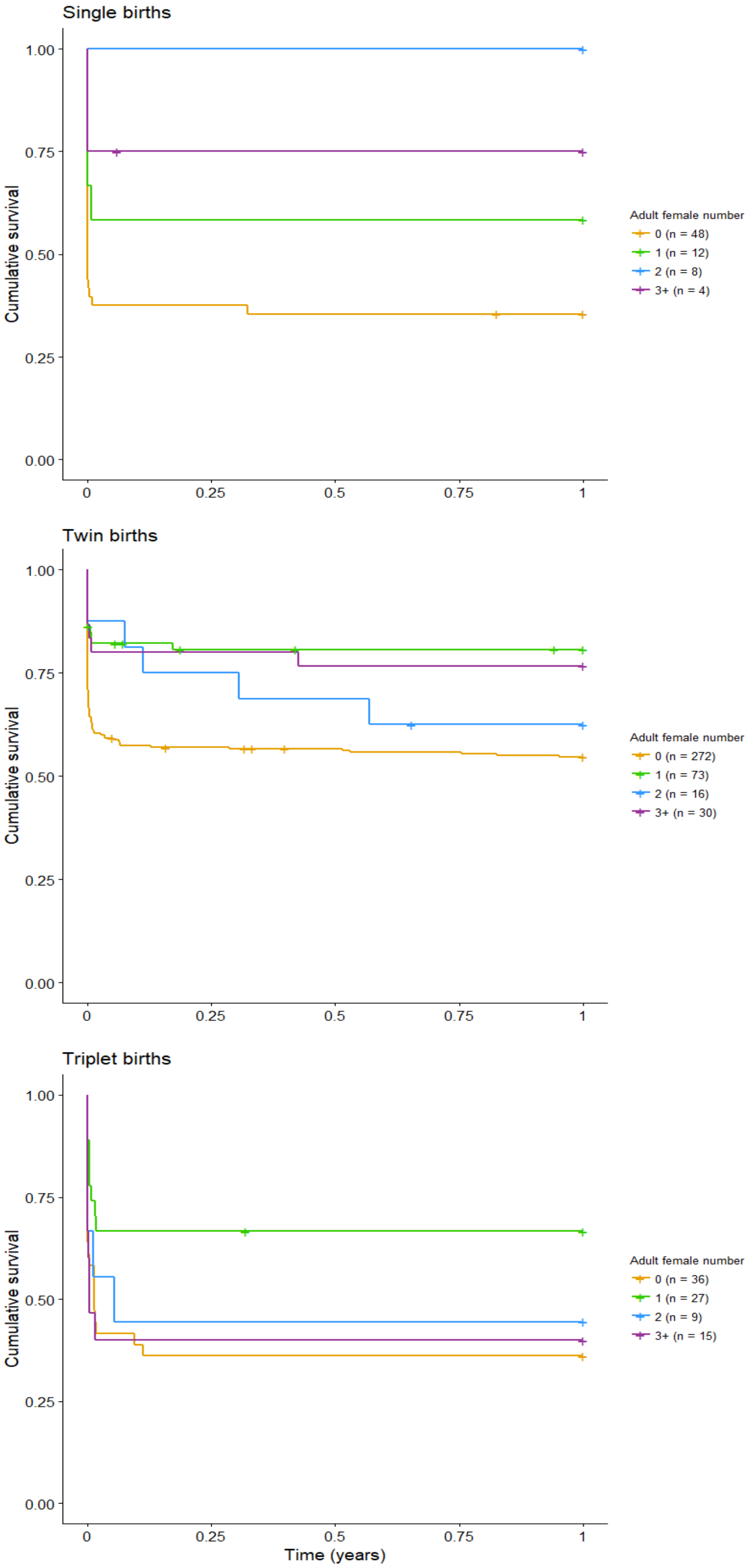


Figure 3. Cumulative survival to 1 year of golden lion tamarin offspring with different numbers of adult females in the group, split by litter size. Crosses denote censored cases.

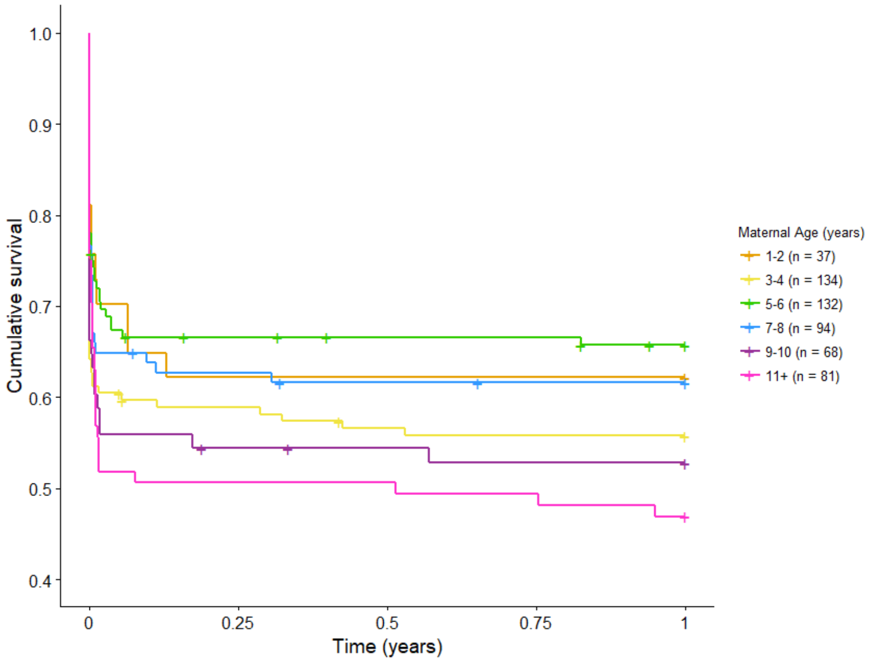


Figure 4. Cumulative survival to 1 year of golden lion tamarin offspring with different maternal ages. Crosses denote censored cases. Maternal age is categorised for the plot but was a continuous variable in the model.

Table 3. Results of a GLMM investigating the effects of group composition on offspring survival to 1 day in golden lion tamarins. Bold indicates significant results.

	Estimate	SE	Z value	P
Adult males	0.21	0.16	1.27	0.20
Adult males*litter size	-0.07	0.76	-0.87	0.38
Adult females	0.22	0.16	1.38	0.17
Adult females*litter size	-0.09	0.07	-1.17	0.24
Young	0.33	0.22	1.50	0.13
Young*litter size	-0.13	0.10	-1.30	0.19
Litter size	**0.42**	**0.18**	**2.36**	**0.02**
Maternal age	-0.01	0.02	-0.79	0.43
Random effects	Variance	SD		
Location	0.00	0.00		
Female	0.00	0.00		

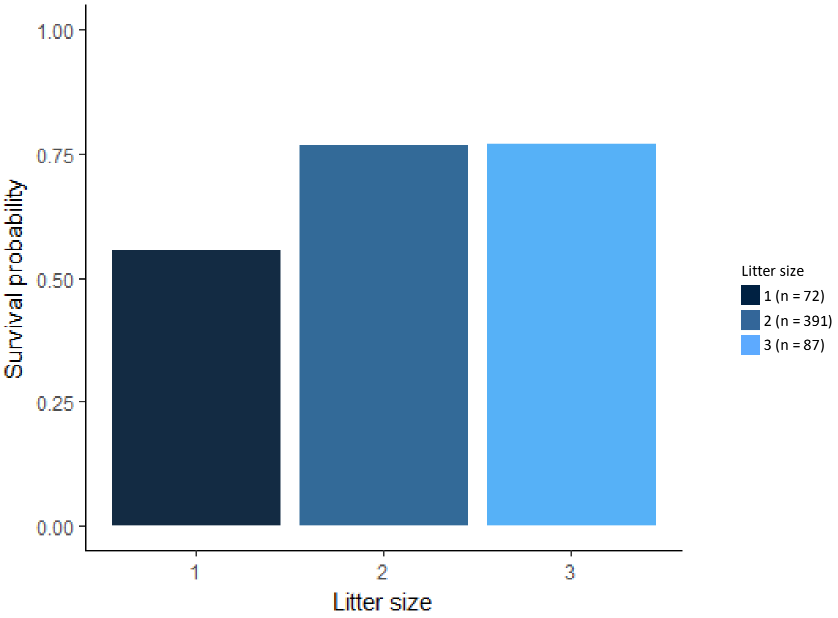


Figure 5. Survival probability for golden lion tamarin offspring in different litter sizes at birth.

3.2.2 Goeldi's monkey survival

The number of adult males and adult females present in the group did not predict offspring survival during the first year in the Goeldi's monkey data set, but the number of young was positively associated with survival (Tables 4 & 5). Increasing the number of young present by one (with all other covariates held constant) increased the probability of offspring survival 36% between birth and 1 year, and 32% between 1 day and 1 year. Offspring in groups with no other young present had lower survival during the first few days of life, after which the survival curves of groups with zero, one and two young present are approximately parallel (Figure 6). No offspring from groups with three or more present died from the day of birth to 1 year, but the low sample sizes limit the interpretation of this pattern. Although variation in offspring survival is predominantly seen in the first few days of life, the association was also significant when deaths on or before the first day were excluded (Table 5).

There was no significant effect of maternal age on offspring survival from birth or after 1 day in Goeldi's monkeys (Tables 4 & 5).

Table 4. Results of a Cox's proportional hazards model investigating the effect of group composition on offspring survival in Goeldi's monkeys. Bold indicates significant results.

	coef	Exp(coef)	SE(coef)	Z value	P
Adult males	-0.10	0.91	0.07	-1.34	0.18
Adult females	-0.16	0.98	0.06	-0.26	0.80
Young	**-0.45**	**0.64**	**0.10**	**-4.63**	**<0.001**
Maternal age	0.03	1.03	0.02	1.16	0.25
Random effects	Variance	SD			
Location	0.31	0.56			
Female	0.31	0.48			

Table 5. Results of a Cox's proportional hazards model investigating the effect of group composition on offspring survival after the first day in Goeldi's monkeys. Bold indicates significant results.

	coef	Exp(coef)	SE(coef)	Z value	P
Adult males	-0.12	0.89	0.09	-1.30	0.19
Adult females	-0.04	0.96	0.08	-0.47	0.64
Young	**-0.39**	**0.68**	**0.12**	**-3.15**	**<0.005**
Maternal age	0.01	1.01	0.03	0.34	0.73
Random effects	Variance	SD			
Location	0.51	0.72			
Female	$4.00e^{-4}$	0.02			

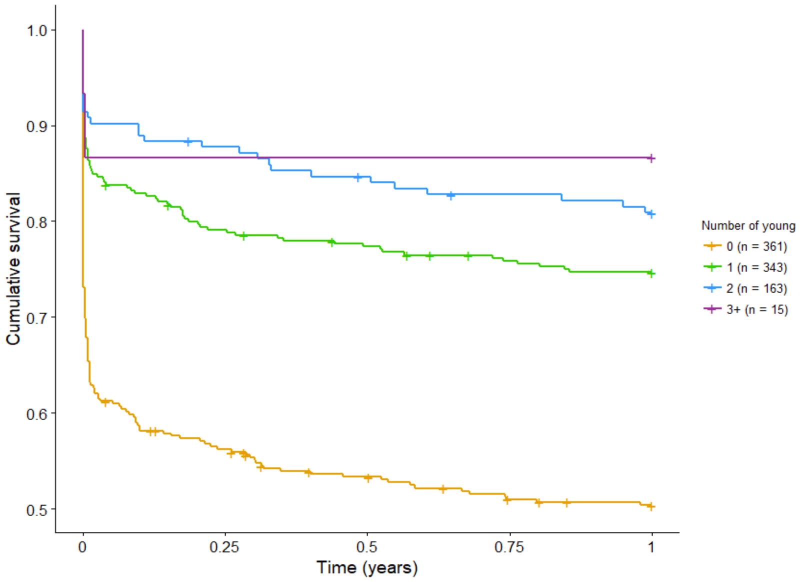


Figure 6. Cumulative survival to 1 year of Goeldi's monkey offspring with different numbers of non-littermate young. Crosses denote censored cases.

3.3 Inter-birth interval

Golden lion tamarins had significantly longer inter-birth intervals than Goeldi's monkeys (Cox proportional hazards test: coef = 0.47, Z=5.90, N=1105, P<0.001, Figure 7). The hazard ratio of 1.59 (95% confidence intervals = 1.36 – 1.86) corresponds to a 59% longer inter-birth interval in golden lion tamarins. For both species almost all births occurred between 6 months and 2 years of the previous birth.

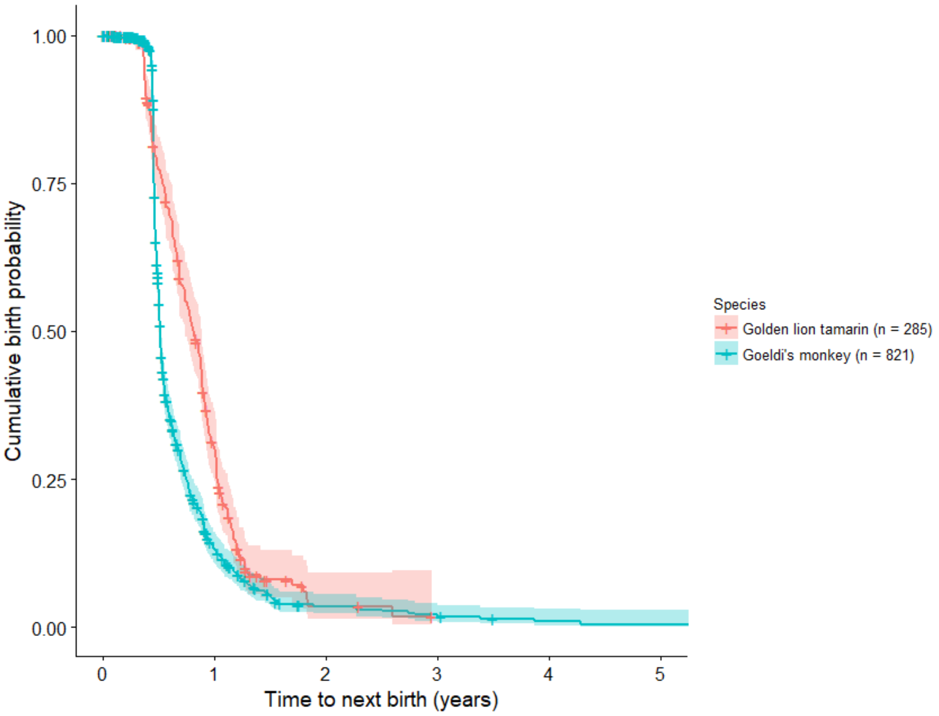


Figure 7. Cumulative survival curves comparing inter-birth intervals in golden lion tamarins and Goeldi's monkeys. Crosses denote censored cases and shading indicates 95% confidence intervals.

3.3.1 Golden lion tamarin inter-birth interval

None of the variables examined significantly predicted inter-birth interval in golden lion tamarins (Table 6).

Table 6. Results of a Cox's proportional hazards model investigating the effect of group composition on inter-birth interval in golden lion tamarins.

	coef	exp(coef)	SE(coef)	Z value	P
Adult males	0.14	1.15	0.27	0.51	0.61
Adult males* litter size	-0.04	0.97	0.14	-0.26	0.79
Adult females	-0.15	0.86	0.33	-0.47	0.64
Adult females* litter size	0.03	1.03	0.16	0.21	0.83
Young	0.16	1.18	0.27	0.61	0.54
Young*litter size	-0.04	0.96	0.13	-0.28	0.78
Maternal age	-0.03	0.97	0.02	-1.36	0.17
Litter size	0.19	1.21	0.26	0.74	0.46
Random effects	Variance	SD			
Location	0.01	0.10			
Female	$3.70e^{-4}$	0.02			

3.3.2 Goeldi's monkeys inter-birth interval

Neither the number of adult males nor the number of adult females were significantly associated with inter-birth interval in Goeldi's monkeys (Table 7). However, the number of young present was significantly associated with inter-birth interval (Table 7). A high proportion of births occurred around 6 months after the previous birth. For inter-birth intervals of longer than 6 months, females with more young present at the first birth had shorter inter-birth intervals than those with fewer or no young present (Figure 8). An increase of one young present at the previous birth corresponded to a 26% shorter inter-birth interval if all other covariates were constant.

Maternal age was also associated with the inter-birth interval in Goeldi's monkeys, with older females being more likely to have longer inter-birth intervals than younger females (Table 7,

Figure 9). However, the effect was small: an increase in maternal age of one year increased inter-birth interval by 4% if all other covariates were constant.

Table 7. Results of a Cox's proportional hazards model investigating the effects of group composition on inter-birth interval in Goeldi's monkeys. Bold indicates significant results.

	Coef	exp(coef)	SE(coef)	Z value	P
Adult males	0.06	1.06	0.04	1.41	0.16
Adult females	-0.07	0.93	0.04	-1.93	0.05
Young	**0.23**	**1.26**	**0.06**	**3.86**	**<0.001**
Maternal age	**-0.04**	**0.96**	**0.016**	**-2.74**	**0.01**
Random effects	Variance	SD			
Location	0.10	0.31			
Female	0.05	0.22			

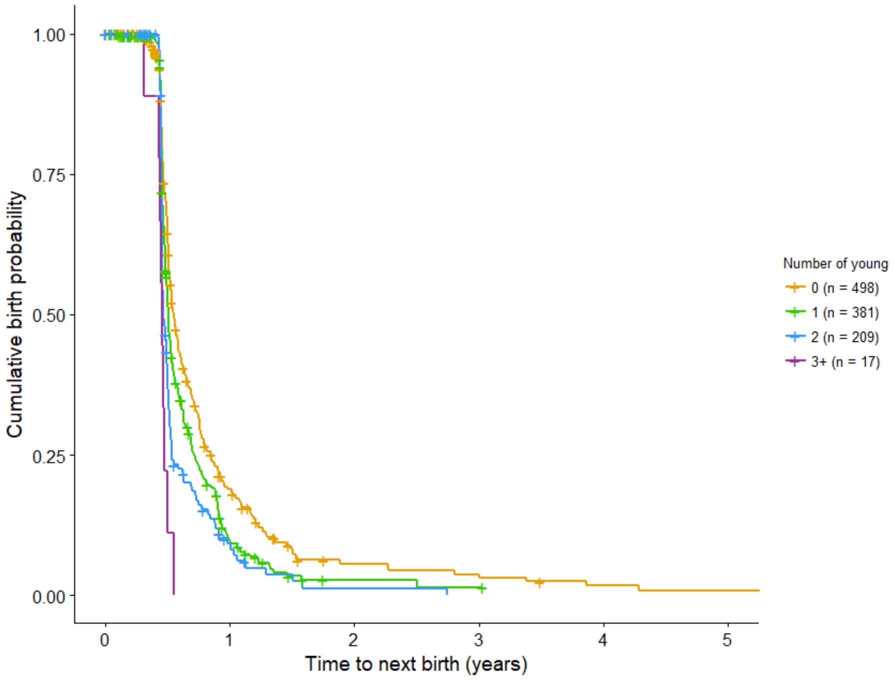


Figure 8. Cumulative survival curves for Goeldi's monkey inter-birth intervals for different numbers of non-littermate young. Crosses denote censored cases.

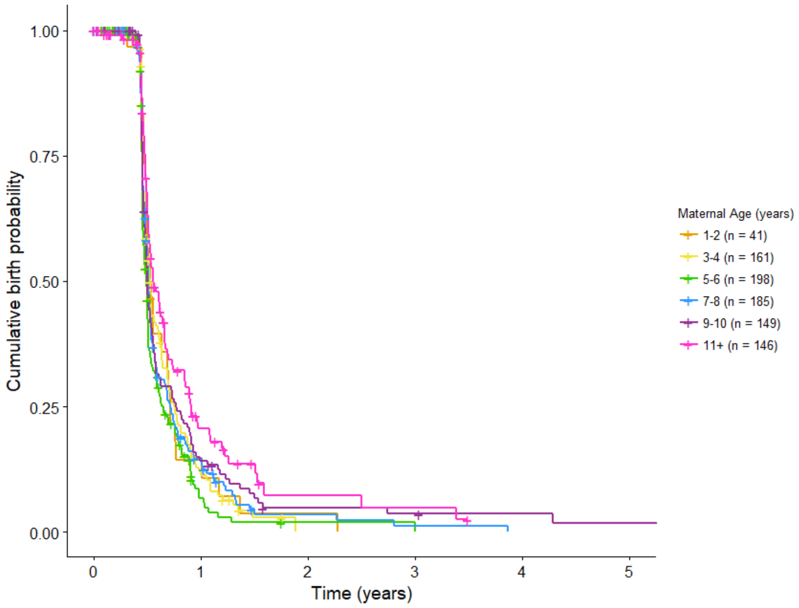


Figure 9. Cumulative survival curves for Goeldi's monkey inter-birth intervals for different maternal ages. Crosses denote censored cases. Maternal age is categorised for the plot but was a continuous variable in the model.

3.4 Litter size

3.4.1 Golden lion tamarin litter size

None of the variables examined significantly predicted the litter size at the next birth in golden lion tamarins (Table 8).

Table 8. Results of a GLMM investigating the influence of group composition on the next litter size in golden lion tamarins.

	Estimate	SE	Z value	P
Adult males	-0.06	0.15	-0.41	0.68
Adult males*litter size	0.04	0.07	0.58	0.56
Adult females	-0.13	0.19	-0.72	0.47
Adult females*litter size	0.06	0.09	0.73	0.46
Young	0.01	0.22	0.03	0.97
Young*litter size	$3.00e^{-3}$	0.11	0.03	0.98
Maternal age	-0.01	0.02	-0.38	0.70
Litter size	-0.03	0.16	-0.20	0.84
Random effects	Variance	SD		
Location	0.00	0.00		
Female	0.00	0.00		

4 Discussion

Cooperative breeding has evolved in species where breeders or helpers receive fitness benefits from allocare. Allomaternal investment often increases maternal success through the quality or quantity of offspring produced (Williams 1966; Trivers 1972; Clutton-Brock 1991; Royle, Smiseth & Kölliker 2012). Maternal fitness may increase though increased offspring success if mothers employ additive care strategies (maintaining their own level of care), or higher maternal reproductive output if mothers undertake load-lightening strategies in response to additional investment from allocarers (reducing their own level of care). I investigated the effects of group composition on female reproductive success in golden lion tamarins and Goeldi's monkeys to better understand the influence of allocarer presence on female reproductive strategies in a captive environment. My results do not support the hypotheses that mothers employ additive care or load-lightening strategies, as neither offspring success nor reproductive output was associated with the number of allocarers in either species.

Allocare may evolve where the net costs and benefits to mothers are neutral, but helpers accrue fitness benefits (Clutton-Brock, Brotherton, O'Riain, *et al.* 2000; Clutton-Brock 2002; Dickinson & Hatchwell 2004). Allocaring behaviours are tolerated, and even encouraged, by callitrichid mothers, suggesting that they benefit in some way (Fite, Patera, French, *et al.* 2005). Across species, the maternal benefits of non-maternal investment are expressed through cryptic traits such as egg size and offspring reproductive success (Russell & Lummaa 2009; Savage et al. 2015). The maternal benefits of allocare in callitrichids may therefore be expressed through traits which I did not measure here. Variation in the amount of allocare undertaken by helpers may also mask the maternal fitness benefits. The amount of allocare undertaken varies with individual characteristics, and with the social environment (Schradin & Anzenberger 2001b). In callitrichids, investment from individual allocarers decreases with increasing number of helpers (Price 1992a). This pattern may be selected for due to diminishing returns of increasing investment, and should occur where allocarers benefit from indirect fitness benefits, or direct benefits from the outcome of allocare (for example increasing groups size) rather than the behaviours themselves (for example via social 'prestige' or 'rent payment') (Heinsohn 2004). It may not be appropriate to assume the amount of allocare increases with the number of helpers, leading to a more complex pattern of benefits to mothers.

4.1 Comparison of female reproductive success between study species

In these datasets most deaths occurred early in life, with 26% of golden lion tamarin offspring and 16% of Goeldi's monkey offspring dying on or before the first day of life. This is consistent with the high neonatal mortality and low subsequent mortality found across the callitrichid family (Jaquish, Cheverud, Tardif, *et al.* 1996; Jaquish, Tardif & Cheverud 1997; French 1996; Leong, Terrell & Savage 2004; Savage, Soto, Medina, *et al.* 2009; Anderson & Dennis 2018) and New World monkeys more generally (Debyser 1995).

My results support previous findings for offspring survival and inter-birth intervals in the two study species. Overall, I found that golden lion tamarins had a lower survival to 1 year than Goeldi's monkeys, supporting patterns reported in previous studies of these species in captivity (Kohler, Laurie & Lackey 2006; Lynch, Zeigler, Wells, *et al.* 2010). The mean inter-birth interval was longer for golden lion tamarins than Goeldi's monkeys. Both species are capable of biannual births, although they may occur more frequently in captivity than in the wild (Dietz, Baker & Miglioretti 1994; French 1996; Porter 2001). The rate of biannual births and average inter-birth intervals are not well reported, but lion tamarins have been suggested to have fewer biannual births than most other callitrichid species, including Goeldi's monkeys (Porter & Garber 2004; but see Baker & Woods 1992). My finding of a longer mean inter-birth interval in golden lion tamarins than Goeldi's monkeys supports this.

Golden lion tamarins had a mean litter size of 1.9, while Goeldi's monkeys had predominantly singletons. However, golden lion tamarin offspring had a higher mortality before 1 year than Goeldi's monkeys. Combined with the shorter inter-birth interval in Goeldi's monkeys, this suggests that singleton births may be associated with an equivalent, or higher, reproductive success for Goeldi's monkeys than twin births in golden lion tamarins and other callitrichids. I estimated the overall reproductive success to 1 year between the two study species using the average litter size (golden lion tamarin = 1.9, Goeldi's monkey = 1.0), probability of offspring survival to 1 year (golden lion tamarin = 0.58, Goeldi's monkey = 0.66), and average inter-birth interval (golden lion tamarin = 0.77, Goeldi's monkey = 0.64), and found that golden lion tamarins in this study had a higher average number of offspring surviving to 1 year (golden lion tamarin = 2.5, Goeldi's monkey = 0.97). This estimate suggests that the evolutionary reduction in litter size in Goeldi's monkeys has led to lower overall reproductive success. However, a more accurate comparison of reproductive success in the two species would include the effect of litter size and offspring survival on subsequent reproduction and on the reproductive lifespan of a female.

4.2 Group composition and offspring survival

I predicted that the probability of offspring survival would correlate positively with the number of male and female helpers relative to litter size. In the analysis from birth, an increase in the number of adult male golden lion tamarins was associated with increased offspring survival, depending on litter size. However, this effect was mainly seen neonatally and the association was not significant in the analysis from 1 day. Allocare begins approximately 1 month after birth in golden lion tamarins (Hoage 1982; Santos, French & Otta 1997). This suggests that allocaring behaviours of adult males do not increase offspring survival since the number present during the allocaring period was not significant. Female callitrichids are capable of late-term pre-natal litter size reduction without spontaneous abortion which may be influenced by the local conditions, including the social environment (Jaquish, Cheverud, Tardif, *et al.* 1996; Windle, Baker, Ridley, *et al.* 1999). However, the number of adult males was not associated with late-term abortions and still-births in this data set.

The number of adult females relative to the litter size was associated with both measures of offspring survival (from birth to 1 year, and from 1 day to 1 year) in golden lion tamarins. Offspring in all litter sizes born in groups with no other adult females present had a lower probability of survival to 1 year than those born in groups with adult females present. However, the relationship was not linear: offspring born in groups with more than two females were less likely to survive than those born in groups with one or two adult females. This may because of the high level of intra-sexual aggression between females in callitrichids, including golden lion tamarins (French & Inglett 1989; Snowdon & Pickhard 1999; Burkart 2015). This aggression can be directed towards offspring in instances of plural breeding but plural breeding was rare in this data set and most instances of female-female aggression in the literature are directed towards adult females, making it unlikely that intra-sexual aggression explains this association. The interpretation of this finding is limited by the small number of groups with a large number of adult females, but plural breeding and dominance status may be factors to investigate in future studies and a consideration in captive group management.

The interaction between group composition and litter size in golden lion tamarins is interesting. Litter size has frequently been found to affect infant survival, but previous studies have not analysed group composition relative to the litter size. Most studies of golden lion tamarins and across callitrichids have found that twins have better survival than triplets, with some also reporting that singletons have a lower survival probability than twins (Jaquish, Gage & Tardif 1991; Leong, Terrell & Savage 2004; Savage, Soto, Medina, *et al.* 2009; Ward, Buslov & Vallender 2014). The effects of litter size on offspring survival have previously been found to be restricted to early life (to 1 month), rather than until reproductive maturation or throughout an individual's lifespan (Jaquish, Gage & Tardif 1991). My analysis suggests litter size influences neonatal survival: litter size was the only significant factor affecting golden lion tamarin survival to 1 day. In my dataset singleton litters had the lowest survival to 1 day. Singletons have a higher neonatal body mass than twins, which is associated with better survival (Bales, French & Dietz 2002; but see Jaquish, Tardif & Cheverud 1997). However, singletons may be more likely to be stillborn or non-viable than larger litter sizes. Their high neonatal body mass may result in birth complications, or prenatal litter size reduction may increase the likelihood of late-term abortions or stillbirths (Leutenegger 1979; Jaquish, Gage & Tardif 1991; Jaquish, Cheverud, Tardif, *et al.* 1996).

The single births and later onset of allocare in Goeldi's monkeys compared to other callitrichids (except lion tamarins), has led to the suggestion that allocare is less important for Goeldi's monkeys than for twinning callitrichids (Porter 2001; but see Rapaport, Kloc & Warneke 2013). My results support this: in Goeldi's monkeys, neither the number of adult males nor the number of adult females was associated with offspring survival birth or from 1 day. This suggests that the allocaring behaviours of Goeldi's monkeys do not increase maternal reproductive success through an increase in offspring survival.

As non-littermate young present in a group also receive care from allocarers, I predicted that the probability of offspring survival would correlate negatively with the number of non-littermate young present. This was not the case in golden lion tamarins, which suggests that the presence of other young does not decrease investment enough to affect survival. In Goeldi's monkeys, I found the opposite pattern to my prediction: an increase in the number of young was associated with a higher probability of offspring survival. This was mainly due to the presence, rather than the number of, other young. Juveniles and subadults show less allocare than adults in most callitrichid species, but Goeldi's monkeys have similar investment levels before and after maturation (Schradin & Anzenberger 2001b). The positive association between the presence of young and offspring survival could suggest that the helping behaviours of the young have a considerable impact in this species. However, although offspring survival increased in the presence of young, survival did not increase with a larger number of young present, and my data did not support an association between the numbers of adults and offspring survival. Therefore, I found no other support that the number of potential allocarers increases survival in Goeldi's monkeys. Groups including individuals younger than 1 year have helpers with rearing experience, and offspring born are likely to be from the same female due to the reproductive skew towards the dominant female and the practise of keeping callitrichids in family groups in captivity. The association between offspring survival and the presence of young is therefore likely to indicate that groups or breeding females which have successfully reared an infant are more likely to be successful again.

4.3 Group composition and female reproductive output

In addition to offspring survival, a female's reproductive success is also affected by her fecundity. If female golden lion tamarins or Goeldi's monkeys employ load-lightening strategies (Mitani & Watts 1997), then I predicted that time to the next birth would correlate negatively with the number of male helpers and the number of female helpers relative to the litter size at the current birth. These predictions were not supported in either golden lion tamarins or Goeldi's monkeys. I also predicted that the inter-birth interval would correlate positively with the number of young. This was not supported in golden lion tamarins, but an increase in the number of young was associated with a shorter inter-birth interval in Goeldi's monkeys. This association is the opposite of that predicted. I suggest that this is an indirect association as maternal age was also associated with the inter-birth interval, and local or female conditions have previously been found to correlate with inter-birth intervals in callitrichids and in other cooperatively breeding species (Nias & Ford 1992; Mitani & Watts 1997; Hodge, Manica, Flower, *et al.* 2008).

Female reproductive output is also affected by litter size at each birth. In golden lion tamarins multiple births are common and the mean litter size in this study is similar to previous reports (Jaquish, Gage & Tardif 1991). I predicted that the next litter size would correlate positively with the number of male helpers and the number of female helpers relative to the litter size and would correlate negatively with the number of young present relative to the litter size. These predictions were not supported in golden lion tamarins. This result is in line with a previous study which did not find a correlation between the number of live-born offspring produced in a year (a measure which incorporates both live-born litter size and inter-birth interval) and the total number of helpers, the number of adult males (Bales, O'Herron, Baker, *et al.* 2001). I therefore found no evidence for an increase in maternal output with increasing allocare, and no support for load-lightening strategies in golden lion tamarins. Goeldi's monkeys rarely have multiple births and there were only three cases of Goeldi's monkeys twins in this data set, similar to the frequency reported in previous studies (Altmann, Warneke & Ramer 1988; Rapaport, Kloc & Warneke 2013). Of the three sets of twins, one set was dead at 1 day, another set were alive but aged <1 year at the end of the study, and another set survived past 1 year. The rearing status of the surviving twins was not recorded, but Goeldi's monkeys have only previously been reported to both survive when one is hand-reared (Altmann, Warneke & Ramer 1988; Sodaro 2000) The small sample size prevents conclusions from being drawn about the factors affecting the probability of twins, or the effect of litter size on offspring survival in Goeldi's monkeys.

In some callitrichid species, allocarers, rather than mothers, load-lighten and alter their investment levels according to the local conditions (Price 1992a; Santos, French & Otta 1997; Bales, Dietz, Baker, *et al.* 2000). If this occurred then an increase in allocaring behaviours would not be expected to correlate with an increase in female reproductive success, but with the success of other group members. The extent of allocare may also influence a female's lifetime reproductive success through factors that were not examined here, such as offspring growth rate, female reproductive tenure, or female survival.

4.4 Other factors affecting female reproductive success

4.4.1 Female age and identity

Maternal age was not associated with offspring survival from birth to 1 year in either species, but offspring of older females were less likely to survive from 1 day to 1 year in golden lion tamarins. This suggest that maternal age may be important to post-natal offspring survival in this species, but that the high proportion of deaths on the first day mask the effect of maternal age in subsequent survival. Across species, age-related decline in breeding females selects against continued investment in offspring production due to the lower probability of success from breeding to maturation (Rockwell, Cooch, Thompson, *et al.* 1993; Paul, Kuester & Podzuweit 1993), although this may be less important in callitrichids as allocare means that offspring can survival maternal death before they are fully weaned (Bales, O'Herron, Baker, *et al.* 2001). Maternal age was not correlated with female reproductive output in golden lion tamarins, supporting a previous study of this species (Bales, O'Herron, Baker, *et al.* 2001). Older females had slightly longer inter-birth intervals than younger females in Goeldi's monkeys, as in other callitrichid species (Smucny *et al.* 2004; but see Box & Hubrecht 1987).

Maternal ID had a low contribution to maternal reproductive output and offspring survival in both species I studied. This does not support findings that callitrichid females have individual histories of either low or high reproductive success, although this difference may have been determined by the female's body mass (Bales *et al.* 2001). It does, however, support the low repeatability of litter size in both callitrichids and other litter-bearing species (Jaquish *et al.* 1996). Ideally, I would have included female body mass at conception in the model as this has consistently been found to predict reproductive success in callitrichids (Tardif & Jaquish 1997; Bales *et al.* 2001; Ash & Buchanan-Smith 2014). However, I had insufficient data, and those data available were more likely to have been taken when the individual was in poor condition and examined by a veterinarian, biasing the data set.

4.4.2 Captive conditions

Using historical databases from zoos enabled me to analyse the factors affecting reproductive success without the high environmental variability associated with wild studies. However, differences in husbandry practices affect female reproductive success in callitrichids (Kirkwood 1983; Jaquish, Gage & Tardif 1991; Nuss & Warneke 2010; Steinmetz *et al.* 2011). The human determination of breeding pairs and groups compositions in captivity may also affect individual's reproductive strategies. In other species, individuals paired with a 'less preferable' mate produced fewer offspring, or offspring with lower viability, than those paired with a 'more preferable' mate, so the quality of the available mate or the absence of mate selection may influence female reproductive success (Drickamer, Gowaty & Holmes 2000; Bluhm & Gowaty 2004a, 2004b).

The high energy diet and restricted ranging leads to a higher body mass in captivity than in the wild (Araújo *et al.* 2000). In callitrichid females this is associated with and larger litter sizes at birth (Kirkwood 1983; Tardif & Jaquish 1997). Historically, these large litter sizes in captivity were followed by greater neonatal mortality in captivity than in the wild (Jaquish, Gage & Tardif 1991). However, wild studies underestimate litter size and neonatal death rate, as offspring are frequently first observed and recorded a few days after birth and improvements in callitrichid husbandry and breeding programmes have led to increases in neonatal survival in captivity (Windle *et al.* 1999; but see Savage *et al.* 2009). This study provides a recent measure of neonatal survival in zoo conditions, which is higher than previous reports from zoos and captivity generally (Debyser 1995).

Levels of relatedness and group composition differ between wild and captive conditions. The flexible mating systems present in wild callitrichid groups are infrequently replicated in captivity in the interests of group stability (De Vleeschouwer, Leus & Van Elsacker 2003; Anzenberger & Falk 2012). The resulting predominantly monogamous mating system and long reproductive tenures may affect the costs and benefits of allocare to the individuals involved (Löttker, Huck & Heymann 2004). The low flexibility in group membership in captivity may also mean that an individual's presence in group is an inaccurate proxy for investment level. Although individuals are separated after intense or continued aggressive behaviours, captive groups may have low social tolerance before aggression occurs (De Vleeschouwer, Leus & Van Elsacker 2003; Burkart 2015). Captive groups may have social compositions that would not be stable in the wild and include individuals that would have dispersed if that was an available option. Such individuals would have been included as helpers in my analysis but may not have shown substantial allocare. This reduction in social tolerance may explain the non-linear association between the number of adult females and offspring survival. Captive callitrichid groups with a higher proportion of females have a lower overall level of prosociality, the effects of which may also have masked the effects of allocare by adult males (Burkart 2015). Future studies integrating the sex ratio of the group and sex as individual factors could explore this.

The allocaring behaviours of callitrichids have been suggested to have less effect on maternal reproductive success in captivity than in the wild (Rothe, Koenig & Darms 1993; but see Rapaport, Kloc & Warneke 2013). Across cooperative breeding species, an increase in the number of helpers has the largest effect on reproductive success in poor conditions (Heinsohn 2004). My results support the general finding that captive callitrichids have larger average litter sizes and higher rates of biannual breeding than wild callitrichids, and that infant mortality mostly occurs neonatally (Dietz, Baker & Miglioretti 1994; Jaquish *et al.* 1996; Jaquish, Tardif & Cheverud 1997; French 1996; Leong, Terrell & Savage 2004; Savage *et al.* 2009). The effects of varying group composition may therefore be less pronounced in captivity than in the wild: load-lightening will not increase fecundity if a female's current reproductive output is already high, and additive care will not affect offspring survival if it is not restricted by the level of investment received.

4.5 Implications for the evolution of allocare

My results do not support the hypothesis that an increase in allocarers increases maternal fitness through either offspring success or reproductive output in captive golden lion tamarins or Goeldi's monkeys. If golden lion tamarin and Goeldi's monkey mothers do not receive fitness benefits from allocare then its evolution in callitrichids may not relate to indirect fitness benefits to helpers. Instead, direct fitness benefits such as increases in parental experience or reproductive success would be the direct fitness benefits behind its evolution and maintenance. This would not include 'rent payment' by subordinate females as mothers would have no incentive to reduce aggression or delay eviction of subordinate females if they did not receive direct fitness benefits from allocare

However, it is possible that allocare does increase maternal fitness, but that maternal reproductive success does not increase linearly with allocarer numbers. The number of allocarers is negatively associated with the investment undertaken by each helper, with the father benefiting most from decreased carrying time (Santos et al. 1997; Zahed et al. 2010).

Mothers may undertake additive care, and maintain their investment levels, whilst allocarers undertake load-lightening behaviours, altering their helping behaviours according to the group composition. If this is the case, helper numbers would not be associated with total investment in offspring, and therefore would not predict maternal success.

I found an association between group composition and offspring survival to 1 day in golden lion tamarins. I included this measure to ensure that my results were not affected by aborted and stillborn offspring. Although this overcompensated for aborted and stillborn offspring, without this measure the numbers of male and female adult helpers would have appeared to influence offspring survival in golden lion tamarins. Most studies do not remove stillborn individuals or examine offspring survival only during the allocaring period (Jaquish et al. 1991). Associations between allocarer numbers and offspring survival may therefore be a measure of the effect of group composition on late-term abortion, stillbirth or neonatal death. The effect of allocare on reproductive success may not be as evident or widespread as reported, and the importance of group composition on maternal prenatal and neonatal success may have been overlooked in previous studies (Jaquish et al. 1991). Explanations for this association may include a breeding females' position in a feeding hierarchy, since nutrition is associated with ovulation number and litter size at birth, or other group characteristics such as group stability which relates to infant survival in captive cebidae (Debyser 1995).

4.6 Conclusion

Overall, this study shows that group composition affects reproductive success in golden lion tamarins through offspring survival. An increase in the number of adults of both sexes relative to the litter size was associated with an increase in offspring survival. However, the effect mostly occurred before allocare begins in this species, and the number of adult males was not significantly associated with offspring survival if stillbirths and deaths on the first day were not included the analysis. This suggests that the association may not be caused by allocare. I found no evidence of an increase in female reproductive output in response to increasing helper numbers in golden lion tamarins. In Goeldi's monkeys, the number of adult males and females did not correlate with any of the measures of reproductive success I investigated. Unexpectedly, the number of young present was associated with higher reproductive success but this is likely to be an indirect association rather than a result of the allocaring behaviours of young Goeldi's monkeys.

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Appendix A – Locations of breeding groups

Table 1. The number of offspring born and breeding females of golden lion tamarins and Goeldi's monkeys at each location. Location names correspond to the studbooks and may differ from the institution's name.

	Golden lion tamarins			Goeldi's monkeys		
Location	Births	Breeding females	Additional information	Births	Breeding females	Additional information
AALBORG	11	3	Outdoor enclosure	26	3	Indoor enclosure
ALBUSTAN				3	1	
ALFRISTON				14	2	
AMIENS				5	1	
AMSTERDAM				12	5	
ANTWERP				15	3	
APELDOORN	23	2	Free-ranging	11	2	Free-ranging
ASSON				9	2	
AUGSBURG				2	1	
BANDHOLM				4	3	
BANHAM	16	2		16	2	
BARCELONA				18	2	Indoor/outdoor enclosure
BASEL	17	2	Indoor enclosure			
BASILDON				2	1	Indoor enclosure
BAYRAMOGL				2	2	
BEAUVAL	27	3		15	4	1 birth from unknown mother
BELFAST	1	1		2	2	Indoor enclosure
BERN				18	7	
BESANCON				22	2	
BIRMNGHAM	3	1		5	1	
BLACKPOOL				14	2	Indoor and outdoor enclosure
BOISSIERE	2	1		4	2	
BRISTOL	9	2		22	4	Indoor enclosure

BROXBOURN				1	1	
BUDAPEST	2	1		2	1	
CALDERGLE				7	1	
CALVIAC				2	2	
CHARD				1	1	
CHEMNITZ				9	3	
COLCHESTR	19	2	Outdoor walk-through enclosure	19	2	Outdoor walk-through enclosure
COMBE MAR				3	1	
DRESDEN				10	3	
DUBLIN	5	1	Indoor enclosure	21	4	Indoor enclosure
DUDLEY				8	2	Indoor enclosure
DUISBURG	12	4		5	1	
DVURKRALV	19	1	Indoor/outdoor enclosure			
EBERSWALD				1	1	
EDINBURGH				32	3	Indoor enclosure
EICHBERG				10	3	
EXMOOR				1	1	
FAUNIA				23	2	Indoor enclosure
FONTAINE	20	3				
FRANKFURT	26	2	Indoor enclosure	10	3	Indoor enclosure
GOTEBORGS				2	1	
HALLE				29	3	Indoor enclosure
HAMERTON				12	2	Indoor/outdoor enclosure
HEIDELBURG	8	1				
HELSINKI	16	2		8	1	Indoor enclosure
ISL AM				10	2	
JEREZ				3	3	
JERSEY	8	2	Free-ranging	8	1	
JERUSALEM	8	3	Indoor enclosure			
JIHLAVA	11	2		8	2	

KARLSRUHE				11	2	
KARSUPKE				5	1	
KATOWICE				8	1	
KERZERS				6	1	
KOBENHAVN	64	4	2 births from unknown mother. Indoor enclosure			
KOLN				8	2	
KREFELD	9	1	2 births from unknown mother			
KRISTIANS	2	1				
LA FLECHE	5	1	Outdoor enclosure			
LA PALMYR	29	2	Outdoor enclosure	14	2	
LANDAU	2	1				
LILLE				3	1	
LISBON	24	2		9	1	
LONDON	3	1	Indoor enclosure	19	3	Indoor enclosure
MARLOW				4	1	
MARWELL	13	1		15	3	
MOTZKIN				2	1	
MULHOUSE				14	4	Indoor enclosure
MUNSTER	17	4				
NESLES				1	1	
NEUWIED				4	2	
NEWBURY				6	1	Indoor enclosure
NOVOSIBRK	7	1		9	3	
NYKOBING				5	1	
ODENSE				3	2	
OLOMOUC	12	3		1	1	
OMEGA PAR				5	1	
OPOLE				4	1	
OVERLOON				19	3	

PAIGNTON				9	3	
PEAUGRES	19	3				
PELISSANE				11	2	
PISTOIA				2	1	
PITENCRIF				3	1	
PLOCK				10	4	
PUNTAVERD				2	1	
RANDERS				17	3	Indoor walk-through enclosure
RIGA				14	3	
ROMAGNE	14	2	Free-ranging			
SANDWICH				4	2	
SANTILLIAN	9	1		18	2	
SERVION				11	3	
SHALDON	1	1		3	1	
SKANAKV				11	2	
STOCKHOLM	13	1				
STUTTGART				16	3	Indoor enclosure
SZEGED	5	1		3	1	
TORUN				2	1	
TROPIQUAR				5	1	
TWYCROSS	4	1		2	1	
USTI	16	1	Indoor enclosure			
VIENNA				5	2	
WALTER				22	4	
WELS				34	8	
WHIPSNADE				2	1	
WITTENBRG				7	2	
ZURICH	19	2		10	1	

Appendix B – Data

The link below is for the data set for all offspring born from golden lion tamarins and Goeldi's monkeys. The data set was used to analyse the difference in offspring survival between the two species (Appendix C.1, BothBirths.csv), the species were analysed individually for the survival models (Appendix C.1), and the data were arranged by litter for the analysis of inter-birth interval (Appendix C.2) and litter size (Appendix C.3).

https://docs.google.com/spreadsheets/d/1puqBfgVVgQvqK5L-n5v57XzqBj6nKWWDQWskMTZ3ARM/edit?usp=sharing

Appendix C. R codes for data analysis

Appendix C.1 Analysis of offspring survival

```
#======================================================================================
#  SURVIVAL ANALYSIS of POST-NATAL SURVIVAL OF GOLDEN LION TAMARINS AND GOELDI'S MONKEYS
# Author K FLACH
#======================================================================================

library(survival)
library(coxme)
library(ggplot2)
library(survminer)
library(lme4)

GLT = read.csv("GLTforsurvival2017.csv")
GM = read.csv("GMbirthscorrect2017.csv")
BOTH = read.csv("BothBirths.csv")

# CONVERT .csv data from 1 day to a Survival Object (Right censored)
surv_obj <- Surv(time = GLT$daysurvtime, event = GLT$daysurvstat)
surv_obj2 <- Surv(time = GM$daysurvtime, event = GM$daysurvstat)

# CONVERT .csv data from birth to a Survival Object (Right censored)
surv_obj0.1 <- Surv(time = GLT$survtime, event = GLT$survstat)
surv_obj2.1 <- Surv(time = GM$survtime, event = GM$survstat)
surv_obj3.1 <- Surv(time = BOTH$survtime, event = BOTH$survstat)


#SURVIVAL ANALYSIS - species comparison
res.cox0 <- coxph(surv_obj3.1 ~ species, data=BOTH)
summary(res.cox0)

# Plot baseline survival fuction for both species
BOTHsurvplot <- survfit(surv_obj3.1 ~ species, data = BOTH)
ggsurvplot(BOTHsurvplot, conf.int = TRUE, xlab= "Time (years)", ylab = "Cumulative survival", legend = "right",
legend.title = "Species", legend.labs = c("Golden lion tamarin (n = 550)", "Goeldi's monkey (n = 884)"), ylim = c(0.5,
1))


# GLT OFFSPRING SURVIVAL
# surv from birth
res.cox2.2a <- coxme(surv_obj0.1 ~ AdM + AdF_1 + AllJuv + AdM*ls + AdF_1*ls + AllJuv*ls +  damage + ls + (1|dam) +
(1|loc), data = GLT)
summary(res.cox2.2a)

# surv from 1 day
res.cox2.2b <- coxme(surv_obj ~ AdM + AdF_1 + AllJuv + AdM*ls + AdF_1*ls + AllJuv*ls + damage + ls + (1|dam) +
(1|loc), data = GLT)
summary(res.cox2.2b)

#Plot significant factors from birth

#Adult Males*litter size
#Single births
GLTsurvAdMls1.1 <- survfit(surv_obj0.1 ~ GraphAdM.ls1, data = GLT)
ggsurvplot(GLTsurvAdMls1.1, xlab = "", ylab = "Cumulative survival", palette = c("#E69F00", "#33CC00","#3399FF",
"#993399"), title = "Single births", legend = "right", legend.title = "Adult male number", legend.labs = c("0 (n =1)", "1
(n = 41)", "2 (n = 20)", "3+ (n = 10)"))
```

```
#Twins
GLTsurvAdMls2.1 <- survfit(surv_obj0.1 ~ GraphAdM.ls2, data = GLT)
ggsurvplot(GLTsurvAdMls2.1, xlab = "", ylab = "Cumulative survival", palette = c("#33CC00","#3399FF", "#993399"),
title = "Twin births", legend = "right", legend.title = "Adult male number", legend.labs = c("1 (n = 240)", "2 (n = 67)",
"3+ (n = 84)"))

#Triplets
GLTsurvAdMls3.1 <- survfit(surv_obj0.1 ~ GraphAdM.ls3, data = GLT)
ggsurvplot(GLTsurvAdMls3.1, xlab = "Time (years)", ylab = "Cumulative survival", palette = c("#33CC00","#3399FF",
"#993399"), title = "Triplet births", legend = "right", legend.title = "Adult male number", legend.labs = c("1 (n = 36)",
"2 (n = 24)", "3+ (n = 27)"))

#Adult females and litter size interaction
#Single births
GLTsurvAdF_1ls1.1 <- survfit(surv_obj0.1 ~ GraphAdF_1.ls1, data = GLT)
ggsurvplot(GLTsurvAdF_1ls1.1,xlab = "", ylab = "Cumulative survival", palette = c("#E69F00", "#33CC00","#3399FF",
"#993399"), title = "Single births", legend = "right", legend.title = "Adult female number", legend.labs = c("0 (n = 48)",
"1 (n = 12)", "2 (n = 8)", "3+ (n = 4)"))

#Twins
GLTsurvAdF_1ls2.1 <- survfit(surv_obj0.1 ~ GraphAdF_1.ls2, data = GLT)
ggsurvplot(GLTsurvAdF_1ls2.1, xlab = "", ylab = "Cumulative survival", palette = c("#E69F00", "#33CC00","#3399FF",
"#993399"), title = "Twin births", legend = "right", legend.title = "Adult female number", legend.labs = c("0 (n = 272)",
"1 (n = 73)", "2 (n = 16)", "3+ (n = 30)"))

#Triplets
GLTsurvAdF_1ls3.1 <- survfit(surv_obj0.1 ~ GraphAdF_1.ls3, data = GLT)
ggsurvplot(GLTsurvAdF_1ls3.1, xlab = "Time (years)", ylab = "Cumulative survival", palette = c("#E69F00",
"#33CC00","#3399FF", "#993399"), title = "Triplet births", legend = "right", legend.title = "Adult female number",
legend.labs = c("0 (n = 36)", "1 (n = 27)", "2 (n = 9)", "3+ (n = 15)"))

#Maternal age
GLTdamage1 <- survfit(surv_obj0.1 ~ DamageGraph2, data = GLT)
ggsurvplot(GLTdamage1, xlab = "Time (years)", ylab = "Cumulative survival", ylim = c(0.4,1), break.y.by = c(0.1),
palette = c("#E69F00", "#F0E442", "#33CC00","#3399FF", "#993399", "#FF33CC"), legend = "right", legend.title =
"Maternal Age (years)", legend.labs = c("1-2 (n = 37)", "3-4 (n = 134)", "5-6 (n = 132)", "7-8 (n = 94)", "9-10 (n = 68)",
"11+ (n = 81)"))

#GLMM for deaths between birth and 1 day
GLTGLMMbd <- glmer(survbd ~ AdM + AdF_1 + AllJuv +AdM*ls + AdF_1*ls + AllJuv*ls + damage + (1|dam) + (1|loc),
data = GLT, family = poisson(link='log'))
summary(GLTGLMMbd)

#Pot-hoc - Litter size birth to 1 day
GLTbdls <-ggplot(data = GLT, aes(ls, survbd, fill = ls)) + stat_summary(fun.y=mean, geom="bar") + labs(x = "Litter
size", y = "Survival probability")  + ylim(0, 1) + theme_classic()
GLTbdls


#GM OFFSPRING SURVIVAL
# surv from birth
res.cox4.1 <- coxme(surv_obj2.1 ~ AdM + AdF_1 + AllJuv + damage + (1|dam) + (1|loc), data = GM)
summary(res.cox4.1)

# surv from 1d
res.cox4.1a <- coxme(surv_obj2 ~ AdM + AdF_1 + AllJuv + damage + (1|dam) + (1|loc), data = GM)
summary(res.cox4.1a)

#Plot significant factors
#Other young
GMsurvAllJuv1 <- survfit(surv_obj2.1 ~ GraphAllJuv, data = GM)
ggsurvplot(GMsurvAllJuv1, xlab = "Time (years)", ylab = "Cumulative survival", ylim = c(0.5, 1), palette =
c("#E69F00", "#33CC00","#3399FF", "#993399"), legend = "right", legend.title = "Number of young", legend.labs =
c("0 (n = 361)", "1 (n = 343)", "2 (n = 163)", "3+ (n = 15)"))
```

Appendix C.2 Analysis of inter-birth interval

```
#=====================================================================================
#  ANALYSIS of IBI OF GOLDEN LION TAMARINS AND GOELDI'S MONKEYS
# Author K FLACH
#=====================================================================================

library(survival)
library(coxme)
library(ggplot2)
library(survminer)

GLTibi = read.csv("GLTallbirthevents2017.csv")
GMibi = read.csv("GMlitterscorrect2017.csv")
BOTHibi = read.csv("BothLitters.csv")

# CONVERT .csv data to a Survival Object (Right censored)
ibi_obj <- Surv(time = GLTibi$ibitime, event = GLTibi$ibistatus)
ibi_obj2 <- Surv(time = GMibi$ibitime, event = GMibi$ibistatus)
ibi_obj3 <- Surv(time = BOTHibi$ibitime, event = BOTHibi$ibistat)

#SURVIVAL ANALYSIS - comparison of inter-birth interval between species
res.coxibi0 <- coxph(ibi_obj3 ~ species, data = BOTHibi)
summary(res.coxibi0)

# Plot baseline survival fuction for both species
BOTHibiplot <- survfit(ibi_obj3 ~ species, data = BOTHibi)
ggsurvplot(BOTHibiplot, xlab = "Time to next birth (years)", ylab = "Cumulative birth probability", conf.int = TRUE, legend = "right", legend.title = "Species", legend.labs = c("Golden lion tamarin (n = 285)", "Goeldi's monkey (n = 821)"))

# IBI GLT
res.coxibi1.2a <- coxme(ibi_obj ~ AdM + AdF_1 + AllJuv + AdM*ls + AdF_1*ls + AllJuv*ls + damage + (1|loc) + (1|dam), data = GLTibi)
summary(res.coxibi1.2a)

#No significant factors

#IBI GM
res.coxibi2.1 <- coxme(ibi_obj2 ~ AdM + AdF_1 + AllJuv + damage + (1|loc) + (1|dam), data = GMibi)
summary(res.coxibi2.1)

#Plot significant factors
#Other young
GMibiAllJuv1 <- survfit(ibi_obj2 ~ GraphAllJuv, data = GMibi)
ggsurvplot(GMibiAllJuv1,  xlab = "Time to next birth (years)", ylab = " Cumulative birth probability ", palette = c("#E69F00", "#33CC00","#3399FF", "#993399"), legend = "right", legend.title = "Number of young", legend.labs = c("0 (n = 498)", "1 (n = 381)", "2 (n = 209)", "3+ (n = 17)"))

#Damage
GMibidamage <- survfit(ibi_obj2 ~ DamageGraph1, data = GMibi)
ggsurvplot(GMibidamage, xlab = "Time (years)", ylab = "Cumulative birth probability", palette = c("#E69F00", "#F0E442", "#33CC00","#3399FF", "#993399", "#FF33CC"), legend = "right", legend.title = "Maternal Age (years)", legend.labs = c("1-2 (n = 41)", "3-4 (n = 161)", "5-6 (n = 198)", "7-8 (n = 185)", "9-10 (n = 149)", "11+ (n = 146)"))
```

Appendix C.3 Analysis of litter size

```
#================================================================================================
# GLMM for LITTER SIZE OF GOLDEN LION TAMARINS
# Author K FLACH
#================================================================================================

library(Matrix)
library(lme4)
library(ggplot2)

GLTlsn = read.csv("GLTallbirthevents2017.csv")

#GLMM
#GLT NEXT LS
LSNext2 <- glmer(lsnext ~ AdM + AdF_1 + AllJuv + AdM*ls + AdF_1*ls + AllJuv*ls + damage + (1|dam) + (1|loc), data =
GLTlsn, family = poisson(link='log'))
summary(LSNext2)

#No significant factors
```