Social and Environmental Factors Influencing Reproductive Success in a Cooperatively Breeding Primate

by

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A thesis submitted in conformity with the requirements for the degree of Master of Science
Department of Ecology and Evolutionary Biology
University of Toronto

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Abstract

Cooperative breeding is a system where non-breeding individuals care for another individual’s offspring. In primates, cooperative breeding is only found in the family Callitrichidae. *Leontopithecus chrysomelas* (the golden-headed lion tamarin) is an endangered callitrichid that is facing high rates of habitat loss and fragmentation. For this study, I analyzed the influence of social, parental and environmental variables on reproductive success in *L. chrysomelas*, using data previously collected during the first long-term study on a wild population of this species. I found that infant survival was negatively associated with group size, but this was tempered by the presence of multiple adult males. The use of secondary forest was associated with high body condition, as well as high resting and reproductive rates, indicating that it can act as a good quality habitat under certain conditions. In addition, secondary forest use and the presence of multiple males were associated with faster infant growth and higher adult weights.
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1 Introduction

Life history traits are vital for understanding the evolution and behaviour of all organisms. Quantifying and understanding these traits facilitates the identification of selective forces as well as factors driving animal behaviour. In addition, life history traits can act as indicators of population health and growth, and can be used to measure the effectiveness of conservation strategies. Among life history traits, reproduction is particularly crucial. The ability to successfully reproduce is in itself an important selective trait, but it is the success of the resulting offspring that will truly determine an individual’s fitness.

Infant success, as measured in both infant survival and growth, can have important implications for population health and growth. Moreover, identifying the factors that influence infant success is vital for understanding animal behaviour, and the creation of effective conservation strategies. Infant mortality can act as a strong selective force, particularly in species with low fecundity and low effective population sizes. Infant mortality removes individuals from the population before they reproduce, and can have far reaching impacts on the fitness of the parents. Where reproduction has a high energetic cost to the parents, investment in the current offspring can reduce the parents’ capability to reproduce in the future (Zera and Harshman, 2001), an investment that is wasted if the current offspring does not survive to maturity. Early infant growth is another measurement of infant success that can act as a selective force, as variation in early growth can lead to variation in lifetime fitness (Rödel et al., 2008). Thus studying reproductive behaviour and its mediating factors is vital for understanding selection, quantifying effective population sizes and creating conservation strategies (Sutherland, 1998).

Reproduction and infant success can be influenced by a variety of factors. In many organisms, both the parents and the environment can have strong impacts on birth rates as well as survival and growth of the resulting offspring (Altmann and Alberts, 2005; Rödel et al., 2005). Environmental factors include predation (Ross, 2001) and resource availability (Altmann and Alberts, 2005). Influential parental characteristics include the condition of the parents (Rödel et al., 2008) and, when parental care is present, their previous reproductive experience (Hastings and Testa, 1998). These effects have been researched in a wide variety of taxa (Pluháček et al., 2007; Smuts and Nicolson, 1989). In species with complex social systems, another important
factor can influence reproductive success. Organisms that exhibit a high degree of alloparental care often rely on the infant care contributions of non-parent individuals (Bales et al., 2000; Lukas and Clutton-Brock, 2012b). As a result, a parent or infant’s social environment may exert equal influence to environmental or parental effects (Russell et al., 2002), and should not be overlooked as a mediator of reproductive success.

Cooperative breeding is a specialized social system found sparsely distributed across various taxa, including mammals, fish and birds (Lukas and Clutton-Brock, 2012b). The defining characteristic of this system is the provision of infant care by non-breeding members of a social group to another individual’s offspring (Bergmüller et al., 2007). As a result, social environment is thought to play an important role in the reproductive success of cooperative breeders (Russell et al., 2002), influencing birth rates (Bales et al., 2001), infant growth (Brouwer et al., 2014) and infant survival (Rood, 1990). In addition, cooperative breeders typically exhibit reproductive suppression of most or all other females in the group (Lukas and Clutton-Brock, 2012a), leading to high reproductive skew and low effective population sizes.

Cooperative breeding is found in several mammalian clades, but within primates, it is found only in the family Callitrichidae (Lukas and Clutton-Brock, 2012a). Callitrichids are arboreal New World primates comprising the marmosets, tamarins and lion tamarins (Sussman and Kinzey, 1984). The callitrichids exhibit a combination of high reproductive skew and low effective population size characteristic of cooperative breeders (Henry et al., 2013). The majority of callitrichids exhibit a social system where a single female reproduces within a group, and other sexually mature females experience low offspring survival, or do not reproduce at all (Henry et al., 2013). Reproductive suppression of subordinate females in the callitrichids can occur through hormonal (Barrett et al., 1993; Snowdon et al., 1993) or behavioural mechanisms (Henry et al., 2013).

Cooperative breeding is thought to have evolved in the callitrichids in order to accommodate the high cost of raising infants (Clutton-Brock, 2009). Callitrichids are the only primates that regularly twin, increasing the cost of reproduction. Infants have proportionally high birth weight to adult body weight (Heymann, 2000), and these heavy infants must be carried for several months (Santos et al., 1997) over large home ranges (Hankerson and Dietz, 2014). Infants also
require extended care involving food-provisioning for up to six months after carrying has ceased (Rapaport, 2011). Callitrichids have some of the highest lactation costs among primates, with maternal energetic needs increasing by approximately 100% during lactation (Key and Ross, 1999; Nievergelt and Martin, 1998). In addition, these small-bodied primates face high predation rates, particularly among infants and juveniles (Oliveira and Dietz, 2011; Zeigler et al., 2013). The high reproductive cost and infant mortality likely necessitates cooperative breeding in order to attain any consequential reproductive success.

It is well-documented in callitrichids that social environment can play an important role in reproductive success. This seems particularly true of infant survival, likely due to the high degree of alloparentral care. While it might be intuitive that infant survival would correlate with the number of available helpers, this is not always the case. The presence of helpers has been well documented to improve survival compared to parent pairs alone (Bales et al., 2000; Johnson et al., 1991), but the number of helpers may not be additive in all species. Some callitrichids show a positive association between infant survival and group size (Heymann and Soini, 1999), but others show a weak association or a non-linear relationship with the number of helpers (Bales et al., 2000; Rothe et al., 1993). In contrast to the effects of group size, callitrichids show a highly consistent relationship between helper sex and reproductive success. A positive association between infant survival and the number of available male helpers has been documented in multiple species (Bales et al., 2000; Garber et al., 1984; Koenig, 1995), likely due to the family-wide tendency for males to exhibit higher rates of helping behaviour. Males tend to carry more (Cleveland and Snowdon, 1984) and provision food at higher rates (Burkart et al., 2007). Social factors can also influence birth rates, and group size has been documented to have a positive impact on birth rates in wild *Leontopithecus rosalia* (Bales et al., 2001; Henry et al., 2013). This may be due to food-provisioning of breeding individuals by helpers (Ferrari, 1987; Hoage, 1982), or the ability of parents to reduce investment in the current infant in the presence of helpers (Cleveland and Snowdon, 1984; Santos et al., 1997).

Parental characteristics are also a common focus of research into reproductive success, particularly in species with extended parental care and/or high reproductive costs. Maternal effects are common, particularly in environments with low resource availability and in species where reproductive costs are high (Tardif et al., 2001). Callitrichid females increase their energy
intake up to 100% during lactation (Nievergelt and Martin, 1998) and so maternal condition would be expected to be influential on infant success. Unsurprisingly, better quality milk (Tardif et al., 2001) and higher investment in infant care (Bales et al., 2002) have both been associated with maternal body size in the callitrichids. In *L. rosalia*, female body mass is also a predictor of the number of live births per reproductive season (Bales et al., 2001). Among the callitrichids, males generally provide the highest degree of infant carrying (Hoage, 1982; Schradin and Anzenberger, 2004), a costly activity that limits mobility (Schradin and Anzenberger, 2001) and foraging ability (Tardif, 1994). Captive callitrichid males experience significant weight loss due to infant care (Achenbach and Snowdon, 2002; Sanchez et al., 1999), suggesting that male care could vary with body condition. As a result, infant survival may be closely linked to both maternal and male condition.

In species with social learning and extended parental care, previous parental experience may be also be influential for infant success. Within the callitrichids, primaparous mothers show higher infant rejection rates (Johnson et al., 1991) and lower infant survival (Rapaport et al., 2013). In addition, the within-group reproductive status of *Leontopithecus* mothers can have a large impact on infant survival, as subordinate females likely experience reproductive suppression through group behavioural cues, including infanticide (Henry et al., 2013). Reproductive experience is less studied as a factor in paternal behaviour, but the hormone prolactin has been repeatedly linked to paternal care behaviour (Schradin and Anzenberger, 1999), and an increase in callitrichid male prolactin levels has been linked with paternal experience (Schradin and Anzenberger, 2004) and even correlated with the number of previous experienced births (Ziegler et al., 1996). Experienced marmoset fathers show greater attentiveness to infants (Zahed et al., 2008), adding further evidence to the idea that paternal experience could function in a similar manner to maternal experience. As most callitrichids participate in sibling care before dispersing from their natal group or reproducing themselves, it is likely that this experience also influences future infant care ability. Individuals with sibling experience have shown higher infant survival (Hoage, 1982; Kirkwood et al., 1985; Tardif et al., 1984) and lower infant rejection rates (Johnson et al., 1991). It seems likely that sibling-rearing experience improves reproductive success in addition to direct reproductive experience in callitrichids.
Habitat use can have a direct impact on many life history parameters, including infant survival, growth and birth rates. It is especially important to understand habitat use in species facing habitat loss or degradation. Predation rates can impact infants disproportionately compared to other age classes (Ross, 2001), particularly in species with altricial infants. Callitrichids carry their infants for the first several months (Hoage, 1982), and this behaviour likely evolved in response to high rates of predation (Ross, 2001). As small-bodied primates, callitrichids have a high number of natural predators (Franklin et al., 2007), and this predation rate may also be influenced by anthropogenic disturbance. It’s likely that varying predation risks between habitat types will differentially impact reproductive success. Similarly, resource availability can differ by habitat, and can be even more influential on reproductive success than predation. Lactation is extremely costly in callitrichids (Key and Ross, 1999; Nievergelt and Martin, 1998), indicating that low resource availability could severely restrict their ability to raise offspring. The presence of helpers could offset this danger. A captive study on L. chrysomelas found that helpers provision food to mothers and infants at higher rates when food is difficult to obtain (Moura et al., 2010). However, helping effort in other cooperative breeders is condition-dependent (Russell et al., 2003) and this seems more likely to be the case in wild callitrichids, where helpers could face starvation if they are unable to obtain enough resources for themselves. This may be especially true when it comes to infant carrying, which is well known to be energetically costly (Achenbach and Snowdon, 2002; Schradin and Anzenberger, 2001). Resource availability can also limit the initial reproductive efforts of the parents and thus affect birth rates (Noma et al., 1998).

For my thesis, I examined the role of social, parental and environmental factors on reproductive success in a wild population of Leontopithecus chrysomelas, the golden-headed lion tamarin. The lion tamarins (genus Leontopithecus) are endemic to the Atlantic Forest of Brazil (Perez-Sweeney et al., 2008). The four species are found in distinct geographic locations, and are all of conservation concern due to extreme habitat loss and fragmentation. An ongoing field study in Poço das Antas, Brazil, has provided a great deal of insight into the social behaviour of Leontopithecus rosalia, the golden lion tamarin (Baker et al., 1993). L. chrysomelas is the second most studied species in the genus, however unlike L. rosalia, little is known about their reproductive patterns. For my research, I analyzed data collected during a long-term field study on L. chrysomelas conducted by B.E. Raboy and J.M. Dietz between 1991 and 2007. I used
survival analysis to determine the influence of habitat use in early life, parental condition and experience, and group composition (including size and sex ratio) on infant survival rates. For a broader view of reproductive success in this species, I also used growth functions to identify environmental and social factors influencing infant growth rates, and compared reproductive rates between habitat types.

*Leontopithecus chrysomelas* are frugi-faunivores (Raboy and Dietz, 2004) and face predation from raptors, snakes, and carnivores such as cats and tayras (Oliveira and Dietz, 2011, B.E. Raboy, unpublished data). The species is considered Endangered with a decreasing population (Kierulff, 2008), and is currently found in highly heterogeneous and fragmented habitat patches due to expansive anthropogenic degradation (Raboy et al., 2010). Recent work on *L. chrysomelas* has shown that shade cocoa, a highly modified habitat, can have both positive effects, on body condition and birth rates (Oliveira et al., 2011), and negative effects in the form of higher predation rates (Oliveira and Dietz, 2011). As a species with large home ranges (Raboy et al., 2004), *L. chrysomelas* likely uses a variety of habitats, and represents an interesting study system for comparing reproductive success in mature and degraded habitat. As one of the few cooperatively breeding primates, they also offer an opportunity to understand how environmental and social factors may influence reproductive success in a complex social system.

2 Methods

2.1 Data collection

Data were collected during a field study headed by J.M. Dietz and B.E. Raboy from 1991-2007, in and bordering the Una Biological Reserve in Southern Bahia, Brazil. The study region is characterized as lowland moist tropical forest, and includes mature, regenerating, and shade cocoa forest (Raboy et al., 2004). *L. chrysomelas* in the study population were habituated to individual observers following the methods of Dietz et al. (1996). Bi-annual captures were used to take individual measurements, record age and sex class, and administer numeric tattoos and dye marks on tails to facilitate individual identification in the field. One or two monkeys per
group were also fitted with radiotelemetry collars to allow observers to track the group. Infants born into the groups were first captured at an average of 147 days old (approximately five months), after which individual identification of twins was possible. Once habituated, each group was followed for 2-10 days a month, depending on the research schedule. Observation days were either full days (emergence from sleeping site in the morning to entrance into sleeping site in the evening) or partial days. On partial days the lion tamarins were tracked from emergence from their sleeping site until 1300 hr, or from 1100 hr until they entered their evening sleeping site. Data were collected year round by a team of observers that were trained together for several months. The eight groups analyzed herein were followed for 2-12 years. Groups were monitored from the time they were habituated until October 2007, with the exception of the group PRIN which was followed from 1992-1994.

Every time a group was observed, membership was noted at the outset. Observers conducted behavioural scans of all individuals at 20-minute intervals. Behaviours recorded included travelling, remaining stationary, resting, eating animal prey, fruit or flowers, foraging for animal prey, fruit or flowers, social and other less frequent behaviours. Throughout observation days, observers also made ad-libitum field notes on behaviour, which included instances of aggression, scent-marking and infant care behaviour outside of the scans. Observers noted each time a group visited fruit trees, including the location and type of the tree when known, and the duration of the visits. Geographic location of the group was also recorded at 20-minute intervals, including X-Y coordinates and habitat type.

2.2 General demographic methods

I used observer field notes to determine group membership for the duration of the study. I considered an individual to be a group member if they were recorded with the group on three consecutive observation-days. If an individual was not sighted with the group for three consecutive observation-days and the exact date of emigration, death or disappearance was not known, I estimated the date as the mid-point between the last day they were seen with the group and the first day the group was seen without them. If the individual was found dead, or an individual was sighted with another group before their original group was sighted without them, that date was used instead to calculate the mid-point.
I assigned a birth date to all individuals born into the study, calculated as the mid-point between the last day the group was seen without infants and the first day the group was seen with infants. Infants whose birth-date could not be determined within a 28-day period were excluded from all analyses involving survival or growth, but included in analyses involving counts of births. Of the infants included in survival analyses (n=117), ninety percent of the infants had birth dates known within a two week period.

I then assigned a sex and age class to each individual based on capture measurements. Individuals who were never captured were not included in analyses requiring sex or age, with the exception of individual “TOK” in group KIT, who was never captured but was known to be an adult female as she gave birth several times during the study. I created an aging protocol (Appendix A) based on captures of individuals of known age, using weight, length, scent gland development and tooth eruption to assign an individual of unknown birth date to one of four age classes: infant 0-90 days (weaning), juvenile 91-270 days (age of first possible immigration), subadult 271-540 days (sexual maturity) and adult 541 days and over. The aging protocol was used for individuals who immigrated into the study population or who were born before the study began. Some individuals could only be aged within two classes.

For survival analyses, infant lifespan was defined as the number of days between birth-date and last-known-date. I determined the last-known-date using four methods, corresponding to the fate of the infant: alive when study ended, disappearance, confirmed death or assumed death. For individuals still alive when the study ended, I considered the last-known-date to be the last date the individual was directly observed. Individuals were considered “disappearances” if they disappeared from the group past nine months of age, as it was unknown if they died or immigrated outside the study population. For these individuals, I considered the last-known-date to be the last date the individual was seen in the study. Individuals alive when the study ended and those that disappeared were considered to be “censored” data for survival analyses, as their ultimate fate was unknown. Individuals were considered “confirmed deaths” if their body was found. For these individuals, I calculated the last-known-date as the mid-point between the last day the individual was seen alive and the day the body was found. All deaths were known within a 16-day period. Individuals were considered assumed deaths if they disappeared from their group under nine months of age, as nine months is considered the first possible age of dispersal.
from the natal group (B.E. Raboy, pers comm.). For assumed deaths, I calculated the last-known-date as the mid-point between the last day the individual was seen with the group and the first day the group was seen without the individual, and these dates were all known within a 28-day period.

2.3 Infant success: Social group characteristics

I determined group composition during each infant’s first three months of life. During this period, the infant is completely dependent on milk from its mother and carrying from group members (Santos et al., 1997). I calculated group composition characteristics as the average values between composition at birth and composition at three months of age. I did not include the focal infant (and their twin, if present) in any counts of group characteristics. I characterized each infant by: group size, the number of adult helpers, the presence of single or multiple adult males, the ratio of adult males and females, the presence of single or multiple reproductive females, and the presence of other dependent individuals. I considered group size to be the number of individuals in the group, excluding the infant and its twin if present. For adult male presence, I classed infants as “multiple-male presence” if two or more adult males were present in the group for more than three consecutive observation days during the first three months of life, and “single-male presence” if only one adult male was present the entire first three months. No infants were raised in groups without adult males. I considered infants to have multiple reproductive females present if another female gave birth in the group within the first three months of life, or if infants (<90 days of age) were present at the time of birth. I measured the number of helpers and the adult sex ratios using the average number of adults between birth and three months (individuals over 540 days). I divided the adult sex ratios into three categories: males outnumbering females, equal sex ratio and females outnumbering males. I considered infants to have other dependents present if any individuals under 270 days of age (juvenile or infant) were present at the time of birth, or if another infant was born during the first three months and survived more than three consecutive observation days. Infants were not included in certain analyses if group membership could not be confirmed for the time period, or if group members could not be aged or sexed appropriately.

I used Kaplan-Meier survival estimates for initial comparisons between categorical group characteristics. Log-rank tests were used to compare the survival curves between categories, and
variables with significant differences were included in a Cox proportional hazards model, as described below under 2.6 Multivariate Survival Analysis. For the reproductive female analysis, sample size was much higher for infants with a single reproductive female than infants with multiple reproductive females, and so I performed a Fisher’s exact test on observed and expected survival to nine months of age. I divided continuous variables into two categories, above the average value or below the average value, and used Kaplan-Meier survival curves to compare them as well. Continuous variables were included in a Cox proportional hazards model if they showed a visible trend for differences in survival between the two categories, regardless if the log-rank test demonstrated significance, due to the loss of information when categorizing continuous variables.

I also classified infants by adult male presence in order to compare infant growth rates. Forty-eight infants lacked capture measurements, and thus these infants could not be included in growth rate analysis. Infants were first captured between 21 and 436 days old (mean=147 days). Weight was used as a measurement of growth. Individual identity was included as a random effect to account for repeated captures of the same individuals. 213 captures on 69 individuals were used for the analysis. The effect of male presence on both growth rate and asymptotic (adult) weight was tested using Von Bertalanffy growth functions. Three growth functions were calculated, one with no effect included, one with male presence included as an effect on growth rate, and one with male presence included as an effect on both growth rate and asymptotic weight. The three nested models were compared using a likelihood ratio test to determine if male presence significantly improved the function’s fit to the data.

2.4 Infant success: parental characteristics

I determined maternity for all infants through behavioural observations and capture measurements. For the majority of infants, I used observations of nursing to establish maternity. I considered ongoing nursing to be a reliable indicator of maternity. In 17 years of behavioural observations, allo-nursing was recorded only once, involving a young female who had recently lost her infant and was observed nursing her younger sister a single time. Where nursing observations were not available, I determined maternity through the detection of pregnancy or lactation from captures near the birth, and by carrying behaviour (as callitrichid mothers carry more than their female helpers (Cleveland and Snowdon, 1984)). In rare cases for infants born
early in the study, I assigned maternity by eliminating all other possible mothers (through age, lack of lactation or lack of previous reproductive status). This method was necessary when nursing and carrying were not consistently recorded, such as the beginning of the study when demographics were not known as intimately as later years.

Paternity was impossible to verify without genetics. Instead, I assigned a “primary male caregiver” to 79 infants based on behaviour. I designated the primary male caregiver as the male who exhibited the highest amount of carrying within the first two weeks of life, determined by the number of behaviour scans that noted infant carrying. For 10 infants, scans were either unavailable for the first two weeks, or no male was listed as carrying in the scans. Instead, I counted the number of times each individual was observed to pick up or carry the infant in the observer’s ad-libitum field notes. This method was less accurate than using behaviour scans, as groups often contained one adult male with a radio collar, who was thus easier to track and observe. For the remaining 28 infants, no primary male caregiver could be designated due to lack of carrying observations or lack of male carrying, likely due to low social status of the mother.

2.4.1 Parental condition

For each infant, I recorded the condition of the mother and primary male caregiver. Maternal condition was determined using measurements from the captures occurring closest to the birth, provided they were within a year of the birth and the female was not pregnant at the time. Adjusted body weight was calculated by dividing an individual’s weight in grams by the knee-heel length in millimetres, in order to account for individual differences in height. Maternal condition was then determined as the average of the two adjusted body weights per individual (pre and post birth; n=47 infants), or from a single capture when no second capture was available (n=53 infants). Seventeen infants could not be included due to lack of non-pregnant captures within the specified time frame. For a preliminary analysis, I separated infants into mothers with “high” condition (above the average) and “low” condition (below the average) in order to plot Kaplan-Meier curves. I recorded primary male caregiver condition in the same manner, using measurements from captures that occurred within a year of the birth and calculating condition as weight in grams divided by the knee-heel length in millimetres. Condition was calculated as an average between two captures for 52 infants, and from a single capture for 26 infants. For 39 infants, primary male caregiver could not be determined, or no eligible captures existed. To plot
Kaplan-Meier curves, I assigned the infant’s primary male caregivers with “high” or “low” condition in the same manner as maternal condition.

2.4.2 Parental experience

I determined maternal experience in three different ways. First, I assigned a within-group reproductive status to the mother. Within-group reproductive status was assigned if the female had been previously observed giving birth within her current social group. Females were considered to have within-group non-reproductive status if they had never been observed giving birth within their current social group, or if all previous reproductive attempts had ended in observed infanticide by group members. If a female was within the group when observations began, her first observed infants were not included in this analysis as her within-group reproductive status could not be determined. Second, I counted the number of previous parturition events for each mother. For females with unknown history but a nipple length \( \geq 3.0 \) mm before their first observed birth, I counted the number of previous observed parturition events and added one. For females with unknown history but a nipple length over 5.0 mm before their first observed birth, I counted the number of previous observed parturition events and added two. I used captures of females of known parity to determine these cut-offs. Among females of known parity with non-pregnant, non-lactating nipple lengths \( \geq 3.0 \) mm, 97% had given birth previously. Among females of known parity with non-pregnant, non-lactating nipple lengths over 5.0 mm, 89% had given birth at least twice previously. Third, I counted the number of sibling litters each female was exposed to prior to giving birth for the first time. Sibling litters were only counted if at least one infant survived more than three consecutive observation-days, and were not counted if they occurred during the female’s first pregnancy. I could only determine sibling experience for the mothers of 43 infants out of 117 (37%). This is because the early histories of many reproductive females were unknown. All females of known history had sibling experience.

For primary male caregivers, I determined parental experience in three ways. First, I determined if the male had previously acted as primary male caregiver for any litters. Second, I counted the number of previous infants where the male had acted as primary male caregiver. These values could only be determined for 62 infants out of 117 (53%). Third, I counted the number of sibling litters males had experienced before they first acted as primary male caregiver. Sibling
experience could only be determined for the primary male caregivers of 26 infants out of 117 (22%). As with mothers, all primary male caregivers of known history had sibling experience.

I used Kaplan-Meier curves and log-rank tests for preliminary analysis of parental characteristics. Categorical variables were included in a Cox proportional hazards model if a log-rank test found a significant difference between categories. Continuous variables were categorized as above or below the average value, and were included in a Cox proportional hazards model if a log-rank test found a significant difference between the categories, or if there was a visual trend for differences in survival. The methods for the Cox proportional hazards model are described below in 2.6 Multivariate Survival Analyses.

2.5 Habitat use

Habitat types were defined as outlined in Raboy, Christman et al (2004):

1. **Mature Forest**: canopy 25-35 metres in height, relatively open understory, abundance of vines and epiphytes

2. **Secondary Forest**: canopy 5-15 metres in height, trees of small diameter, dense understory, includes small areas of newly regenerating fields

3. **Shade Cocoa Forest**: canopy similar in height to mature forest, presence of epiphytes, distinguished by the presence of cacao and banana trees, sparser understory and mid-canopy, absence of vines

4. **Swamp Forest**: muddy ground or standing water, dense understory

I used indirect measurements to determine predation risk and resource availability for each habitat. For predation risk, I analyzed observations of predation events recorded during the study. I determined three predation risk measurements for each habitat type: predation attempts, predator species observations and total predation events. First, predation attempts were defined as the number of events where a predator was observed to attempt predation on one of the study individuals. Second, the predator species observations were defined as the number of observations of potential predators, including predation attempts. I excluded all observations where the lion tamarins reacted with alarm calls but the animal eliciting the reaction was
identified as a non-predator, or where the animal could not be identified at all. I also excluded all observations where the lion tamarins made alarm calls in response to humans, with the exception of one event where the human was a hunter. Third, for total predation events, I included all events where a predator was observed or the lion tamarins reacted with alarm calls, even if the predator was unknown. The only events I excluded from total predation events were events where the predator was positively identified as a non-predatory animal. I compared predation risk measurements across the main habitat types against expected scores, using a chi-square goodness-of-fit test. Expected scores were calculated based on proportion of overall geographic points recorded in each habitat type.

Sample sizes for predation events were very small, so as another proxy for predation risk, I calculated resting scores for each main habitat type. Behaviours were scored as resting when the individual was reclining (ventrally or dorsally) on a substrate, a vulnerable position unlikely to be observed when predation was an immediate risk. To calculate resting scores, I divided the total number of scans where the behaviour was recorded as resting by the total number of scans per individual within each habitat, then averaged across individuals in that habitat. Individuals were only included in this analysis if they had at least 300 scans recorded in the focal habitat type. To analyze these results I conducted a one-way ANOVA on resting scores between all the main habitat types. I then ran a post-hoc Tukey HSD test to calculate pairwise comparisons between habitat types. As vigilance behaviour commonly decreases in large groups (Roberts, 1996), I also compared resting scores with group size to identify if group size could be a confounding factor. I calculated the yearly resting score for each group by averaging across all individuals in the group with at least 300 scans recorded within the year, regardless of habitat. I calculated yearly group size and number of adult males for each group by averaging between the group composition on the group’s first and last observation day of the year. I plotted average yearly resting score against average group size and average number of adult males. I conducted Pearson’s product-moment correlation tests to calculate the correlation coefficient and p-value for group size and adult males versus resting scores.

I also determined resource availability for each habitat type. Trophic resource abundance data were not available for the study site, so I tested three indirect measurements using lion tamarin behaviour and condition. First, I calculated foraging efficiency scores using behaviour scans of
any individual with at least 50 total scans in the focal habitat type. Foraging efficiency scores were calculated by dividing the number of animal prey eating scans by the number of animal prey foraging scans. I conducted a one-way ANOVA on the foraging efficiency scores for each habitat type. Second, I measured fruit tree visitation as a proxy for fruit abundance. I divided the number of fruit tree visits in each habitat by the number of geographic points recorded in each habitat per group. I calculated fruit tree visitation for each habitat by group and by year, as fruit abundance may vary between years. I conducted a one-way ANOVA between habitat types using fruit tree visitation for each group-year pair. This analysis was done on a subset of the data for groups ENT, PIA, ONÇ, PIT and TAP. Third, I calculated body condition for all individuals over 1000 days and compared condition to habitat use. For each individual, I averaged condition (weight/knee-heel length) across all captures over the age of 1000 days. The age cut-off was chosen because growth in weight plateaus around 1000 days, ensuring that I was not measuring developmental growth instead of condition. Each individual was assigned a most-used habitat based on the percentage of time their group spent in each habitat, averaged across the included years. I ran a one-way ANOVA on body condition across the main habitat types, and then ran a post-hoc Tukey HSD test for pairwise comparisons between habitat types. I plotted body condition against average percentage of time spent in both secondary and mature habitat types, and ran Spearman’s rank correlation tests on each comparison. I also classed individuals as “high” or “low” body condition relative to the average, and used student’s t-tests to compare mean time spent in secondary or mature forest between high and low condition individuals.

2.5.1 Habitat use and reproductive rates

I analyzed the relationship between reproductive rates and habitat use by female rather than by group, due to the inconsistency of group membership over long periods of time. Females were only included if they were observed for three reproductive seasons starting with their first reproductive attempt. In addition, they were excluded if they did not reproduce two seasons in a row. Reproductive rates were calculated as the number of infants born divided by the number of years the female was observed to be reproductive. The number of years was calculated from the first date the female joined the study, provided she reproduced in the reproductive season immediately following the start of inclusion in the study. For females born into a group, the number of years was calculated from January 1st of the year including her first reproductive
attempt. For one female (individual 36 in PIA), geographic points were not available until July 1998, and so the number of years was calculated from that point and her litter of twins from October 1997 was not included. I used geographic points recorded for each group to calculate habitat use per female. I measured the proportion of time spent in each habitat by calculating the percentage of geographic points recorded per habitat type for each female’s group while she was a member. Two females who met the reproductive requirements, individual 39 in PIA and individual 42 in ONÇ, could not be included due to a lack of geographic points in the early data. Reproductive rates were compared to secondary and mature forest use because they were the most commonly used habitats, as well as presenting a comparison between relatively pristine and degraded habitat. Pearson’s product-moment correlation tests were used to compare reproductive rates with secondary and mature forest use. I also used a Pearson’s product-moment correlation test to determine the association between secondary and mature habitat use per female.

2.5.2 Habitat use and infant survival

I calculated the habitat use during early life for each infant as the percentage of group geographic points recorded in each habitat for the first three months of life. Infants were only included if a minimum of 70 scans were recorded for their group within the first three months of life (n=75). I then classified each infant based on the most-used habitat in the first three months of life. I did a preliminary analysis on the effects of these habitats using Kaplan-Meier survival curves for infants whose most-used habitat was primary versus all others, and infants whose most-used habitat was secondary versus all others.

The method of assigning habitat use based on scans in early life excluded infants who died before scans could be collected. In order to include a larger proportion of infants, I conducted an extended Fisher’s exact test on infant survival to nine months, based on the most-used habitat of their natal group in the year containing their birth. This analysis allowed the inclusion of 104 infants.

2.5.3 Habitat use and infant growth

I analyzed the effect of the most-used habitat type for the population, secondary forest, on infant growth using nested Von Bertalanffy growth functions. Infants were included if they survived long enough to be captured and I was able to determine their most-used habitat in early life. 167
captures from 54 infants were used to construct the growth functions. Weight was used as a measurement of growth. Infants were classed as using secondary habitat or any other habitat the most in early life. Individual identity was included as a random effect to account for repeated captures of the same individuals. The effect of secondary habitat use on both growth rate and asymptotic (adult) weight was tested using Von Bertalanffy growth functions. Three growth functions were calculated: one with no effect included, one with secondary habitat use included as an effect on growth rate, and one with secondary habitat use included as an effect on both growth rate and asymptotic weight. The three nested models were compared using a likelihood ratio test to determine if accounting for secondary habitat use significantly improved the function’s fit to the data. I also calculated three growth functions in the same manner to determine if accounting for mature habitat use significantly improved the function’s fit to the data.

2.6 Multivariate survival analyses

Survival statistics are generally used in medical research to measure predicted survival outcomes for diseases or drug trials. They allow for the use of “censored” data, where an individual’s ultimate fate is unknown but their time in the study is still able to be included in the research. I chose to use survival analysis so that I could include the large number of *L. chrysomelas* infants who disappeared past nine months of age and whose ultimate fate was unknown.

Preliminary analyses of social, parental and environmental factors were conducted using Kaplan-Meier survival curves and log-rank tests, as described in sections 2.3, 2.4 and 2.5.2. Categorical variables with significant log-rank test results (p<0.05), as well as continuous variables that showed a visible trend for variation in survival, were used to build two Cox proportional hazards models.

To determine the combined effects of social factors on survival, I constructed a proportional hazards model using social variables that met the conditions for inclusion in preliminary analyses. To determine the combined effects of parental factors on survival, I constructed a proportional hazards model using the parental variables that met the assigned conditions. I did not combine the two models, due to a reduced sample size for parental characteristics.
For each model, I used both the method of forward selection and the method of best subsets. I compared the resulting models from each method using AIC values or, if the models were nested, a likelihood ratio test, and chose one model that demonstrated the best fit to the data for social or parental variables.

All statistical analyses were run in R 3.1.2. The packages “survival” and “glmulti” were used for survival analyses, and the package “nlme” was used for growth analyses.

3 Results
3.1 General reproduction in wild L. chrysomelas

3.1.1 Infant demographics and survival

Between 1992 and 2007, there were 79 confirmed births in the eight study groups, producing 132 infants. Table 1 describes the distribution of births among the groups, as well as the time period during which each group was included in the study. Across the study population, 70% of infants (n=92) survived to weaning and 56% (n=69) survived to the age of first possible dispersal. There were 53 births recorded as twins and 26 births recorded as “singleton”, where only one infant was observed. However, “singleton” does not necessarily mean the female only bore one offspring, as the death of a twin following birth may not have been observed. Infant sex could only be determined for infants that survived long enough to capture (n=82), but the sex ratio was evenly divided with 41 males and 41 females. Infant survival showed no difference between sexes, as measured by percentage surviving to nine months ($\chi^2=0.37$, df=1, p=0.54) or overall survival (log-rank $\chi^2=0.7$, df=1, p=0.42; Figure 1). It should be noted that due to the inability to sex infants who died before being captured, a skew in survival between the sexes could occur at a very early age and be missed with these data. Infant survival also showed no difference between singleton and twin litters as measured by percentage surviving to nine months ($\chi^2=0.57$, df=1, p=0.45). Survival curves showed a trend for lower survival among singletons (Figure 2), but a log-rank test did not find the difference to be significant ($\chi^2=3.4$, df=1, p=0.07). Litter size
was not included in further analyses due to both the lack of a significant finding and the uncertainty of that classification.

3.1.2 Reproductive skew

During the study, 32 sexually mature females were observed for at least one reproductive season. Of these females, approximately one third (n=10) were not observed to reproduce. Among the females who did reproduce (n=22), 15 successfully reared an infant to weaning age and 4 lost offspring in infancy. One female (individual 112) lost an initial offspring in infancy, but the status of her second infant could not be confirmed as she reproduced a week before the study ended. Two other females (individuals 10 and 27) were known to have reproduced, but the status of their infants at weaning age could not be confirmed. Among the females who reproduced (n=22), 16 females were observed to reproduce more than once, and 6 females were only observed reproducing once. On 10 occasions, two females were observed concurrently reproducing in the same group. The two reproductive females were almost always mother-daughter pairs, with one possible exception in group PIA where the young female’s mother could not be determined. On each of these occasions, only one female’s infants were observed surviving to the first age of possible dispersal. In the majority of cases, one litter died before reaching weaning age. Only two mother-daughter pairs successfully reared both their offspring to the age of weaning (90 days). In group PIT, the mother and daughter both raised twins to the age of weaning, but the daughter’s twins later died at 5 months of age. In group P2, the older female was at least 12 years old when she gave birth, and her single offspring died between weaning and 9 months of age. In almost every case, the surviving infants were the offspring of the older female. The exceptions were the birth in P2 to a female of substantial age, and a twin litter in group PIT, where the daughter killed the mother’s infants (see 3.1.3 Infanticide). No more than two females were ever observed to reproduce within the same group and reproductive season, although on 7 occasions, more than two sexually mature females were present in the same group during a reproductive season.

3.1.3 Infanticide

Infanticide by group members was observed directly on four occasions during the study. The social context of the four events differed in maternal reproductive history, composition of the
group, and the chronological proximity to another female’s reproductive attempt within the group (Table 2). The demographics of the participants also differed between events. For two events, an adult male in the group initiated the infanticide and was joined by other males. Both of these events occurred in group PIA and involved infants born to the same mother (individual 36). On a third occasion, an adult female (aunt to the infants) initiated the infanticide and an adult male joined the interaction. On the fourth occasion, an adult female with infant offspring killed her mother’s newborn offspring without participation by the rest of the group. For three of the four events, another female in the group was either pregnant or nursing newborn infants. The fourth event occurred in PIA, and another sexually mature female in the group may have been pregnant, but no infant was ever observed. One possible consistency between events was the size of the group and adult sex ratio. For three of the four events, the group size was 6, there were 3 sexually mature females present, and adult females outnumbered adult males. For the fourth event, a third sexually mature female disappeared two weeks before the birth, reducing the group to 5 individuals and changing the adult sex ratio from equal to male biased.

3.2 Infant success: social group characteristics

3.2.1 Helper presence

The majority of infants (98%, n=129) were born into groups with at least one non-breeding helper. On two occasions, births were observed to occur in groups with no helpers present, producing one set of twins and one singleton. Both occurrences were observed in group ONÇ, although the mother and primary male caregiver were different for each birth. Both occurrences also took place after individuals split off from ONÇ to form new groups (PIT and TAP). Infant 69 was born four months after three individuals split off to form PIT. Twins 116 and 117 were born eight months after four individuals split off to form TAP. Following the birth of infant 69, another adult male joined the group within three months. As a result, 116 and 117 were the only infants raised without helpers present throughout infancy. Only 3 out of 132 infants were born without helpers present (2.3% of infants and 2.5% of parturition events), and all 3 survived past the age of first possible dispersal.
3.2.2 Social factors and infant survival

The effects of social variables on infant survival were initially assessed by Kaplan-Meier survival curves and log-rank tests before inclusion as potential variables in model building. Infant survival showed a trend for higher survival in smaller than average groups (Figure 3a). A log-rank test did not show this to be significant ($\chi^2=2.9$, df=1, $p=0.09$). However, as group size was a continuous variable and showed a trend when categorized, it was included in model building despite the lack of a significant log-rank result. Infant survival showed no difference in survival between high and low numbers of helpers ($\chi^2=0$, df=1, $p=0.98$; Figure 3b). Infants showed significantly lower survival when other dependents were present in the group ($\chi^2=5.2$, df=1, $p=0.02$; Figure 4). Survival was significantly higher in the presence of multiple adult males than in the presence of a single adult male ($\chi^2=11$, df=1, $p=0.0009$; Figure 5a). There was no significant difference in survival with multiple or single reproductive females present ($\chi^2=2.7$, df=1, $p=0.10$; Figure 5b). Sample size was highly uneven for this variable due to a low number of infants with multiple reproductive females present (24 out of 117). Survival to nine months was also tested with a Fisher’s exact test ($p=0.35$), providing no evidence that survival outcome to nine months was dependent on presence of multiple or single reproductive females. Survival curves showed a trend for lower survival with female-biased adult sex ratios (Figure 5c), however a log-rank test found no significant difference between the three sex ratio categories ($\chi^2=4.4$, df=2, $p=0.12$).

Based on preliminary analyses, group size, male presence, and the presence of other dependents were chosen as initial variables for a multivariate Cox proportional hazards model. The proportional hazards assumption was assessed for all variables using a Pearson’s product-moment correlation between the Schoenfeld residuals and log(time). There was no evidence of any variable violating the proportional hazards assumption (all $p$-values > 0.05). The linearity assumption was assessed for group size using the Martingale residuals. The LOESS line for the Martingale residuals showed no clear directional trend (Figure 6), indicating that the linearity assumption was not violated. The model was built using the forward selection model. Male presence and group size were both found to significantly improve the model’s fit, while presence of dependents showed no significance and was thus removed from the model. An interaction between group size and male presence was also found to be significant. An alternate model was
generated with the same variables using the method of best subsets. The best model using the method of best subsets included group size, male presence, dependent presence, and an interaction between male presence and group size. The forward selection model was nested within the best subsets model, so a likelihood ratio test was used to compare their fit. The model including dependent presence showed no significant improvement over the forward selection model ($\chi^2=1.99$, df=1, p=0.16). Consequently, the final social model included male presence, group size and an interaction between the two terms. Table 3 shows the hazard ratios for the final model, in which only the interaction shows a significant p-value (p=0.007). For each unit increase of group size, the relative risk of death for infants with a single male present increases by 1.95 relative to the risk for infants with multiple males present.

3.2.3 Male presence and infant growth

Likelihood ratio tests of nested Von Bertalanffy growth functions showed a significant effect of multiple adult males on both growth rate and adult weight (Table 4). Infants in the presence of multiple adult males showed faster growth rates and higher adult weights than infants in the presence of a single adult male (Figure 7).

3.3 Infant survival: parental characteristics

The effects of parental characteristics on infant survival were initially assessed using Kaplan-Meier survival curves and log-rank tests. Infant survival did not differ significantly between infants with primary male caregivers of high or low body condition relative to the average ($\chi^2=2.7$, df=1, p=0.10; Figure 8a). A log-rank test also found no significant difference between infants with mothers of high or low body condition relative to the average ($\chi^2=1.8$, df=1, p=0.18; Figure 8b), or between infants with mothers of high or low parity relative to the average ($\chi^2=0.8$, df=1, p=0.37; Figure 9a). Survival did differ significantly between infants based on their mother’s previous reproductive status in the group ($\chi^2=4.7$, df=1, p=0.03; Figure 9b).

All quantitative variables showed non-significant trends when compared categorically, and were therefore included along with maternal reproductive status as initial variables in a Cox proportional hazards model, with the exception of maternal condition. The maternal and male condition variables were each missing data for a large number of infants, potentially interfering with the model results and reducing the power of the analysis. Male condition showed a stronger
trend in the Kaplan-Meier survival curves, and so maternal condition was left out of the model and the dataset was reduced to include only infants who had data on male condition available. This reduction excluded 32% of the full dataset. Values and ranges for social factors and other parental characteristics were compared between the full dataset and reduced dataset, and showed no prominent differences (Table 5). The proportional hazards assumption was assessed for all included variables using a Pearson’s product-moment correlation between the Schoenfeld residuals and log(time). There was no evidence of any variable violating the proportional hazards assumption (all p-values > 0.05). The linearity assumption was assessed for male condition score and maternal parity using the Martingale residuals. The LOESS line for the Martingale residuals showed no clear, consistent directional trend in either case (Figure 10), indicating that the linearity assumption was not violated. The forward selection method was initially used to build the parental model, but demonstrated no significant effects from male condition, maternal parity or maternal reproductive status. All potential models generated with the forward selection method had likelihood ratio test results well over p=0.05, representing no improvement in fit over the null. The method of best subsets produced the 10 best models with the provided variables, and similarly found no models that showed a significant improvement in fit, and no significant main effects. The top model produced by the method of best subsets had a lower AIC than any of the univariate forward selection models. The results of that model are reported in Table 6. These results may be due to the reduced dataset reflecting the limitations of the data rather than a true lack of significance.

Outside of maternal parity, analysis of maternal and primary male caregiver (PMC) experience was very limited by the data. This was due to the unknown history of most mothers and PMCs. Only 6 PMCs and 10 mothers were known prior to sexual maturity. Sibling-care experience could only be determined for the mothers of 43 infants and the PMCs of 26. In all cases, the mothers and PMCs had participated in sibling-care. There were no known cases of reproductive individuals that had not experienced sibling-care. Sibling-care experience ranged between 1-6 litters for both mothers and PMCs. The average number of sibling-care experiences was 2.5 litters for males and 2.9 litters for females. Primary male caregivers were also ranked by the number of times they had previously acted as primary male caregiver, but this could only be determined for the PMCs of 62 infants. The majority of infants had experienced primary male caregivers (n=52) with only 10 infants known to have inexperienced PMCs. A Fisher’s exact test
found no significant difference in survival to nine months between experienced and inexperienced PMCs (p=0.71).

3.4 Habitat use and reproductive output

3.4.1 Characterizing habitat types

There was no significant difference between foraging efficiency for animal prey in shade cocoa, mature, secondary or swamp forest ($F_{3,217}=0.78$, p=0.50; Table 7). Fruit tree visitation also showed no difference between shade cocoa, abandoned shade cocoa, mature, secondary and swamp forest ($F_{3,14}=1.78$, p=0.20; Table 8), instead showing wide variation in fruit tree use between groups (Figure 11). Predator species observations ($\chi^2=7.7$, df=4, p=0.10) and total predation events ($\chi^2=5.8$, df=4, p=0.21) did not differ from the expected distribution based on the proportion of time spent in each habitat type. Predation attempt scores were not calculated due to the extremely low sample size (n=14 for all habitat types combined). The scores for foraging efficiency, predation risk and resting activity are presented for each habitat in Table 9.

Body condition scores differed significantly between shade cocoa, mature and secondary forest ($F_{2,36}=3.908$, p=0.03; Table 10). Post hoc comparisons using the Tukey HSD test found no pairwise comparisons to be significant (Table 11). Individual body condition was not correlated with the percentage of time spent in mature forest (Pearson’s correlation, $r=0.30$, df=129, p=0.99; Figure 12a). Individual body condition was weakly correlated with the percentage of time spent in secondary forest (Pearson’s correlation, $r=0.48$, df=129, p<0.0001; Figure 12b). When individuals were classed as “high” or “low” condition relative to the average, secondary forest made up a significantly higher percentage of habitat use in high condition individuals (mean=0.62, SD=0.34) than low condition individuals (mean=0.27, SD=0.30; $t (129)=-6.25$, p<0.0001). Individuals with high body condition also spent significantly lower percentages of time in mature forest (mean=0.24, SD=0.31) than individuals with low body condition (mean=0.40, SD=0.24; $t (129)=-2.93$, p=0.004).

Resting scores showed a significant difference between habitat types ($F_{4,94}=3.89$, p=0.006; Table 12). Post hoc comparisons using a Tukey HSD test showed a significant difference between mature and secondary forest (p=0.003; Table 13), with higher average resting scores in secondary (mean=0.028, SD=0.016) than mature (mean=0.016, SD=0.010). Resting scores did
not show a correlation with average yearly group size (Pearson’s correlation, \( r=0.18, \) \( df=38, \) \( p=0.27; \) Figure 13a) or with average number of adult males (Pearson’s correlation, \( r=0.18, \) \( df=37, \) \( p=0.30; \) Figure 13b).

Secondary and mature forest accounted for 76% of all habitat use (Table 9), and so further analyses on habitat classified individuals by their use of these two habitat types.

### 3.4.2 Habitat use and reproductive rates

Social groups experienced membership and habitat use changes over time, and so reproductive rates were calculated per reproductive female. While the sample size was small (n=6 females), reproductive rate showed a strongly positive correlation with secondary habitat use (Pearson’s correlation, \( r=0.92, \) \( df=4, \) \( p=0.005; \) Figure 14a). Reproductive rate showed a negative correlation with mature habitat use (Figure 14b), but a Pearson’s product-moment test did not find this to be significant (\( r=0.77, \) \( df=4, \) \( p=0.96). \) Mature habitat use was not significantly correlated with secondary habitat use (Pearson’s correlation, \( r=0.85, \) \( df=4, \) \( p=0.98; \) Figure 14c).

### 3.4.3 Habitat use and infant survival

A comparison of Kaplan-Meier survival curves showed no significant difference in survival between infants who mostly used secondary forest and infants who mostly used other habitats in early life (\( \chi^2=0.2, \) \( df=1, \) \( p=0.70; \) Figure 15a). There was also no significant difference in survival between infants who used mature forest and infants who used other habitats the most in early life (\( \chi^2=0.3, \) \( df=1, \) \( p=0.60; \) Figure 15b). Due to lack of significance, habitat variables were not assessed with a Cox proportional hazards model. A Fisher’s exact test found no evidence that infant survival to nine months was dependent on the group’s most-used habitat for the year containing the birth (\( p=0.24. \))

### 3.4.4 Habitat use and infant growth

Likelihood ratio tests of nested Von Bertalanffy growth functions showed a significant effect of secondary habitat use on both growth rate and adult weight (Table 14). Infants who used secondary forest the most in early life showed higher growth rates and adult weights (Figure 16). Secondary habitat use and the presence of multiple adult males were not independent of each other (\( \chi^2=7.0, \) \( df=1, \) \( p=0.008). \) 77% of the growth data points were infants who both used
secondary habitat the most and had multiple males present. There was not enough data to analyse the effects of multiple males and secondary forest use separately from each other.

A comparison of nested Von Bertalanffy growth functions showed a significant effect of mature habitat use on growth rate but not adult weight (Table 15). The growth function results indicate that infants who used mature forest the most in early life showed lower growth rates (Figure 17), but this sample size was very small. Only 32 captures were available for 13 individuals who used mature forest the most, while 135 captures were available for 41 individuals who used other habitats the most. Mature forest use and the presence of multiple males were independent of each other ($\chi^2=3.45$, df=1, p=0.06).

4 Discussion

This was the first research to examine multiple factors influencing reproductive success in wild *L. chrysomelas*. I demonstrated that females have limited breeding opportunities, and I found that both social and environmental variables can have important impacts on reproductive success in this species. Less than 60% of all infants survived to the age of first possible dispersal. Adult male presence and group size interacted to influence survival, with large group sizes negatively impacting infant survival to a greater extent in the presence of a single male compared to multiple males. Male presence also affected infant growth, the first time this has been analyzed in callitrichids. Infants raised with multiple adult males grew faster to larger adult weights than infants raised with a single adult male. I found no effect of parental characteristics on infant survival. Habitat use influenced reproductive success through reproductive rates and infant growth, although it appeared to have no effect on infant survival. Female reproductive rates were correlated with secondary forest use, and infants raised in secondary forest grew faster to larger adult weights than infants in other habitats. Individuals also had better body condition and rested at higher rates in secondary forest, suggesting that this degraded forest type can act as a good quality habitat under certain conditions.
4.1 Limited reproductive opportunities for females

*L. chrysomelas* females have limited opportunities to achieve a reproductive position, particularly within their natal groups. Reproduction was generally limited to a single female within each social group, and concurrent breeding attempts always ended in the death of one litter at a young age. Infanticide was documented on four occasions, and on three of those occasions another female group member was pregnant or nursing infants at the time of the event. In the fourth event, another sexually mature female was suspected to be pregnant, although she was never observed with infants. Infanticide was only observed directly four times in the current study, but multiple females were never observed successfully rearing young concurrently. In 63% of these cases, infants born to young, previously non-reproductive females disappeared before reaching weaning age. It is possible therefore that infanticide was occurring at higher rates than anecdotal evidence indicates, although abandonment, lack of care or insufficient resources could be alternative explanations. Regardless of the reason for these losses, it is clear that groups will not tolerate caring for simultaneous litters. This is contrary to *L. rosalia* (Baker et al., 1993), where multiple breeding females have been observed successfully raising infants within the same group and timeframe. However, similar to *L. rosalia*, the majority of *L. chrysomelas* females do experience pregnancy, and reproductive skew is enforced post-partum (Henry et al., 2013). In the current study, a third of *L. chrysomelas* females did not reproduce in their natal group at all. Additionally, only one or two females were observed to reproduce concurrently within a group, even when more than two sexually mature females were present. This could be the result of self-restraint due to the threat of infanticide, as proposed for cooperatively-breeding meerkats and *Callithrix jacchus* (Digby and Saltzman, 2009; Young et al., 2008).

In the current study, only three *L. chrysomelas* females were ever observed to successfully rear infants to independence within their natal group. This represents 12% of the females that were observed for at least one reproductive season within their natal group. In two instances, a young female successfully reared infants in her natal group after the previously reproductive female had disappeared. Only one female was ever observed successfully reproducing in her natal group while the previously reproductive female was still present. This female, individual 100, was observed to kill her mother’s infants in an apparent “takeover” of the reproductive position. Her
infants did survive, but she disappeared approximately six months later and her mother resumed the reproductive position for several more years. The other two instances may also represent takeovers, or inheritances, of the reproductive position in their natal group. This reflects the pattern seen in meerkats, where females are only expected to experience reproductive success in their natal group through overthrow or inheritance of the reproductive position (Kutsukake and Clutton-Brock, 2006). A similar pattern is seen in another callitrichid, *Callithrix jacchus*, where infanticide is also used to restrict reproductive competition or facilitate the takeover of a dominant position by a subordinate female (Saltzman et al., 2008). My results suggest that in wild *L. chrysomelas*, it is uncommon for natal females to inherit or takeover a reproductive position, as only three females were observed to achieve such a position in their natal group.

In general, turnovers of reproductive females were uncommon across the population. Over 53 group-years, only eight turnovers were observed. This is likely a by-product of the long tenures held by established reproductive females, as seen in meerkats (Kutsukake and Clutton-Brock, 2006). The three turnovers noted above likely constitute inheritances or takeovers by natal females. Five additional turnovers involved the immigration of a new female into the group. While females face limited opportunities in their natal groups, the occurrence of females immigrating into reproductive positions was equally low, suggesting that dispersal might not necessarily represent a better solution. Other work on this study population suggests that *L. chrysomelas* females are more likely to end up as lone “floaters” than males (Hu, Raboy et al., in prep). In marmosets and *L. rosalia*, females have been shown to immigrate less than often than males into established groups (Baker and Dietz, 1996; Ferrari and Diego, 1992). *L. rosalia* females also face aggression from both sexes when trying to join a group (Baker and Dietz, 1996), likely because they pose a threat to an established reproductive female. As a result of limited reproductive opportunities through dispersal and in the natal group, it seems likely that a high number of *L. chrysomelas* females do not attain any reproductive success, resulting in a very low effective population size.

4.2 Multiple males have several fitness benefits

I found that the presence of multiple adult males was associated with several fitness benefits for infants. Multiple males mitigated the costs of group size on infant survival. This is consistent with previous work in the callitrichids that has found an association between adult males and
infant survival (Bales et al., 2000; Koenig, 1995). Infants raised by multiple males also grew faster to larger adult weights than infants raised by a single male. This is the first time infant growth has been analyzed in the context of male presence in callitrichids. Fast early growth and high adult body weights have been linked to lifetime fitness benefits in several mammals, including primates (Altmann and Alberts, 2003, 2005; Clutton-Brock et al., 2006; Rödel et al., 2008; Wauters and Dhondt, 1989). It should be noted that male presence is not independent of habitat use, which also affected infant growth, and it was not possible to tease the two effects apart with the available data.

The fitness benefits of increased survival and growth likely occur due to the high level of infant care displayed by callitrichid males. In several callitrichid species, field and captive studies have documented fathers and adult male helpers contributing the highest rates of infant carrying (Baker et al., 1993; Heymann, 1990; Price, 1992a; Sanchez et al., 1999). Several field studies have also documented multiple males within a social group carrying at equally high rates (Baker et al., 1993; Goldizen, 1987; Heymann, 1990), indicating that multiple males could substantially increase care. It is less clear if males also provision food at higher rates. In studies of food transfers from adults to infants, callitrichid fathers almost always display the highest provisioning rates (Brown et al., 2004), but research on marmosets has not found that male helpers provision food to infants at higher rates than other group members (Price, 1992a). Shared paternity between multiple males has been documented in two species of *Saguinus* tamarins, even within a single litter (Díaz-Muñoz, 2011; Huck et al., 2005). If fathers provision food at higher rates than helpers and a group contains multiple fathers, the presence of multiple males could indeed increase the amount of provisioning juveniles receive.

### 4.3 The benefits of males temper the costs of group size

I found that the presence of multiple males interacted with group size to mitigate the negative effects of increasing group size on infant survival. As group size increased, infant survival decreased at a greater rate when a single male was present than when multiple males were present. The negative association between group size and infant survival is in contrast to the positive association documented in many cooperative breeders (Clutton-Brock et al., 2001; Magrath, 2001; Rood, 1990). Previous work in callitrichids has generally found no association between group size and infant survival (Bales et al., 2000; Rothe et al., 1993), although number
of helpers was positively associated with infant survival in *L. rosalia* (Bales et al., 2000). However, previous studies have frequently compared groups with and without helpers (Schaffner and French, 1997), overlooking the effect of increasing numbers of helpers and juveniles. It has been suggested that callitrichids may be unable to raise infants without helpers in free-ranging populations, due to the high cost of reproduction (Goldizen, 1987). In this study, 98% of infants were raised with helpers present. The near-universal presence of helpers suggests that they do play an important role in infant care, but I found that further increases in group size resulted in a cost to infant survival. This effect has been documented in the Seychelles warbler, a cooperatively breeding passerine, where reproductive success initially increased with group size but both reproductive success and overall survival decreased in groups larger than 5 members (Brouwer et al., 2006). There is also some evidence for a decrease in reproductive return with the addition of more than 2-3 helpers in marmosets and *Saguinus* tamarins (Koenig, 1995; Schaffner and French, 1997).

There are three possible explanations for the presence of multiple males limiting the costs of large group sizes. One straight-forward explanation is that males provide more infant care, and thus groups with multiple adult males will have higher overall amounts of care. Another explanation is resource competition among group members, as seen in gorillas (Watts, 1985), and the Seychelles warbler (Brouwer et al., 2006). Group size is constrained by available food resources in many primate species (Wrangham et al., 1993). In *L. rosalia*, groups with multiple adult males had larger territory sizes than other groups (Hankerson and Dietz, 2014), suggesting that groups with multiple adult males had access to more resources and might therefore experience less resource competition. However, larger groups in general also had larger territory sizes (Hankerson and Dietz, 2014), and so it seems counterintuitive that infant survival would still decrease with group size if this pattern held true in *L. chrysomelas*.

A third explanation for the interaction between males and group size is the increased risk of reproductive competition in large groups. *L. chrysomelas* groups are largely made up of older offspring who have not yet dispersed. I found no bias in the birth sex-ratio of this population, nor any difference in survival between male and female offspring. As a result, larger groups are more likely to contain multiple sexually mature females and thus more likely to experience reproductive competition. In *L. rosalia*, both subordinate and dominant females are more likely
to give birth in large groups (Henry et al., 2013). An increase in birth rate might be interpreted as a positive effect on reproductive success, but multiple litters could actually strain resources and result in lower infant survival overall.

In the current study, three of the four recorded infanticides involved adult males as participants. In each infanticide involving male participants, the mother was young and either primaparous, or had had her previous infants killed. Infanticide has been documented in free-ranging populations for three other callitrichid species (Hilário and Ferrari, 2010; Saltzman et al., 2009). However, the infanticides documented in those species were all committed by females – either the dominant female, another reproductive female, or the mother herself (Saltzman et al., 2009). This is the first time males have been observed committing infanticide in the callitrichids. The infanticide observations in the current study suggest that male L. chrysomelas might actively enforce the reproductive skew within a group by targeting litters born to inexperienced mothers, and maximizing the survival of one litter rather than risking two. Interestingly, multiple breeding females in captive L. chrysomelas groups have resulted in infanticide, group member deaths and breakdowns of the social group cohesion (De Vleeschouwer et al., 2001). As previously indicated, multiple L. chrysomelas females in this study were never observed to successfully rear infants concurrently. Together with the infanticides committed by male and non-breeding group members, these results suggest that multiple litters present a particular risk to L. chrysomelas groups compared to other callitrichids. As such, the presence of multiple males in large groups could act to minimize the threat of multiple litters through direct enforcement of reproductive skew.

4.4 Secondary forest can act as high quality habitat under certain conditions

I found several indicators that secondary forest can act as a high quality habitat for L. chrysomelas, including a positive effect on reproductive rate and infant growth. Individuals in secondary forest had better body condition and spent a greater proportion of time resting than in other habitats. This could mean that individuals were able to dedicate less time to anti-predator or foraging behaviour, without an associated decrease in body condition. Secondary forest also had an impact on reproductive success. Female reproductive rates were highly correlated with secondary habitat use. While I found no effect of habitat on infant survival, the end result was a
greater number of surviving infants in secondary forest due to the greater number of infants born into the habitat. In addition, infants in secondary forest grew faster to larger adult weights.

Fast infant growth and high birth rates have been associated with high food resource availability in a variety of mammals, including primates (Altmann and Alberts, 2005; Asquith, 1989; McAdam and Boutin, 2003; Persson, 2005). I found no difference in resource availability between habitats using the indirect measurement of foraging behaviour. However, body condition, resting frequency, rates of reproduction and infant growth all suggest high food resource availability within secondary forest.

High food resource availability could also provide an explanation for the lack of independence between male presence and secondary forest use. A high proportion of infants in secondary forest also benefitted from the presence of multiple males, and the two effects on growth could not be teased apart with the available data. Extensive work has been done on captive Saguinus tamarins documenting the costs males face by providing infant care (Achenbach and Snowdon, 2002; Schradin and Anzenberger, 2001). In captive Saguinus, carrying restricts mobility (Schradin and Anzenberger, 2001) and foraging (Price, 1992b), and males have been documented to experience a striking weight loss during periods of infant care (Achenbach and Snowdon, 2002). Despite these costs, Saguinus males are not known to increase food intake when providing infant care (Sanchez et al., 1999). As a result, it may be particularly important for male caregivers to be in good body condition at the start of a reproductive attempt. The higher average body weight of L. chrysomelas individuals in secondary forest could reduce the danger of weight loss during infant care, allowing more males to invest more care into infants.

There are two important considerations that should be taken into account before generalizing my results on habitat to the rest of L. chrysomelas’ range. First, the quality of secondary forest for L. chrysomelas could depend on its proximity to other habitats. The secondary forest in this study was part of a mosaic of forested habitats almost entirely contiguous to one other, including relatively pristine mature forest (Raboy et al., 2004). Contrary to my results, a one year study on the species in a secondary patch isolated by cattle pasture found very high infant mortality (Guidorizzi, 2008). This is particularly concerning because the Atlantic Forest is so highly fragmented, with 80% of remaining fragments less than 50 ha in size (Ribeiro et al., 2009). In
addition, very little of the remaining forest is protected and further fragmentation is expected (Ribeiro et al., 2009).

A second consideration that should be taken into account is the floristic composition of secondary habitat, which can vary widely by location. The secondary forest in this study contained a high density of dendê (*Elaeis guineensis*), commonly known as African oil palm (Raboy and Dietz, 2004). Dendê is an introduced species that serves as a resource on multiple levels for *L. chrysomelas*, offering fruit and animal prey in addition to sleeping sites (Oliveira et al., 2010, B.E. Raboy, pers. comm.). It is possible that the dendê in this secondary forest served a similar role to jackfruit in the shade cocoa habitat of another study site (Oliveira et al., 2011), providing a high quality resource in a habitat that might otherwise be average or low quality.

### 4.5 Future directions for *L. chrysomelas* research

My research demonstrates that *L. chrysomelas* can reproduce at high rates in secondary habitat. High reproductive rates were previously documented in shade cocoa, another type of degraded forest, when jackfruit was abundant (Oliveira et al., 2011). It is apparent that the species can do well in some human-modified habitats in terms of reproductive success. It is less clear if these results can be applied to degraded habitat patches that lack close proximity to mature forest, or that lack high densities of resource-rich exotics. *L. chrysomelas* are currently facing high rates of habitat degradation and fragmentation, and a large part of their range is now degraded forests (Raboy et al., 2010). The Bahian landscape is however dynamic, and regeneration is occurring in some places. A crucial direction for future work will thus involve analyzing how reproductive success varies by forest characteristics, and degree of degradation.

Another vital focus for future work is the relationship between habitat use and group composition. My research has demonstrated that both social and habitat characteristics can play a strong role in influencing reproductive success in this species. I also found a lack of independence between multiple male presence and secondary habitat use. Understanding how habitat use and social group composition directly influence each other could provide a promising tool for future conservation management. If habitat use influences the composition of the social group, identifying habitats that promote smaller groups with more males could allow the focus of conservation initiatives on habitats that will optimize reproductive success.
Finally, I found no effect of parental characteristics on infant survival. It is possible that social characteristics have largely replaced parental effects, as seen in meerkats (Russell et al., 2002). However, it is also possible that my results might not reflect a true lack of biological significance, due to low power of the parental analysis. The effects of parental characteristics are another direction for future research, to ensure that a potential influence on reproductive success is not overlooked.

4.6 Conclusions

My results show that both social and environmental factors can have a strong influence on reproductive success in *L. chrysomelas*. I identified a strong reproductive skew and limited reproductive opportunities for females. I also documented the social circumstances of the first recorded infanticides in wild *Leontopithecus*. I showed that adult males are critical for infant growth and survival, and I demonstrated that secondary habitat, previously believed to be a poor quality habitat, can actually correspond to increased reproductive success under certain conditions. In addition, I found some evidence that habitat use and social characteristics can act together to influence reproductive success. These results have important implications for conservation management of this endangered primate, in addition to providing new insight into the relationship between social factors and reproductive success in a cooperative breeding system.
References


## Tables

Table 1. Number of births and years studied for each group included in the analyses.

<table>
<thead>
<tr>
<th>Group Name</th>
<th>Number of Years</th>
<th>Years Studied</th>
<th>Number of Births</th>
<th>Number of Infants</th>
</tr>
</thead>
<tbody>
<tr>
<td>PIA</td>
<td>12.66</td>
<td>1995-2007</td>
<td>18</td>
<td>25</td>
</tr>
<tr>
<td>ONÇ</td>
<td>12.17</td>
<td>1995-2007</td>
<td>16</td>
<td>27</td>
</tr>
<tr>
<td>ENT</td>
<td>8.25</td>
<td>1999-2007</td>
<td>16</td>
<td>28</td>
</tr>
<tr>
<td>PIT</td>
<td>6.66</td>
<td>2001-2007</td>
<td>12</td>
<td>23</td>
</tr>
<tr>
<td>P2</td>
<td>5.25</td>
<td>2002-2007</td>
<td>5</td>
<td>7</td>
</tr>
<tr>
<td>TAP</td>
<td>4.33</td>
<td>2003-2007</td>
<td>5</td>
<td>9</td>
</tr>
<tr>
<td>KIT</td>
<td>2.58</td>
<td>2005-2007</td>
<td>4</td>
<td>8</td>
</tr>
<tr>
<td>PRIN</td>
<td>2.50</td>
<td>1992-1994</td>
<td>3</td>
<td>5</td>
</tr>
</tbody>
</table>
Table 2. Social context for each observed infanticide event. Group composition lists the number of adult males (AM), adult females (AF), subadult males (SAM), subadult females (SAF), and infants (INF). For participants in the infanticide, their relationship to the mother is listed in parentheses.

<table>
<thead>
<tr>
<th>Group Name</th>
<th>Reproductive Season</th>
<th>Reproductive History of Mother</th>
<th>Group Composition</th>
<th>Closest Birth to Different Mother</th>
<th>Age of Infants (at death)</th>
<th>Participating Individuals</th>
<th>Additional Observations</th>
</tr>
</thead>
<tbody>
<tr>
<td>PIA</td>
<td>1997-1998</td>
<td>Primaparous</td>
<td>2 AM</td>
<td>1 week after birth</td>
<td>8 days</td>
<td>2 AM (unknown)</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>3 AF</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>1 SAM</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PIA</td>
<td>1998-1999</td>
<td>Previous infants killed (above)</td>
<td>3 AM</td>
<td>5 months before (infant died before this birth)</td>
<td>1 day</td>
<td>2 AM (unknown)</td>
<td>No other reproductive female in group</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>2 AF</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PIT</td>
<td>2005-2006</td>
<td>Successfully reproduced 5 times previously in group</td>
<td>1 AM</td>
<td>2 months before (infants alive at time of birth)</td>
<td>1 day</td>
<td>AF (daughter; mother of older infants)</td>
<td>Twin disappeared 6-10 days after event</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>3 AF</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>2 INF</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ONÇ</td>
<td>2006-2007</td>
<td>Primaparous</td>
<td>1 AM</td>
<td>3.5 months after</td>
<td>1 day</td>
<td>AF (sister), AM (likely father)</td>
<td>Twin disappeared 2-7 days after event</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>3 AF</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>2 SAF</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 3. Cox proportional hazards regression model of the effect of social variables on infant survival. The hazard ratio for Male Presence – Single indicates the relative risk of death for infants with a single male present compared to infants with multiple males present. The hazard ratio for Group Size indicates the relative risk of death for infants between each unit increase in group size. The hazard ratio for the interaction indicates the relative risk of death for infants with a single male present compared to multiple males present, for each unit increase of group size.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Hazard Ratio</th>
<th>Lower 95% CI</th>
<th>Upper 95% CI</th>
<th>Z</th>
<th>P-Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male Presence (Single)</td>
<td>0.1663</td>
<td>0.0126</td>
<td>2.187</td>
<td>-1.36</td>
<td>0.1723</td>
</tr>
<tr>
<td>Group Size</td>
<td>1.1608</td>
<td>0.9743</td>
<td>1.383</td>
<td>1.67</td>
<td>0.0951</td>
</tr>
<tr>
<td>Interaction: Male Presence (Single) by Group Size</td>
<td>1.9508</td>
<td>1.1957</td>
<td>3.183</td>
<td>2.68</td>
<td>0.0075</td>
</tr>
</tbody>
</table>
Table 4. Likelihood ratio test results comparing nested Von Bertalanffy growth functions to test the effect of multiple male presence on infant growth. M0 represents the null hypothesis, with no effects included. M1 includes an effect of male presence on growth rate, and M2 includes an effect of male presence on both growth rate and asymptotic weight.

<table>
<thead>
<tr>
<th>Model</th>
<th>Df</th>
<th>AIC&lt;sup&gt;1&lt;/sup&gt;</th>
<th>BIC&lt;sup&gt;2&lt;/sup&gt;</th>
<th>LogLik&lt;sup&gt;3&lt;/sup&gt;</th>
<th>L.Ratio&lt;sup&gt;4&lt;/sup&gt;</th>
<th>P-Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>M0</td>
<td>7</td>
<td>2152.275</td>
<td>2175.804</td>
<td>-1069.137</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M1</td>
<td>8</td>
<td>2150.011</td>
<td>2176.901</td>
<td>-1067.005</td>
<td>4.264023</td>
<td>0.0389</td>
</tr>
<tr>
<td>M2</td>
<td>9</td>
<td>2145.649</td>
<td>2175.901</td>
<td>-1063.825</td>
<td>6.361402</td>
<td>0.0117</td>
</tr>
</tbody>
</table>

1 The Akaike’s information criterion for the given model
2 The Bayesian information criterion for the given model
3 Log likelihood value for the given model
4 The likelihood ratio comparing the given model against the previous listed models.
Table 5. Comparison of social and parental variable ranges between the full dataset and the reduced dataset used for the parental proportional hazards model, which included only infants with data available on primary male caregiver condition.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Full Dataset Values</th>
<th>Reduced Dataset Values</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Range: 2-11 individuals</td>
<td>Range: 2-11 individuals</td>
</tr>
<tr>
<td>Group Size</td>
<td>Mean = 5.64</td>
<td>Mean = 5.41</td>
</tr>
<tr>
<td>Male Presence</td>
<td>Multiple Males: 68%</td>
<td>Multiple Males: 63%</td>
</tr>
<tr>
<td></td>
<td>Single Male: 32%</td>
<td>Single Male: 38%</td>
</tr>
<tr>
<td>Presence of Dependents</td>
<td>Dependents Present: 48%</td>
<td>Dependents Present: 47%</td>
</tr>
<tr>
<td></td>
<td>Dependents Absent: 52%</td>
<td>Dependents Absent: 53%</td>
</tr>
<tr>
<td>Adult Sex Ratio</td>
<td>Male-Biased: 36%</td>
<td>Male-Biased: 28%</td>
</tr>
<tr>
<td></td>
<td>Equal: 28%</td>
<td>Equal: 33%</td>
</tr>
<tr>
<td></td>
<td>Female-Biased: 36%</td>
<td>Female-Biased: 38%</td>
</tr>
<tr>
<td>Number of Rep. Females</td>
<td>Multiple: 21%</td>
<td>Multiple: 14%</td>
</tr>
<tr>
<td></td>
<td>Single: 79%</td>
<td>Single: 86%</td>
</tr>
<tr>
<td></td>
<td>Mean = 7.007</td>
<td>Mean = 7.052</td>
</tr>
<tr>
<td></td>
<td>Mean = 4.60177</td>
<td>Mean = 4.922078</td>
</tr>
<tr>
<td>Maternal Rep. Status</td>
<td>Previously reproductive: 74%</td>
<td>Previously reproductive: 84%</td>
</tr>
<tr>
<td></td>
<td>Prev. non-reproductive: 26%</td>
<td>Prev. non-reproductive: 15%</td>
</tr>
</tbody>
</table>
Table 6. Cox proportional hazards regression model of the effect of parental variables on infant survival. No model showed a significant improvement over the null, and so the model with the lowest AIC value is presented. No variable showed a significant effect. The hazard ratio for reproductive status indicates the relative risk of death for infants born to mothers of previous non-reproductive status compared to infants born to mothers of previous reproductive status. The hazard ratio for maternal parity indicates the relative risk of death for infants between each unit increase.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Hazard Ratio</th>
<th>Lower 95% CI</th>
<th>Upper 95% CI</th>
<th>Z</th>
<th>P-Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maternal Reproductive Status</td>
<td>0.3538</td>
<td>0.0748</td>
<td>1.674</td>
<td>-1.310</td>
<td>0.190</td>
</tr>
<tr>
<td>(Previously Non-Reproductive)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Maternal Parity</td>
<td>0.8993</td>
<td>0.7723</td>
<td>1.047</td>
<td>-1.368</td>
<td>0.17</td>
</tr>
</tbody>
</table>
Table 7. One-way analysis of variance (ANOVA) testing for a significant difference in foraging efficiency for animal prey between habitats. Shade cocoa, mature, secondary and swamp forest were included as habitat types.

<table>
<thead>
<tr>
<th>Source of Variation</th>
<th>Sum Sq</th>
<th>Df</th>
<th>Mean Sq</th>
<th>F value</th>
<th>F crit</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Between groups</td>
<td>0.01762</td>
<td>3</td>
<td>0.00571</td>
<td>0.782898</td>
<td>2.646205</td>
<td>0.504628</td>
</tr>
<tr>
<td>Within groups</td>
<td>1.585667</td>
<td>217</td>
<td>0.007307</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>1.60283</td>
<td>220</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 8. One-way analysis of variance (ANOVA) testing for a significant difference in fruit tree visitation between habitats. Abandoned shade cocoa, mature, secondary and swamp forests were included as habitat types.

<table>
<thead>
<tr>
<th>Source of Variation</th>
<th>Sum Sq</th>
<th>Df</th>
<th>Mean Sq</th>
<th>F value</th>
<th>F crit</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Between groups</td>
<td>0.042286151</td>
<td>3</td>
<td>0.014095384</td>
<td>1.78382021</td>
<td>3.343889</td>
<td>0.196387</td>
</tr>
<tr>
<td>Within groups</td>
<td>0.110625146</td>
<td>14</td>
<td>0.007901796</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>0.152911297</td>
<td>17</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 9. Average scores in each main habitat type for several predation threat and resource availability proxy measurements. The number of individuals used to calculate the average is given in parentheses for resting activity and foraging efficiency scores, which were calculated using individual behaviour scans. The percentage of observations indicates the percentage of total geographic points recorded in each habitat over the course of the study.

<table>
<thead>
<tr>
<th>Habitat Type</th>
<th>Predator Observation Score</th>
<th>All Predation Events Score</th>
<th>Resting Activity Score</th>
<th>Foraging Efficiency Score (Animal Prey)</th>
<th>Percentage of Observation Time¹</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abandoned Shade Cocoa</td>
<td>0.005</td>
<td>0.005</td>
<td>0.013 (n=4)</td>
<td>0.047 (n=17)</td>
<td>5%</td>
</tr>
<tr>
<td>Shade Cocoa</td>
<td>0.002</td>
<td>0.003</td>
<td>0.023 (n=10)</td>
<td>0.103 (n=27)</td>
<td>11%</td>
</tr>
<tr>
<td>Mature Forest</td>
<td>0.002</td>
<td>0.003</td>
<td>0.016 (n=34)</td>
<td>0.079 (n=67)</td>
<td>33%</td>
</tr>
<tr>
<td>Secondary Forest</td>
<td>0.002</td>
<td>0.002</td>
<td>0.028 (n=45)</td>
<td>0.094 (n=85)</td>
<td>43%</td>
</tr>
<tr>
<td>Swamp Forest</td>
<td>0.003</td>
<td>0.003</td>
<td>0.023 (n=6)</td>
<td>0.080 (n=42)</td>
<td>7%</td>
</tr>
</tbody>
</table>

¹ Habitats with extremely low observation times were not included in analyses, but make up the other 1% of observations.
Table 10. One-way analysis of variance (ANOVA) testing for a significant difference in body condition scores between habitat. Shade cocoa, mature and secondary forest were included as habitat types.

<table>
<thead>
<tr>
<th>Source of Variation</th>
<th>Sum Sq</th>
<th>Df</th>
<th>Mean Sq</th>
<th>F value</th>
<th>F crit</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Between groups</td>
<td>2.353269</td>
<td>2</td>
<td>1.176634</td>
<td>3.9082</td>
<td>3.259446</td>
<td>0.029106</td>
</tr>
<tr>
<td>Within groups</td>
<td>10.83845</td>
<td>36</td>
<td>0.301068</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>13.19172</td>
<td>38</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 11. Post hoc Tukey HSD test comparing mean body condition between pairs of most-used habitats.

<table>
<thead>
<tr>
<th>Pairwise Comparison</th>
<th>Difference in Avg Means</th>
<th>Lower 95% CI</th>
<th>Upper 95% CI</th>
<th>Adjusted P-Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mature – Shade Cocoa</td>
<td>0.2921866</td>
<td>-0.44240674</td>
<td>1.0267800</td>
<td>0.5988745</td>
</tr>
<tr>
<td>Secondary – Shade Cocoa</td>
<td>0.7168896</td>
<td>-0.03783331</td>
<td>1.4716125</td>
<td>0.0654784</td>
</tr>
<tr>
<td>Secondary – Mature</td>
<td>0.4247030</td>
<td>-0.03339645</td>
<td>0.8828024</td>
<td>0.0737780</td>
</tr>
</tbody>
</table>
Table 12. One-way analysis of variance (ANOVA) testing for a significant difference in resting activity scores between habitats. Shade cocoa, abandoned shade cocoa, mature, secondary and swamp forest were included as habitat types.

<table>
<thead>
<tr>
<th>Source of Variation</th>
<th>Sum Sq</th>
<th>Df</th>
<th>Mean Sq</th>
<th>F value</th>
<th>F crit</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Between groups</td>
<td>0.002743</td>
<td>4</td>
<td>0.000686</td>
<td>3.893682</td>
<td>2.468533</td>
<td>0.005702</td>
</tr>
<tr>
<td>Within groups</td>
<td>0.016558</td>
<td>94</td>
<td>0.000176</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>0.019302</td>
<td>98</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 13. Post hoc Tukey HSD test comparing mean resting activity scores between habitats. Asterisk (*) indicates significance.

<table>
<thead>
<tr>
<th>Pairwise Comparison</th>
<th>Difference in Avg Means</th>
<th>Lower 95% CI</th>
<th>Upper 95% CI</th>
<th>Adjusted P-Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mature – Abandoned Shade Cocoa</td>
<td>0.0030441703</td>
<td>-0.016469239</td>
<td>0.022557579</td>
<td>0.9925098</td>
</tr>
<tr>
<td>Secondary – Abandoned Shade Cocoa</td>
<td>0.0141893526</td>
<td>-0.005071371</td>
<td>0.033450076</td>
<td>0.2511691</td>
</tr>
<tr>
<td>Shade Cocoa – Abandoned Shade Cocoa</td>
<td>0.0093914253</td>
<td>-0.012448182</td>
<td>0.031231033</td>
<td>0.7536183</td>
</tr>
<tr>
<td>Swamp – Abandoned Shade Cocoa</td>
<td>0.0091252988</td>
<td>-0.014703666</td>
<td>0.032954264</td>
<td>0.8238155</td>
</tr>
<tr>
<td>Secondary – Mature</td>
<td>0.0111451824</td>
<td>0.002756792</td>
<td>0.019533573</td>
<td>0.0033187*</td>
</tr>
<tr>
<td>Shade Cocoa – Mature</td>
<td>0.0063472550</td>
<td>-0.006932733</td>
<td>0.019627243</td>
<td>0.6736858</td>
</tr>
<tr>
<td>Swamp – Mature</td>
<td>0.0060811285</td>
<td>-0.010265407</td>
<td>0.022427664</td>
<td>0.8386160</td>
</tr>
<tr>
<td>Shade Cocoa – Secondary</td>
<td>-0.0047979274</td>
<td>-0.017703756</td>
<td>0.008107901</td>
<td>0.8389455</td>
</tr>
<tr>
<td>Swamp – Secondary</td>
<td>-0.0050640539</td>
<td>-0.021108104</td>
<td>0.010979996</td>
<td>0.9043393</td>
</tr>
<tr>
<td>Swamp – Shade Cocoa</td>
<td>-0.0002661265</td>
<td>-0.019329299</td>
<td>0.018797046</td>
<td>0.9999999</td>
</tr>
</tbody>
</table>
Table 14. Likelihood ratio test results comparing nested Von Bertalanffy growth functions to test the effect of secondary habitat use on infant growth. S0 represents the null hypothesis, with no effects included. S1 includes an effect of secondary habitat use on growth rate, and S2 includes an effect of secondary habitat use on both growth rate and asymptotic weight.

<table>
<thead>
<tr>
<th>Model</th>
<th>Df</th>
<th>AIC¹</th>
<th>BIC²</th>
<th>LogLik³</th>
<th>L.Ratio⁴</th>
<th>P-Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>S0</td>
<td>7</td>
<td>1644.654</td>
<td>1666.480</td>
<td>-815.3268</td>
<td></td>
<td></td>
</tr>
<tr>
<td>S1</td>
<td>8</td>
<td>1628.055</td>
<td>1652.999</td>
<td>-806.0276</td>
<td>18.598511</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>S2</td>
<td>9</td>
<td>1625.578</td>
<td>1653.640</td>
<td>-803.7889</td>
<td>4.477384</td>
<td>0.0343</td>
</tr>
</tbody>
</table>

1 The Akaike’s information criterion for the given model
2 The Bayesian information criterion for the given model
3 Log likelihood value for the given model
4 The likelihood ratio comparing the given model against the previous listed models.
Table 15. Likelihood ratio test results comparing nested Von Bertalanffy growth functions to test the effect of mature habitat use on infant growth. H0 represents the null hypothesis, with no effects included. H1 includes an effect of mature habitat use on growth rate, and H2 includes an effect of mature habitat use on both growth rate and asymptotic weight.

<table>
<thead>
<tr>
<th>Model</th>
<th>Df</th>
<th>AIC(^1)</th>
<th>BIC(^2)</th>
<th>LogLik(^3)</th>
<th>L.Ratio(^4)</th>
<th>P-Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>H0</td>
<td>7</td>
<td>1644.654</td>
<td>1666.480</td>
<td>-815.3268</td>
<td></td>
<td></td>
</tr>
<tr>
<td>H1</td>
<td>8</td>
<td>1637.971</td>
<td>1662.915</td>
<td>-810.9853</td>
<td>8.683006</td>
<td>0.0032</td>
</tr>
<tr>
<td>H2</td>
<td>9</td>
<td>1638.906</td>
<td>1666.968</td>
<td>-810.4529</td>
<td>1.064862</td>
<td>0.3021</td>
</tr>
</tbody>
</table>

1 The Akaike’s information criterion for the given model
2 The Bayesian information criterion for the given model
3 Log likelihood value for the given model
4 The likelihood ratio comparing the given model against the previous listed models.
Figure 1. Comparison of Kaplan-Meier survival curves for infants of known sex. The red line represents female infants and the blue line males. Vertical marks indicate censored observations. The high rate of survival in these curves is due to the inability to determine sex for infants who died before first capture, resulting in misleadingly high survival rates for infants who could be sexed.
Figure 2. Comparison of Kaplan-Meier survival curves for infants from singleton or twin litters. The red line indicates singleton litters and the blue line twin litters. Vertical marks indicate censored observations.
Figure 3. Comparison of Kaplan-Meier survival curves for infants based on group size. Vertical marks indicate censored observations. A) Infant survival in small (red) or large (blue) groups, relative to the average (5.64 individuals). B) Infant survival in groups with low number of helpers (red) or high number of helpers (blue), relative to the average (3.81).
Figure 4. Comparison of Kaplan-Meier survival curves for infants in relation to other dependents in the group. The blue line indicates infants with other dependents present within the group, the red line infants with no other dependents present. The presence of the focal infant’s twin was not included. Vertical marks indicate censored observations. Dotted lines indicate 95% confidence intervals, and are presented only when a log-rank test found a significant difference between survival curves.
Figure 5. Comparison of Kaplan-Meier survival curves for infants by sex of helpers present in the group. Vertical marks indicate censored observations. (A) Multiple adult males (blue) versus single adult male (red) present in early life. Dotted lines indicate 95% confidence intervals. (B) Multiple reproductive females (blue) versus single reproductive female (red) present in early life. (C) Equal (black), male-biased (blue) and female-biased (red) adult sex ratios.
Figure 6. Martingale residuals against the continuous variable group size for the social proportional hazards regression model. The LOESS line is plotted in blue.
Figure 7. Von Bertalanffy growth functions for infants with multiple adult males present (solid line) or a single adult male present (dashed line) in early life. Male presence was included as an effect on both growth rate and adult weight.
Figure 8. Comparison of Kaplan-Meier survival curves for infants categorized by parental condition. Vertical marks indicate censored observations. (A) Infants born to mothers of lower (red) or higher (blue) than average body condition. (B) Infants with primary male caregivers of lower (red) or higher (blue) than average body condition.
Figure 9. Comparison of Kaplan-Meier survival curves for infants categorized by maternal experience. Vertical marks indicate censored observations. (A) Infants born to mothers of lower (red) or higher (blue) than average parity (number of previous births). (B) Infants born to mothers of previous reproductive (blue) or non-reproductive (red) status within their social group. Dotted lines indicate 95% confidence intervals.
Figure 10. Martingale residuals against the continuous variables that were initially included in the parental proportional hazards regression model (maternal parity and primary male caregiver condition). The blue lines are LOESS lines. While the LOESS lines are pulled by a low number of data points at the extreme values, neither line shows a clear, consistent directional trend, indicating the linearity assumption is not violated for either variable.
Figure 11. Average fruit tree visitation by habitat across group-years. Error bars represent standard deviations. The small error bars for the two shade cocoa habitats may be due to small sample size: there were only three group-years available for abandoned shade cocoa and two for shade cocoa. The other three habitats had five group-years each.
Figure 12. Body condition scores plotted against percentage of time spent in (A) mature and (B) secondary forest. Each point represents an individual over 1000 days of age, with body condition averaged across all captures. A simple linear regression best fit line is shown for body condition and secondary forest use.
Figure 13. (A) Average resting scores against average group size. (B) Average resting scores against average number of adult males in group. Each point represents a group in one year.
Figure 14. Reproductive rate for each female (infants/years studied) plotted against the percentage of time spent in (A) secondary forest or (B) mature forest. (C) shows the percentage of time spent in mature versus secondary habitat for each female used in calculating reproductive rates.
Figure 15. Comparison of Kaplan-Meier survival curves for infants based on habitat use in early life. Vertical marks indicate censored observations. (A) Comparison of infants who spent the most time in secondary habitat (blue) versus other habitats (red) in early life. (B) Comparison of infants who spent the most time in mature habitat (blue) versus other habitats (red) in early life.
Figure 16. Von Bertalanffy growth functions for infants who used secondary (dashed line) versus other habitats (solid line) the most in early life. Secondary habitat use was included as an effect on both growth rate and adult weight.
Figure 17. Von Bertalanffy growth functions for infants who used mature forest (dashed line) versus other habitats (solid line) the most in early life. Mature forest use was included as an effect on growth rate, but not adult weight, as indicated by the results of likelihood ratio tests.
Appendices

Appendix A: Aging protocol for *L. chrysomelas* with unknown birth dates

These guidelines should not be applied in reverse.

<table>
<thead>
<tr>
<th>Measurement</th>
<th>Age of Individual</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Weight</strong></td>
<td></td>
</tr>
<tr>
<td>Weight ≤ 200g</td>
<td>&lt; 90 days old (infant)</td>
</tr>
<tr>
<td>Weight ≤ 300g</td>
<td>&lt; 270 days old (infant or juvenile)</td>
</tr>
<tr>
<td>Weight ≤ 400g</td>
<td>&lt; 500 days old (subadult or younger)</td>
</tr>
<tr>
<td>Weight ≥ 600g</td>
<td>≥ 365 days old</td>
</tr>
<tr>
<td>Weight ≥ 650g</td>
<td>≥ 18 months old</td>
</tr>
<tr>
<td>Weight ≥ 700g</td>
<td>≥ 2.5 years old</td>
</tr>
<tr>
<td><strong>Reproductive Organs</strong></td>
<td></td>
</tr>
<tr>
<td>Males: Testes descended</td>
<td>&gt; 90 days old</td>
</tr>
<tr>
<td>Males: Testes width ≥ 15 mm</td>
<td>&gt; 300 days old</td>
</tr>
<tr>
<td>Females: Nipple length ≥ 3.0mm</td>
<td>≥ 18 months old</td>
</tr>
<tr>
<td><strong>Scent Gland Elevation</strong></td>
<td></td>
</tr>
<tr>
<td>Circumgenital gland at least elevation “1”</td>
<td>≥ 400 days old</td>
</tr>
<tr>
<td>Circumgenital gland elevation “3”</td>
<td>≥ 2.5 years old</td>
</tr>
<tr>
<td>Males: Sternal gland elevation “1”</td>
<td>≥ 270 days old</td>
</tr>
</tbody>
</table>
Females: Sternal gland elevation “1”  ≥ 18 months old

Sternal gland elevation > “1”  ≥ 18 months old

**Scent Gland Length, Width & Characteristics**

Circumgenital gland length > 25mm  ≥ 18 months old

Circumgenital gland width > 20mm  ≥ 18 months old

Circumgenital gland fur, odour, secretion or discolouration recorded as “+” or “++”  ≥ 300 days old

Sternal gland length ≥ 40mm  ≥ 300 days old

Sternal gland width ≥ 15mm  ≥ 300 days old

Sternal gland odour or secretion recorded as “++”  ≥ 18 months old

**Length Divided by Weight**

Length/weight > 2.2  < 90 days old

Length/weight ≥ 1.6  < 270 days old

Length/weight ≤ 1.0  ≥ 365 days old

**Teeth**

Tooth wear recorded as “++”  ≥ 2.5 years old

Upper canines have erupted  ≥ 220 days old

Upper canine length > 6.0mm  ≥ 400 days old

Lower canines have erupted  ≥ 300 days old
<table>
<thead>
<tr>
<th>Deciduous lower incisors present</th>
<th>&lt; 18 months old</th>
</tr>
</thead>
<tbody>
<tr>
<td>Deciduous upper incisors present</td>
<td>&lt; 365 days old</td>
</tr>
<tr>
<td>Deciduous upper middle incisors present</td>
<td>&lt; 200 days old</td>
</tr>
<tr>
<td>All teeth deciduous</td>
<td>&lt; 180 days old</td>
</tr>
</tbody>
</table>