

Multi-male groups positively linked to infant survival and growth in a cooperatively breeding primate

Laura A. Heslin Piper¹ · James M. Dietz^{2,3} · Becky E. Raboy¹

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Abstract

Cooperative breeding is a system where helper individuals care for breeding individuals' offspring. As a result, social environment is likely to play a key role in regulating reproductive success. In primates, cooperative breeding is only found in the family Callitrichidae. Callitrichid males typically provide more infant care than non-breeding females, and in many callitrichid species, the presence of multiple males has been linked to infant survival. *Leontopithecus chrysomelas* (the golden-headed lion tamarin) is an endangered callitrichid found in the Atlantic Forest of Brazil. We used long-term data for wild *L. chrysomelas* to assess the influence of social group composition on reproductive success. Our survival model found that infant survival was negatively associated with group size, but this cost was mitigated by the presence of multiple adult males vs a single adult male. We also found that infants raised in groups with multiple adult males exhibited faster growth rates and higher adult weights than infants raised with a single adult male. This study adds novel evidence for the positive influence of adult males on callitrichid reproduction, demonstrating that adult males influence infant growth, as well as survival, in wild populations of

cooperatively breeding primates. We suggest that social group composition, particularly the presence of adult males, be considered in future conservation strategies given its importance for reproductive success.

Significance statement

In cooperatively breeding species, group members care for breeding individuals' offspring. Due to this care, group composition may have a strong influence on infant success. In cooperatively breeding primates, males often provide more infant care than females. We investigated the influence of group composition on infant success in a cooperatively breeding primate, the golden-headed lion tamarin. Using long-term field data, we found that infant survival decreased as group size increased. However, this effect was reduced when multiple adult males were present in the group compared to a single male. We also found that infants grew faster and reached larger adult weights in the presence of multiple adult males compared to a single male. Our results demonstrate the importance of group composition for cooperative breeders and provide new evidence for the positive influence of adult males on cooperatively breeding primate infants.

Keywords *Leontopithecus chrysomelas* · Callitrichid · Primate · Cooperative breeding · Social behavior · Reproductive success

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✉ Laura A. Heslin Piper
laura.heslinpiper@utoronto.ca

¹ Department of Ecology and Evolutionary Biology, University of Toronto, Toronto, Canada

² Program in Behavior, Ecology, Evolution, & Systematics, University of Maryland, College Park, MD, USA

³ Save the Golden Lion Tamarin, Silver Spring, MD, USA

Introduction

Cooperative breeders (Díaz-Muñoz 2016) exhibit a social system in which groups of three or more individuals collectively raise young of a single brood or litter (Koenig and Dickinson 2016). These groups typically include non-breeding “helper” individuals (Russell 2004; Lukas and Clutton-Brock 2012a;

Koenig and Dickinson 2016). Group composition can affect a wide array of variables in social organisms, including vigilance behavior (Childress and Lung 2003), habitat selection (Fortin et al. 2009), and hunting success (MacNulty et al. 2014). For cooperative breeders, group composition can have a particularly important influence on reproductive success (Russell et al. 2002; Lukas and Clutton-Brock 2012b), due to the caretaking role played by non-parent group members (Russell et al. 2003; Woxvold and Magrath 2005; Clutton-Brock 2006; Mumme et al. 2015). Group size has been positively associated with infant survival in many cooperatively breeding species, including meerkats (Clutton-Brock et al. 2001; Russell et al. 2002), African wild dogs (Courchamp and Macdonald 2001), and a number of birds (Woxvold and Magrath 2005; Canestrari et al. 2008). The relationship between helper number and infant survival is not always straightforward, however. The benefits of helper presence may depend on helper sex (Bales et al. 2000) or population density (Sparkman et al. 2011), and helpers can even be associated with lower offspring survival compared to pairs alone (Covas et al. 2011).

Group composition has also been linked to infant growth in many cooperative breeders. In meerkats, infant growth has been positively linked to overall group size and number of helper individuals (Clutton-Brock et al. 2001; English et al. 2014). Nestling body mass was positively associated with group size in Florida scrub jays, although this effect was complicated by territory quality (Mumme et al. 2015). However, as with survival, the relationship between helpers and infant growth is not consistent between all cooperatively breeding species. In *Canis rufus*, helper presence was positively correlated with pup mass at low densities, but negatively correlated at high densities (Sparkman et al. 2011). It may be particularly important to understand factors affecting growth and body mass in cooperative breeders, due to large potential fitness effects. Fast early growth has been linked to lifetime fitness benefits in several mammals, including primates (Wauters and Dhondt 1989; Altmann and Alberts 2003, 2005; Clutton-Brock et al. 2006; Rödel et al. 2008). In meerkats, body mass has been positively associated with dominance status and subsequent reproductive opportunities (Clutton-Brock et al. 2006). While social structure can vary among cooperatively breeding species, reproductive opportunities are generally very limited, often to a single breeding pair per social group (Koenig and Dickinson 2016). Any influence on future reproductive status may therefore have significant fitness consequences in cooperatively breeding species. As cooperative breeding research has expanded to a larger number of species, high variability has been documented in social structure, mating systems, infant care, and helper contributions (Clutton-Brock 2002; Hauber and Lacey 2005; Koenig and Dickinson 2016). This variability has emphasized the need for long-term, species-specific studies, in order to understand

both larger patterns of cooperative behavior and species-specific details (Koenig and Dickinson 2016). In particular, long-term data are only available for a select few cooperatively breeding mammals, such as the meerkat (Hodge et al. 2008) and the dwarf mongoose (Rood 1990). In order to develop a comprehensive understanding of how cooperative breeding manifests in mammals, intensive studies are needed on a wider variety of species.

Callitrichids are small-bodied arboreal New World primates including marmosets, tamarins, and lion tamarins (Buckner et al. 2015). They are the only primates that demonstrate cooperative breeding (Clutton-Brock 2006). Callitrichids exhibit a combination of high reproductive skew (few females actively reproduce) and low effective population size often seen in cooperative breeders (Lukas and Clutton-Brock 2012a; Henry et al. 2013). Reproduction imposes a high energetic cost on callitrichids (Nievergelt and Martin 1998; Key and Ross 1999). With the exception of the genus *Callimico*, callitrichids regularly twin, producing infants with proportionally high birth to adult body weight (Leutenegger 1973; Dunbar 1995; Heymann 2000). These relatively heavy infants are carried for months (Santos et al. 1997) over large home ranges (Raboy and Dietz 2004; Hankerson and Dietz 2014), and require extended care including food provisioning for up to 6 months (Rapaport 2011). Callitrichids have a relatively high reproductive rate per female compared to other primates (Key and Ross 1999); however, they have a low effective population size due to the limited number of breeding positions available to females (Digby 1995). Other cooperative breeders, such as meerkats, have similar restrictions on breeding opportunities but higher fecundity per litter (Russell et al. 2002). As a result, callitrichids produce a low number of infants across their population, and consequently, infant survival is likely an especially important feature in maintaining callitrichid populations.

Long-term field studies of wild callitrichids have so far been limited to a handful of species (Koenig 1995; Goldizen et al. 1996; Bales et al. 2000). Wild callitrichids are rarely observed raising infants without helpers (Goldizen 1987), suggesting that helpers may be necessary for reproductive success. However, even within the small cohort of studied species, there is variability in helper effects. In *Callithrix jacchus* (Koenig 1995) and *Saguinus mystax* (Garber et al. 1984), no relation was found between group size and infant survival. In contrast, *Cebuella pygmaea* showed a positive relationship (Heymann and Soini 1999), and *Leontopithecus rosalia* exhibited an association between infant survival and number of helpers (Bales et al. 2000). Increasing group size was also associated with higher rates of infant care in *Saguinus oedipus* (Price 1992). These differences are likely due to life history differences between species, as callitrichids have demonstrated a variety of mating systems (Dietz and Baker 1993; Nievergelt et al. 2000; Huck et al. 2005;

Yamamoto et al. 2009). The limited number of field studies, however, makes it difficult to determine the exact reason for this variability.

Callitrichids show a more consistent relationship between reproductive success and the sex of potential helper individuals. The number of potential male helpers has been associated with increased infant survival in *S. mystax*, *C. jacchus*, and *L. rosalia* (Bales et al. 2000). This effect is likely due to male callitrichids' tendency to exhibit high rates of infant care behavior (Tardif et al. 1986; Wright 1990; Baker et al. 1993). Captive work has shown that both males and females can function as non-breeding helpers in callitrichids (Price 1992; Yamamoto et al. 2008). However, male group members tend to carry infants more (Cleveland and Snowdon 1984) and provision food at higher rates (Burkart et al. 2007) than females (with the exception of the mother). It may be that this intensive care effort results in a link between male helpers and infant growth, similar to the link between growth and number of helpers in meerkats (English et al. 2014). However, to our knowledge, no study has yet examined infant growth in the context of social variables in a wild callitrichid. The variability shown in the few studied callitrichids demonstrates the need for data on a greater number of species, in order to understand family-wide patterns and differences. This is particularly important given the high number of threatened and endangered callitrichid populations (IUCN 2014).

We examined the role of group composition on both infant survival and growth in a wild population of *Leontopithecus chrysomelas*, the golden-headed lion tamarin. *L. chrysomelas* is designated Endangered by the IUCN, with a decreasing population (Kierulff et al. 2008). The species is frugivorous (Raboy and Dietz 2004) and faces predation from raptors, snakes, and carnivores (Oliveira and Dietz 2011; BER and JMD, unpublished data). They maintain large home ranges (Raboy et al. 2004) but their groups are relatively small, ranging from 3 to 13 individuals (BER and JMD, unpublished data). There are a growing number of studies on *L. chrysomelas*, particularly focused on habitat use (de Almeida Rocha et al. 2015; Catenacci et al. 2016; De Vleeschouwer

and Oliveira 2017), the effects of ongoing habitat fragmentation (De Vleeschouwer and Raboy 2013; Zeigler et al. 2013; Guy et al. 2016), and disease ecology (Bueno et al. 2015; Aitken et al. 2016). However, little is known about the relationship between group composition and reproductive success. We used data from a long-term study on wild *L. chrysomelas* to examine the relationship between group composition, and infant survival and growth. Specifically, we used a survival model to evaluate the impact of multiple demographic variables on long-term survival and growth models to determine if infants raised with multiple adult males exhibited different growth rates and adult weights than infants raised with a single adult male. We sought to develop a detailed understanding of group composition and reproduction in *L. chrysomelas*, adding another species to the callitrichid literature regarding infant survival. We also sought to identify any association between adult male presence and infant growth, the first time this association has been investigated in a wild callitrichid.

Methods

Data collection

Data were collected by JMD and BER in and at the borders of the Una Biological Reserve in Southern Bahia, Brazil, from 1991 to 2007. *L. chrysomelas* from the study population were habituated to individual observers following the methods of Dietz et al. (1996). Bi-annual captures were used to measure physical characteristics, and numeric tattoos and dye marks were applied to facilitate individual identification. In addition, one or two monkeys per group were fitted with radiotelemetry collars. Once habituated, each group was followed for 2–10 days per month year-round. Trained observers conducted behavioral scans of all individuals at 20-min intervals. Eight breeding groups were followed between 2 and 12 years (Table 1).

It was not possible to record data blind because our study involved focal animals in the field.

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

Group name	Number of years	Years studied	Number of births	Number of infants
PIA	12.66	1995–2007	18	25
ONÇ	12.17	1995–2007	16	27
ENT	8.25	1999–2007	16	28
PIT	6.66	2001–2007	12	23
P2	5.25	2002–2007	5	7
TAP	4.33	2003–2007	5	9
KIT	2.58	2005–2007	4	8
PRIN	2.50	1992–1994	3	5

Infant survival analysis

We used survival analyses to compare the effects of demographic variables on infant survival. Survival analyses incorporate censored data when individuals' fates are unknown, allowing us to include a higher number of infants while accounting for uncertainty in their fates. Lifespan was measured as the number of days between the birth date and the last-known date. Birth dates were calculated as the midpoint between the last date the group was seen without infants and the first date the group was seen with infants. Infants were only included in the analyses if their birth date could be determined within a 28-day period. The last-known date was calculated using one of four methods, dependent on the infant's fate: alive when the study ended, lost to follow-up, confirmed dead, or assumed dead. For individuals who were lost to follow-up or alive when the study ended, the last-known date was the last date the individual was observed. Individuals were confirmed dead if a body was found, in which case the last-known date was calculated as the midpoint between the last day they were seen alive and the day the body was found. Individuals were assumed dead if they disappeared from their group under 9 months of age, as 9 months was the earliest age any individuals were observed to successfully disperse from their natal group (BER and JMD, unpublished data). For assumed deaths, the last-known date was calculated as the midpoint between the last date the individual was seen with the group and the first date the individual was observed to be missing from the group. All deaths, confirmed and assumed, were known within a 28-day period, and 96% were known within a 14-day period. To investigate whether survival was skewed by sex, we compared infant survival to 9 months and overall survival between the sexes using a Fisher's exact test and a log-rank test, respectively.

Demographic variables

We measured group composition during each infant's first 3 months, a period when infants are completely dependent on the group (Santos et al. 1997). Group membership was determined using observer field notes. We considered individuals to be group members if they were recorded in the group for at least three consecutive observation days. Group composition was measured as the average values between group composition at birth and at 3 months of age. The focal infant and its twin, if present, were not included in counts of group characteristics. Individuals of unknown birth date were assigned to one of four age classes: infant 0–90 days (weaning), juvenile 91–270 days (age of first possible dispersal), subadult 271–540 days (sexual maturity), and adult 541 days and over. We created a protocol to estimate age based on weight, scent gland development, and tooth eruption data from individuals of known age. Some individuals could

only be aged to within two age classes. Groups containing individuals that were never captured were excluded from analyses for the relevant time period, with one exception where we confirmed a non-captured female to be a sexually mature adult after observing her successfully reproduce.

We classified each infant based on group composition during the first 3 months of life, by the following demographic variables: group size, single vs multiple adult males, single vs multiple reproductive females, and absence or presence of other dependent individuals. Infants were considered to have multiple males present if the average number of adult males in their social group between birth and 3 months of age was 1.5 or higher, indicating that at least two males were present during the individual's infancy period. No infants were raised in groups without adult males. The majority of infants were raised with one or two adult males. We tested male presence as a binomial variable due to the low number of infants raised with more than two males (only 30 out of 116), which limited our ability to test the additive effect of each additional male. Infants were considered to have multiple reproductive females present if another female gave birth in the group within the first 3 months of life or if infants (< 90 days of age) were present at the time of birth. Due to gestation length, a single female could not have newborn and infant offspring at the same time, so the presence of infants at the time of birth was an indication of another reproductively active female. We considered that there were dependent infants or juveniles present if any individuals under 270 days of age were present at the time of birth or if another infant was born during the first 3 months and survived more than three observation days. If group membership could not be confirmed, or if group members could not be aged and sexed, infants were not included in the relevant analyses.

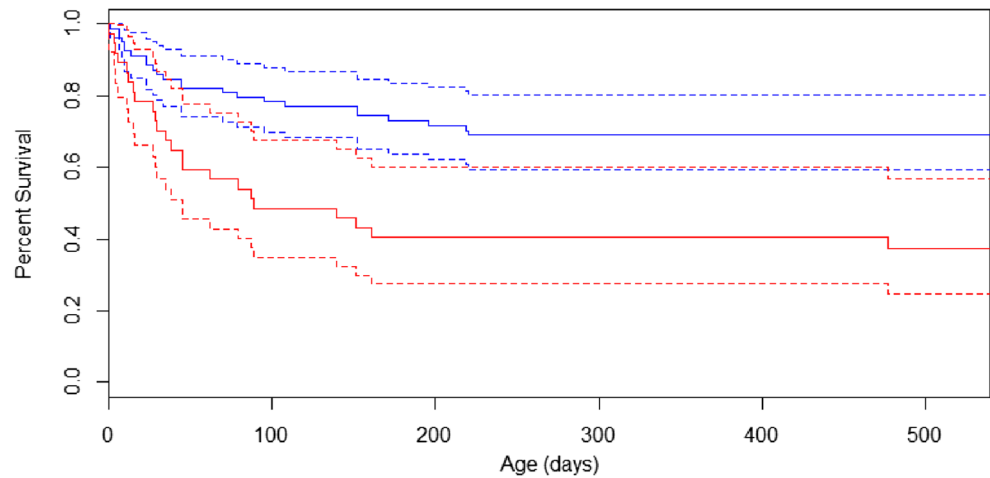
Demographic variable analysis

In order to determine which demographic variables to include in model building, we used log-rank tests to compare Kaplan-Meier survival curves between levels of each categorical variable: multiple vs single adult male, multiple vs single reproductive female, and presence or absence of other dependent individuals. We built a Cox proportional hazards survival model, including all categorical variables that showed significant difference in the log-rank tests, as well as the continuous variable of group size. We built Cox models using two methods: forward selection and the method of best subsets. The resulting models were nested, and so we compared them with a likelihood ratio test in order to choose the final model that demonstrated the best fit to the data. These analyses involved 117 infants.

Infant growth analysis

We analyzed the effect of multiple vs single adult male presence in early life on infant growth using von Bertalanffy

Fig. 1 Comparison of Kaplan-Meier survival curves for infants with multiple adult males (blue) vs single adult male (red) present in early life. Vertical marks indicate censored observations, and dashed lines indicate 95% confidence intervals

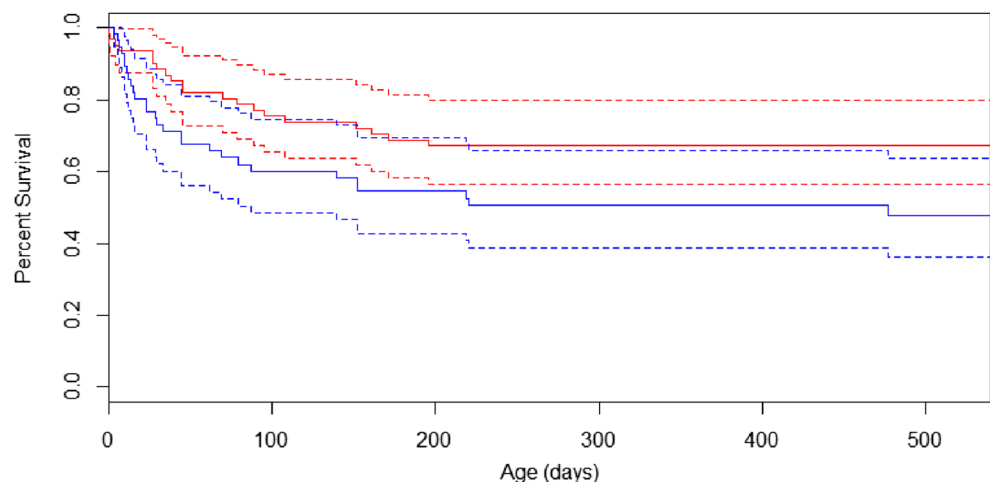


growth functions. Infant growth was measured using weight measurements taken during biannual captures. Individual identity was included as a random effect to account for repeated captures of the same individuals. This analysis included 213 captures of 69 individuals. Three growth functions were calculated: male presence not included (null), male presence included as an effect on growth rate, and male presence included as an effect on both growth rate and asymptotic (adult) 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.

All statistical analyses were run in R 3.1.2 (R Core Team 2016). The survival and glmulti packages were used for survival analyses (Therneau and Grambsch 2000; Calcagno and de Mazancourt 2010; Therneau 2015), and the nlme package was used for growth analyses (Pinheiro et al. 2016). All figures were created in R.

Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Fig. 2 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. Dashed lines indicate 95% confidence intervals



Results

Overview of reproduction in wild *L. chrysomelas*

Between 1991 and 2007, there were 79 confirmed births in the eight study groups, totaling 132 infants (Table 1). Across the study population, 70% ($n = 92$) survived to weaning and 56% ($n = 69$) to the age of first possible dispersal. The sex ratio among infants that survived long enough to be captured was evenly divided with 41 males and 41 females. Infant survival showed no difference between sexes, as measured by percentage surviving to 9 months ($\chi^2 = 0.17$, $df = 1$, $p = 0.68$; $n = 80$ infants) or overall lifetime survival (log-rank $\chi^2 = 0.7$, $df = 1$, $p = 0.42$; $n = 71$ infants).

Infant survival analysis

Demographic variable analysis

The vast majority of infants (98%, 129 of 132) were born into groups with at least three independent individuals, i.e., with at

Table 2 Cox proportional hazards regression model of the effect of social variables on infant survival

Variable	Hazard ratio ^a	Lower 95% CI	Upper 95% CI	Z	p value
Male presence (single)	0.1663	0.0126	2.187	-1.36	0.1723
Group size	1.1608	0.9743	1.383	1.67	0.0951
Interaction: male presence (single) by group size	1.9508	1.1957	3.183	2.68	0.0075*

*Significant effect

^a 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

least one potential helper present. There were three exceptions. One singleton was born into a group containing only a male-female pair, but an adult male joined within the first 3 months of the infant's life. Two infants (twins) were raised by a male-female pair throughout the infants' infancy. In both cases, group membership did not change between time of conception and infant births. All three infants born to groups without potential helpers survived past the age of first possible dispersal.

In the preliminary log-rank tests, infant survival was significantly higher in groups with multiple adult males than in groups with a single adult male ($\chi^2 = 11$, $df = 1$, $p = 0.0009$; Fig. 1). Infants showed significantly lower survival when other dependents were present in the group ($\chi^2 = 5.2$, $df = 1$, $p = 0.02$; Fig. 2) and no significant difference in survival in groups with multiple vs single reproductive females ($\chi^2 = 2.7$, $df = 1$, $p = 0.10$). The number of infants born in groups with multiple reproductive females was very low (24 of 117). A Fisher's exact test also provided no evidence that the reproductive female number influenced survival to 9 months (55% survival with a single reproductive female, 46% survival with multiple reproductive females, $p = 0.50$).

Demographic variable survival model

Multiple vs single adult males, and the presence of dependent individuals, showed significant effects on infant survival in the log-rank tests, and so were included in model building alongside group size. All variables were assessed for proportional hazards and linearity assumptions, and no violations were found. Using the forward-selection model-building method, the best model for the data included multiple vs single adult males, group size, and an interaction between the terms. Using the method of best subsets, the best model included group size, multiple vs single adult males, presence of dependents, and an interaction between the level of adult 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 that included the presence of other dependants showed no significant improvement over the model without dependents presence ($\chi^2 = 1.99$, $df =$

1, $p = 0.16$). Consequently, the final demographic variable model included only multiple vs single adult males, group size, and an interaction between the two terms.

Table 2 lists the hazard ratios for the final survival model. Group size and male presence interacted to have a highly significant effect on infant survival ($p = 0.008$). For each unit of increase of group size, the relative risk of death for infants with a single male present increased by a factor of 1.95 relative to the risk for infants with multiple males present.

Infant growth analysis

The von Bertalanffy growth function that included multiple vs single adult male presence as an effect on both growth rate and adult weight showed a significantly better fit to the data than the null model (Table 3; likelihood ratio $\chi^2 (9) = 6.36$, $df = 9$, $p = 0.017$). Infants in the presence of multiple adult males exhibited faster growth rates and higher adult weights than infants in the presence of a single adult male (Fig. 3). The growth rate estimate for infants with multiple adult males was -5.62 ($SE = 0.05$),

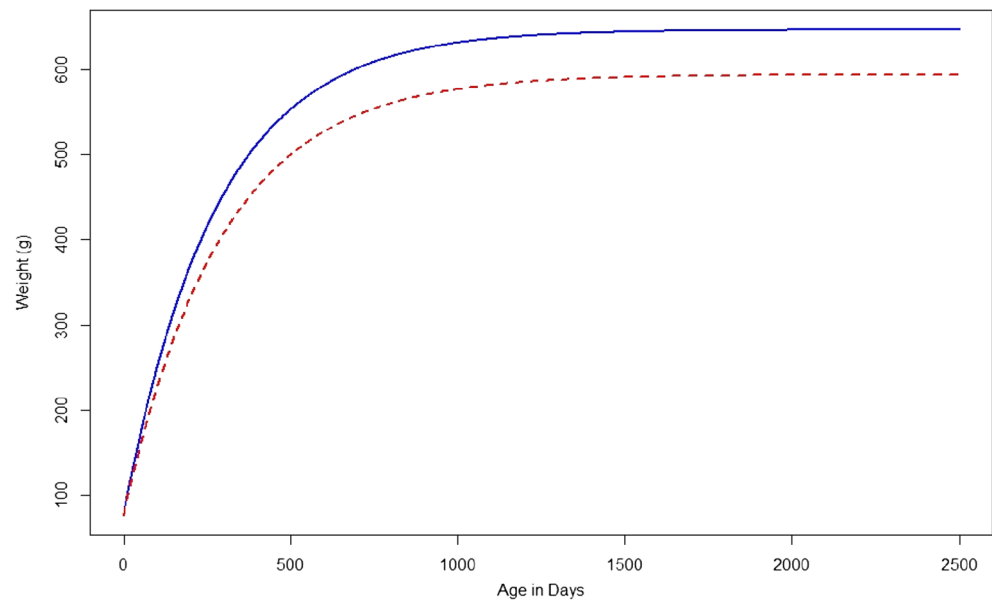
Table 3 Likelihood ratio test results comparing nested von Bertalanffy growth functions to test the effect of multiple male presence on infant growth

Model ^a	Df	AIC ^b	BIC ^c	LogLik ^d	L. ratio ^e	p value
M0	7	2152.275	2175.804	-1069.137		
M1	8	2150.011	2176.901	-1067.005	4.264023	0.0389*
M2	9	2145.649	2175.901	-1063.825	6.361402	0.0117*

*Significant effect

^a 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^b Akaike's information criterion^c Bayesian information criterion^d Log likelihood value^e Likelihood ratio comparing the given model against the previous listed models

Fig. 3 von Bertalanffy growth functions for infants with multiple adult males present (blue line) or a single adult male present (dashed red line) in early life. Male presence (multiple adult males or single adult male present in early life) was included as an effect on both growth rate and adult weight



while the rate for infants with a single adult male was -5.68 ($SE = 0.07$). The asymptotic (adult) weight estimate was 646.77 g ($SE = 9.91$ g) for infants raised with multiple adult males and 594.23 g ($SE = 16.67$ g) for infants raised with a single adult male.

Discussion

Our survival model showed that the presence of multiple males mitigated the negative effects of increasing group size on infant survival. The positive effect of adult males on survival is likely due to the high level of infant care displayed by callitrichid males. Male tamarins, both fathers and non-breeding adult male helpers, have been documented carrying infants at higher rates than other group members in both field and captive studies (Goldizen 1987; Heymann 1990; Price 1992; Sanchez et al. 1999). Field studies on several species have documented multiple males within social groups carrying at equally high rates (Goldizen 1987; Heymann 1990; Baker et al. 1993), suggesting additive benefits. Shared paternity between multiple males has been recorded in two species of *Saguinus* tamarins, even within a single litter (Huck et al. 2005; Díaz-Muñoz 2011). The potential for shared paternity is a possible incentive for multiple callitrichid males in the same social group to provide extensive care. Inclusive fitness benefits from caring for related infants may be another incentive for male helping behavior. However, support for this explanation is mixed in cooperative breeders. In the dwarf mongoose, young adults gained greater fitness benefits staying in their natal group than leaving (Creel and Rabenold 1994). Callitrichid offspring often delay dispersal (Goldizen et al.

1996; Nascimento et al. 2014; Garber et al. 2015), remaining in their natal groups as young adults and potentially benefiting from inclusive fitness. However, the inclusive fitness explanation requires male helpers to be related to the offspring to which they are providing care. In Seychelles warblers, female helping behavior was associated with relatedness of nestlings but male helping behavior showed no such association (Richardson et al. 2003). Adult marmoset males exhibited lower relatedness to other group members than females (Nievergelt et al. 2000). Similarly, in our study population, male helpers were often older immigrants from outside the group (BER and JMD, unpublished data). Thus, while inclusive fitness may influence helping behavior in callitrichids, at least in our study population it seems unlikely to be the driving force behind male helping patterns. Other possible incentives include the possibility of future breeding opportunities (Clutton-Brock 2002) and “paying to stay” in a group so as to avoid the potential risks of dispersal (Hatchwell and Komdeur 2000). Regardless of the incentive, the presence of multiple males may decrease the cost of infant care per male and improve the quality of overall care. In captive *Saguinus oedipus*, males experience striking weight losses during periods of infant care, with the greatest weight losses occurring in the smallest groups (Achenbach and Snowdon 2002), suggesting that the presence of other helpers can reduce the cost of care.

While infant survival has been associated with adult male presence in other callitrichids (Koenig 1995; Bales et al. 2000), the negative association we found between overall group size and infant survival is in contrast to the positive or neutral association documented in many cooperative breeders (Rood 1990; Legge 2000; Clutton-Brock et al. 2001; Magrath 2001). Previous work on callitrichids generally found no

association between group size and infant survival (Rothe et al. 1993; Bales et al. 2000), and the few exceptions suggested a positive relationship (Price 1992; Heymann and Soini 1999; Bales et al. 2000). In our study, 98% of infants were raised with potential helpers present. It has been suggested that callitrichids may be unable to raise infants without helpers in free-ranging populations (Goldizen 1987). The near-universal presence of helpers in our study suggests that helpers are, at the very least, an accepted presence in callitrichid groups. For *L. chrysomelas*, however, further increases in group size have an apparent cost in reduced infant survival. A similar pattern has been documented in the cooperatively breeding Seychelles warbler *Acrocephalus sechellensis* (Brouwer et al. 2006) and the laughing kookaburra *Dacelo novaeguineae* (Legge 2000). A possible explanation of this pattern is resource competition among group members, which may prove detrimental only at larger numbers (Brouwer et al. 2006).

Several potential explanations for multiple males mitigating these large-group costs can be considered. One straightforward explanation is the high level of care demonstrated by callitrichid males. If *L. chrysomelas* males demonstrate the same care patterns as other callitrichids, groups with multiple adult males will have higher overall amounts of care. Another explanation is the potential for intragroup resource competition to increase with group size, as seen in gorillas (Watts 1985) and Seychelles warblers (Brouwer et al. 2006). If the presence of multiple adult males allows groups to maintain larger and higher-quality territories, intragroup competition may be minimized. In the closely related *L. rosalia*, for instance, groups with multiple adult males had larger territory sizes than other groups (Hankerson and Dietz 2014). However, territory size was also positively linked to overall group size (Hankerson and Dietz 2014). If territory size determined infant success, and assuming *L. chrysomelas* follows a similar pattern as *L. rosalia*, we would not expect the negative effect from group size present in our results. A third explanation is the increased risk of reproductive competition in large groups. Callitrichid groups typically contain older offspring who have not yet dispersed (Goldizen et al. 1996; Nascimento et al. 2014; Garber et al. 2015). Larger groups in this study population tended to contain multiple sexually mature females (BER and JMD, unpublished data), which is not surprising as we found no bias in the birth sex ratio and no difference in survival between the sexes. In *L. rosalia*, both subordinate and dominant females are more likely to give birth in large groups (Henry et al. 2013). Multiple litters could strain resources and result in lower infant survival overall. Subordinate breeding has been linked to reduced dominant reproductive success in cooperatively breeding birds and mammals (Koenig et al. 1983; Keane et al. 1994). In our study population, all attempts at breeding by multiple females ended in the failure of at least one litter (BER et al., unpublished data). We found that the presence of multiple reproductive

females had no effect on infant survival; however, the number of infants born in groups with multiple reproductive females was very small (24 out of 117). In comparison, *Callithrix jacchus*, another callitrichid, exhibits high rates of multiple reproductive females per group (Digby and Ferrari 1994). This may indicate that in *L. chrysomelas*, reproductive attempts are largely selected against before breeding, during pregnancy, or immediately after birth, before observers can spot the infants. If so, the selection occurring post-birth may be less obvious and potentially not detectable in our data. In *L. rosalia*, the majority of subordinate female pregnancies do not result in observed live infants (Henry et al. 2013). Adult *L. chrysomelas* males may play an active role in subordinate reproductive suppression, as males in this population were observed committing infanticide in some cases of multiple females breeding within the same group (BER et al., unpublished data).

In addition to increased survival, infants raised in groups with multiple adult males grew faster to larger adult weights than infants raised in groups with a single adult male. Our results provide new evidence that adult males can influence growth as well as survival in callitrichids. High infant growth and body mass have been positively associated with lifetime reproductive success in a variety of mammals and birds (reviewed in Lindström 1999; Festa-Bianchet et al. 2000). In savannah baboons, large juveniles mature earlier (Altmann and Alberts 2005), a trend also documented in deer mice (Jorgenson et al. 1993; McAdam and Millar 1999). In great tits, high nestling mass has been associated with the use of greater-quality breeding territory later in life (Verhulst et al. 1997). High adult body mass has been similarly associated with reproductive success in a variety of mammals, including red squirrels (Wauters and Dhondt 1989), bighorn sheep (Festa-Bianchet et al. 2000), and sifakas (Lewis and Kappeler 2005). In meerkats, female dominance and reproductive status are associated with adult mass (Clutton-Brock et al. 2006) and early growth rate (English et al. 2013). In *L. chrysomelas*, successful reproduction is restricted to a single female per social group (BER et al., unpublished data), and so factors affecting a female's likelihood of achieving a reproductive position would have a strong impact on her lifetime fitness. In the closely related *L. rosalia*, body mass was significantly associated with the number of live births produced by a female (Bales et al. 2001). High growth and adult weight may therefore be particularly important for female *L. chrysomelas*, both for obtaining a reproductive position and for their reproductive success once in the position.

This is the largest sample of wild *L. chrysomelas* infants measured to date, providing valuable information on the relationship between group composition and infant success in this species. Of interest, less than 60% of all infants in this endangered population survived to the age of first possible dispersal, suggesting that factors affecting infant survival could have important consequences for a vulnerable population. Our

study provides new evidence that adult male presence can influence infant growth as well as survival in a wild callitrichid. An important future direction will be to determine how infant growth and adult body weight play a role in an individual's lifetime reproductive success. As more data become available, it will be important to examine the effect of group composition across the entire juvenile period. Moreover, given ongoing habitat destruction in the *L. chrysomelas* range (Raboy et al. 2004; Oliveira et al. 2011), it will be particularly important to understand how habitat characteristics affect group composition and, in turn, infant success.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted. This research complied with the guidelines of the University of Maryland Animal Care and Use Committee (under protocol numbers: R-91-07, R-93-39, R-01-13A, R-01-13B, R-04-43, R-07-75) and all applicable Brazilian laws.

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