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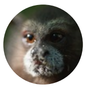

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Modeling Developmental Class Provides Insights into Individual Contributions to Infant Survival in Callitrichids

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Abstract Cooperative breeders live in social groups in which individuals in an age–sex class vary in reproductive development due to reproductive dominance by a few individuals in each group. Among callitrichids, adult males have been implicated in driving group reproductive output, but uneven sampling efforts, the underlying effects of group size, and pseudoreplication at the group and species levels are confounding variables in these analyses. We examined the drivers of group reproductive output in callitrichids by 1) conducting a meta-analysis of published studies of callitrichid group composition; 2) assigning developmental class based on reproductive morphology; and 3) using multivariate modeling to test whether the proportion of individuals of each developmental class predicts the presence and the number of surviving offspring among free-ranging Weddell's saddleback tamarins (*Leontocebus weddelli*) and emperor tamarins (*Saguinus imperator*) in Peru. The meta-analysis revealed that the number of adult females and group size, but not the number of adult males, are significantly correlated with group reproductive output. Statistical models of the new dataset revealed that the proportion of primary breeding males, primary breeding females, and group size predicted whether groups had surviving infants, and that only the proportion of primary breeding females and group size predicted the number of surviving infants. Thus, primary breeding males appear to be necessary for groups to raise any infants, but a higher

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proportion of primary breeding females and a larger group size increase group reproductive output overall.

Keywords Callitrichid · Cooperative breeding · Development · Group composition · Reproductive output

Introduction

Callitrichids exhibit a cooperative breeding system in which offspring receive care from alloparents, or individuals other than biological parents (Garber 1997; Jennions 1994; Sussman and Garber 1987). Groups typically consist of a single breeding female, although other females may be present, and variable numbers of adult and subadult males. Adults and subadult helpers participate in infant rearing, including infant provisioning and transportation (Bales *et al.* 2000; Goldizen and Terborgh 1986; Huck *et al.* 2004). Despite the monopoly of breeding by a single adult female in most cases, callitrichids rarely mate strictly with a single individual, but show a range of flexible mating strategies, both across and within groups over time (Garber 1997; Garber *et al.* 2015; Goldizen 1988; Goldizen *et al.* 1996; Sussman and Garber 1987; Terborgh and Goldizen 1985).

One of the primary hypotheses to explain the presence of helpers, typically unrelated adult males or natal subadults, is that they alleviate the cost of rearing energetically expensive twin offspring that constitute >80% of all births in callitrichids (save *Callimico*) (Tardif 1997; Wislocki 1939). Alloparenting benefits offspring survival, and thus increases group reproductive output (Bales *et al.* 2000, 2001; Boulton and Fletcher 2015; Garber 1997; Heymann 2000; Koenig 1995). By investing in the care of offspring, helpers could incur indirect fitness benefits if they are related to the biological parents; they also benefit from being in a group, e.g., by gaining access to valuable resources or protection from predators, and contribute to it, e.g., via increased vigilance (Bales *et al.* 2000; French 1997; Tardif 1997).

Research suggests that the effects of helpers on group reproductive output vary with helper sex and developmental class (Bales *et al.* 2000). First, species may differ in how helpers of different age–sex classes influence group reproductive output due to differing costs of infant-rearing between species (Díaz-Muñoz 2015; Heymann 2000). For example, *Cebuella pygmaea* have infant-parking strategies (Heymann 2000), while *Callimico goeldii* do not produce twins (Porter 2001), which reduces the cost of infant care in these species. Second, the set of individuals that copulate within a group (the mating system) and the smaller subset of individuals that contribute toward the gene pool of viable offspring (the breeding system) are distinct from each other (Garber 1997). Kappeler and van Schaik (2002) refer to these as the social and the genetic mating systems, respectively. Molecular techniques show that the participants in the genetic mating system, i.e., the biological parents, are usually a single male and female (Garber *et al.* 2015; Huck *et al.* 2005a, 2007; Nievergelt *et al.* 2000). In rare cases, multiple males father offspring in the same litter (Díaz-Muñoz 2011; Huck *et al.* 2005a; Suárez 2007). The social mating system, however, is difficult to describe, since copulation can be cryptic, infrequent, or short (Campbell 2006; Watsa 2013). Nevertheless, the potential to contribute to the gene pool (reflected in varying reproductive development among individuals) may be relevant to understanding group reproductive output in cooperatively breeding primates, because biological parents' efforts are not the sole contributors to infant survival. The factors that describe the social mating system of each group have not been explored in relation to offspring survival, but they could clarify why all adults do not contribute equally to group reproductive output (Garber 1997). These factors can be classified into two broad areas: demographic factors such as age and sex, and the biological factors that could predispose a particular group of individuals to have a greater influence on group reproductive output.

Demographic Factors

The relationship between group reproductive output and demography has been explored in a few callitrichine species with field data from long-term studies. The mean number of infant *Saguinus mystax* that survived to become juveniles was significantly positively correlated with the number of adult male helpers in a group (Garber *et al.* 1984). A follow-up to this study showed that groups with one adult male had one-third the number of dependent offspring of groups with three or more adult males, independent of group size (Garber 1997). A review of research on wild *Callithrix jacchus* found that the number of juveniles was significantly correlated only with the number of adult males among all age–sex classes (Koenig 1995). In a large dataset on *Leontopithecus rosalia*, groups with two adult nonnatal males had more offspring than those with only one such male (Baker *et al.* 1993). In the same population, a more recent analysis showed that in young groups (formed for ≤3 yr), both the number of helpers and adult males were positively correlated with the number of surviving infants, but that in established groups (formed for >3 yr), only the number of helpers correlated with group reproductive output (Bales *et al.* 2000). Here, alloparents were classified in two ways: 1) as "helpers," defined as all individuals >18 mo of age other than the reproductive pair and reproductive subordinate females and 2) "adult males," both breeding and nonbreeding (Garber 1997; as with Garber *et al.* 1984; Koenig 1995). Finally, neither infant nor juvenile numbers were correlated with the number of adult males in a group in an analysis of 21 group-years of *Cebuella pygmaea*; however, juvenile (and not infant) numbers were strongly positively correlated with group size, i.e., the number of adult and subadult group members (Heymann and Soini 1999; Soini 1988).

These studies indicate that more than any other factor, the number of adult males in a group are correlated with increased callitrichine group reproductive output, although in some cases, group size, and numbers of helpers can have similar effects (Heymann 2000; Koenig 1995). However, there are many reasons unrelated to offspring survival why a group might vary in the number of males it contains (Carnes *et al.* 2011; Heymann 2000; Kappeler 2000; Ridley 1986). For instance, the number of adult males in a group has been proposed to increase with shorter breeding seasons (Ridley 1986), since a single male probably cannot successfully monopolize multiple reproductively synchronized females (Carnes *et al.* 2011; Dunbar 2000). However, it has also been suggested that primate males simply "go where females are" (Altmann 1990). Cross-species analyses that control for phylogeny show that these theories are not necessarily exclusive: the number of males is tightly positively correlated with the number of females in primate groups across species (Mitani *et al.* 1996), but either overlap or synchrony of female breeding can predict adult male numbers after female numbers are controlled for (Nunn 1999). Other theories for larger numbers of males in groups include heightened predation risk (Savage *et al.* 1996; van Schaik and Hörstermann 1994) or, as with callitrichids, the necessity for alloparents owing to the high costs of caring for twin infants (Heymann 2000; Tardif 1994, 1997). With the exception of *Callimico*, the number of adult males is positively correlated with litter mass gain and daily path length among callitrichids, implying that adult males are necessary to counter the increased costs of infant care (Heymann 2000). This conclusion was recently supported by an extensive cross-genera analysis of the effect of infant care costs on variation in reproductive behaviors (Díaz-Muñoz 2015), which identified genus *Saguinus* (which previously included all members of the genus *Leontocebus*) as facing the highest infant care costs among all callitrichine genera.

One way to reduce infant care costs among callitrichids is to minimize the number of breeding females in a group in order to keep the number of offspring to a minimum of one set of twins. Several cases of maternal infanticide have been reported for some tamarin species (Bezerra *et al.* 2007; Culot *et al.* 2011; Digby 1995; Tirado Herrera *et al.* 2000), largely in the case of multiple breeding females reproducing in a single group, such as in *Callithrix jacchus*. Moreover, an analysis of *Saguinus mystax* also found that infants were four times as likely to die before reaching the age of 3 mo in groups with two breeding females rather than one (Culot *et al.* 2011).

Studies that have modeled the predictors of group reproductive output in callitrichids, rather than conducting correlation analyses, have shown further factors at play, but there is significant variation between species. For example, a model of the effect of maternal factors on female reproductive output among *Leontopithecus rosalia* showed that female body mass predicted female reproductive output for litters in the first of two birth seasons in a year, whereas the number of helpers (as defined in Bales *et al.* 2000) explained offspring numbers in the second birth season (Bales *et al.* 2001). In this study, mothers with increased helpers carried infants less and were thus in better body condition for the second pregnancy in the year. Among *Saguinus mystax* observed from 1999 to 2008, the number of male helpers, and not female factors per se, significantly affected infant survival to 3 mo (Culot *et al.* 2011). One-third fewer infants survived when two vs. three males were present in the group, and infants died significantly more often when a median of 2.5, rather than three, males were present.

Critical to such analyses are two factors: 1) the nonrandom distribution of group sizes within a study population, and 2) differing effect sizes of studies that confound direct comparisons between them. For example, in a 13-yr. study of Weddell's saddleback tamarins (*Leontocebus weddelli*, formerly *Saguinus fuscicollis weddelli*: Buckner *et al.* 2015; Matauschek *et al.* 2010), 25% (12/47) of groups had one male, 68% (32/47) of groups had two adult males, while only 5% (2/47) had three males, and 2% (1/47) had four males (Goldizen *et al.* 1996). Here, group sizes were not evenly distributed across the population, which could then bias a correlational analysis of the number of adult males with group reproductive output. In a different analysis of group reproductive output across 6 studies on *Callithrix jacchus* spanning 16 groups, adult males were strongly correlated with number of infants, but the authors reported that independence of data could not be ensured, and that they could not consider uneven sampling or random variation between studies that could be achieved through a meta-analytical statistics (Koenig 1995). Subsequently, the large dataset on the demographics of *Leontopithecus rosalia* was analyzed with more powerful statistical methods that accounted for many of the abovementioned confounding factors; however, the focus of that analysis was on female factors, excluding the potential influences of individuals from other age–sex classes (particularly adult males) from the model (Bales *et al.* 2001).

Biological Factors

Callitrichids in the same age–sex class often show varying reproductive capabilities, or developmental classes, which might influence variation in group reproductive output. For example, several studies of both captive and wild populations have shown female reproductive suppression (Barrett *et al.* 1990; Beehner and Lu 2013; Ziegler *et al.* 1987). Among males, wild *Leontopithecus rosalia* showed reproductive suppression in 24 subordinate males unrelated to the dominant breeding male in 14 groups (Bales *et al.* 2006). Additionally, differences of up to 174% have been detected in testicular volumes of male *Saguinus mystax* from the same group (Garber *et al.* 1996), which suggests male reproductive skew. The loose correlation between physical maturity and participation in the mating system (Ginther *et al.* 2001; Ziegler *et al.* 1987) can alter demography, such as delayed dispersal of individuals from natal groups, which has been documented in the wild (Garber *et al.* 2015; Goldizen and Terborgh 1989).

Reproductive status has been assessed using testosterone, estradiol, and prolactin assays among callitrichids in captivity (Ziegler *et al.* 1993) and in the wild (Bales *et al.* 2006; French *et al.* 2003; Löttker *et al.* 2004). However, wild studies are challenged by the inability to collect blood for peptide hormones or adequate numbers of fecal samples from known individuals across multiple ovarian cycles and breeding seasons (Löttker *et al.* 2004). For example, testosterone levels among wild *Saguinus mystax* varied too widely during maturation to reliably indicate reproductive development (Huck *et al.* 2005b). In *Leontopithecus rosalia*, however, androgen levels differed among subordinate males unrelated to the dominant male, and age class had no effect on hormone profiles, suggesting that reproductive capability as reflected by hormone levels was sensitive to group demography but not affected by age class (Bales *et al.* 2006).

Another means to evaluate reproductive development is to assess dominance status in a group, often defined based on behavioral observations. Among females, reproductive dominance has been assessed based on observed mating with breeding males (marmosets: Sousa *et al.* 2005), participation in infanticide and aggression (Bezerra *et al.* 2007; Digby and Saltzman 2009), and simply via age effects, i.e., the oldest female is the breeding female (moustached tamarins: Garber 1997). Among males, since assessments of androgen levels can be inconsistent in some cases (Huck *et al.* 2005b), some researchers have used agonistic interactions to identify a dominant male (Baker *et al.* 1993).

Given these complexities, it is difficult to standardize differentiation of reproductive potential between individuals, particularly in light of species, demographic and site-specific variation. Since all individuals in an age–sex class cannot be assumed to possess similar reproductive potential, it is critical that developmental class, and not only age class, be assessed for possible impacts on group reproductive output. This has been evaluated in callitrichids through measurements of their genitalia (Soini and de

Soini 1990) and scent-gland morphology, which may be representative of an animal's ability to reproduce (French and Cleveland 1984; Moreira *et al.* 2015; Watsa 2013; Zeller *et al.* 1988).

Study Outline

We hypothesized that adult males were critical to group reproductive output while high adult female numbers could negatively affect group reproductive success. Therefore, we predicted that the number of adult males would be significantly positively correlated with group reproductive output across studies on wild callitrichids and high numbers of adult females would have a negative effect on group reproductive output across these studies. To test these predictions, we used a compilation of all published studies on wild callitrichids that provide data on the numbers of individuals in each age–sex class and the numbers of surviving offspring per year. We used meta-analyses to estimate the magnitude of correlations between age–sex classes and group reproductive output across studies (Scheiner and Gurevitch 2001).

We also address two questions regarding development classes and group reproductive output: First, which developmental classes predict whether a group has offspring? Second, which developmental classes predict the number of surviving offspring (zero to three) in a group? To answer these questions, we used a dataset from a 6-yr. study on *Leontocebus weddelli* and *Saguinus imperator* in southeastern Peru, which included group compositions by sex-based developmental classes and the numbers of surviving offspring each year. We used multiple morphological measures of genitalia and scent glands collected via a mark-recapture program to assign individuals to one of three developmental classes independent of age—primary, secondary, and nonbreeders—reflecting their potential to participate in the social mating system of a group.

Methods

Group Reproductive Output in the Literature Review

We used Google Scholar and Scopus to conduct a literature review for published information on demographics and group reproductive output in wild callitrichid populations. We compiled a dataset from 17 studies published from 1976 to 2015 on wild populations of *Saguinus* spp.: *Saguinus geoffroyi*, *S. mystax*, *S. weddelli*, *S. nigrifrons*, *S. illigeri* (now *Leontocebus weddelli*, *L. nigrifrons*, *L. illigeri*: Buckner *et al.* 2015; Matauschek *et al.* 2010), *S. tripartitus*, *S. imperator*, and *S. oedipus*; *Leontopithecus caissara*; *Cebuella pygmaea* and *Callithrix jacchus*. We included studies only if they reported raw numbers of individuals per age–sex class and group reproductive output for a minimum of five group-years (Electronic Supplementary Material [ESM] Appendix 2). For the meta-analysis of the effects of the numbers of adult males on group reproductive output, we included an additional study ($N = 16$) on *Leontopithecus rosalia* by Bales *et al.* (2000) by calculating the effect size from the sample size and Spearman's rank correlations presented in the study. To combine data from multiple studies, we used a Spearman's rank correlation weighted by the number of group-years in the study as a standardized effect size. In this dataset, groups (within a study) and species (across multiple studies) were subject to repeated sampling over time, resulting in pseudoreplication. To address this problem of inflated samples size, we use a more conservative significance level of $P < 0.01$ for the meta-analyses (see Gurevitch *et al.* 1992; Poulin 1994 for detailed explanation of this reasoning). To control for interspecific differences, we added species as a moderator variable in a mixed effect meta-analysis of the dataset. Species did not have a significant effect so we removed it and proceeded with a random effects meta-analysis that does not assume equal effect sizes across studies.

Study Site and Subjects

We studied 21 groups of free-ranging *Leontocebus weddelli* and *Saguinus imperator* at the Estación Biológica Río Los Amigos (12°34′S 70°05′W) in the Madre de Dios Department of southeast Perú from May to August annually across 6 yrs. (2010–2015). We used a mark-recapture program (detailed protocol in Watsa *et al.* 2015) and captured 106 *L. weddelli* and 60 *S. imperator* with a mean of 61 captures per year (range: 42–74), for a total of 331 captures. At capture, infants were 4–7 mo old, based on their facial pelage and dentition, and we tagged them along with the adults using individually distinct beaded collars. We fitted the largest suspected breeding female in each group with a radio collar to facilitate tracking as a part of a larger behavioral study. We followed groups of both species for a mean of 425 h (range: 116–1135 h) each season (May to August) (2127 h across the 6-yr. period) and recorded a total of 143 copulations by 33 males. We could identify all individuals in the study population and censused groups at least twice a month for group composition, noting changes due to immigration, emigration, birth, and death.

Assigning Developmental Class

We used three developmental classes—primary breeders, secondary breeders, and nonbreeders—classified according to the following criteria. A female was a primary breeder if she had a nipple length of >3 mm for *Leontocebus weddelli* or >4 mm for *Saguinus imperator* (Soini and de Soini 1990; Watsa 2013), which indicated that she was parous, regardless of whether multiple adult females or infants were present in the group. We considered males that we observed copulating to be primary breeding males. We identified known secondary breeding individuals as group-members who were born in the previous census year, 1–2 yr. old and sexually mature, but had not yet bred. Thus, groups could consist of primary or secondary breeders of both sexes, as well as any nonbreeding offspring born in that year. Based on these criteria, we identified a subset of individuals of known reproductive developmental class to validate our models to predict reproductive developmental class in other animals.

Like other callitrichids, both study species at Los Amigos twinned frequently and formed groups with multiple breeding females (Garber *et al.* 2015; Watsa 2013). Although these species diverged *ca.* 9.10–10.07 mya and are now placed in separate genera (Buckner *et al.* 2015; Matauschek *et al.* 2010), we found no significant differences between them in mean group size, adult group sex ratios, or mean group reproductive output. Thus, we pooled data from both species for this study.

During capture, we recorded body mass and length and width of genitalia and suprapubic glands to formulate indices of developmental class as follows: vulvar index (length + width), suprapubic gland area (length × width), mean nipple length, and testicular volume (a semispherical estimate of one testicle) (Garber *et al.* 1996; Soini and de Soini 1990). In eight captures, we failed to record a measurement (not always the same one). In these instances, we replaced the missing values with the mean value for the measurement in that developmental class, if known ($N = 4$), or in that age class, if not ($N = 4$). We analyzed males and females separately for each species, and for each group, we mean-centred and scaled all measurements and indices by the standard deviation for use in a principal components analysis (PCA: FactoMiner package in R; Beehner and Lu 2013). Using the individual coordinate values from the first two principal components we conducted a linear discriminant function analysis (LDA) and then used the function to predict the developmental class (either primary breeding, secondary breeding, or nonbreeding) of all individual of uncertain breeding status. Across the study period, we resampled individuals one to four times, with 52% captured at least twice. To avoid pseudoreplication, we used mean individual component scores across years for individuals with known developmental status to train the LDA functions. We checked each species–sex class for normality (q–q normal plots), linear relationships (linear regression), and homoscedasticity between developmental categories (Bartlett's test of homogeneity of variance, $P > 0.05$). We omitted infant males of both species from the LDA due to limited variance causing heteroscedasticity; but since they were <7 mo old, this exclusion had no impact on adult and subadult male classifications. We calculated the percentage of known individuals that were correctly classified by our PCA–LDA model, and used a MANOVA (manova: MASS package in R; Venables and Ripley 2002) to test the null hypothesis that predicted developmental classes were indistinguishable based on individual component scores. We used R v.3.2.2 (R Development Core Team 2015) for all statistical analyses.

Group Reproductive Output in the Los Amigos Dataset

We constructed a mixed-effect logistic regression model with a binomial error structure and a logit link function to predict a binary response variable: offspring presence or absence based on proportions of individuals of each developmental class as fixed factors. As per Bales *et al.* (2001) we also built generalized linear mixed models (GLMMs: lme4 in R [Bates *et al.* 2014]) with a Poisson error structure, response variable of group reproductive output (ranging from zero to three), and proportions of individuals per developmental class as fixed factors. We used saturated fixed-effect models to optimize random structures, and incorporated group identity, species, and year as needed to ensure independence of data points across all models. We ran correlation analyses on all pairwise combinations of explanatory variables and removed redundant fixed factors. We plotted each explanatory variable against the response variable to ensure that there were no nonlinear relationships. We established minimal models using Akaike Information Criterion (Akaike 1994) by backwards non-significant term deletion, retaining terms only if they reduced criteria by two units (Moreno *et al.* 2013). We confirmed minimal models by calculating a likelihood ratio, which compares the difference in log-likelihoods of nested models with a Chi-square distribution. We plotted the residuals of best fit models to ensure that they were randomly distributed around zero. We inferred the relative influence of each breeding class based on the outcome of model selection.

Ethical Note

This study follows the Animal Behaviour Society Guidelines (Rollin and Kessel 2006) and American Society of Mammalogists' Guidelines on wild mammals in research (Sikes and Gannon 2011). The study is part of an ongoing, long-term annual capture-and-release program that began at this site in 2009. In brief, we captured entire groups at baited compartment traps to which they are habituated, and processed and released them on the same day to minimize disruption and discomfort to the subjects. We use a two-step chemical restraint method that has improved recapture rates in comparison to established methods (Savage *et al.* 1993), virtually eliminates capture-related injuries, and has no visible effect on habituation (see Watsa *et al.* 2015 for protocol comparisons). Radio collars placed on the groups will be removed at the end of this study, and are replaced annually on the largest breeding female in each group.

The Peruvian Ministry of the Environment (SERFOR) granted annual research and collection permits, and the Animal Studies Committees of Washington University in St. Louis and the University of Missouri–St. Louis approved protocols.

Results

Meta-analyses of Group Reproductive Output

We found that 23% of group-years in the dataset compiled from past studies contained three or more males, while most group-years considered (77% of 239 group-years) contained two or fewer males. Even the largest dataset available to us, a study at Cocha Cashu on Weddell's saddleback tamarins or *Saguinus fuscicollis* (now *Leontocebus weddelli*) (Goldizen *et al.* 1996), was biased toward groups with one or two males (91%, or 43 of 47 group-years), with groups of three or more males present much less frequently (9%, or 4 group-years). Large confidence intervals are due to the rarity of documenting groups with high numbers of individuals of a particular age–sex class. Overlapping confidence intervals confounded the use of mean group reproductive output as an effective means of comparison across age–sex classes (Fig. 1).

A random-effects meta-analysis combining data from published studies and the present study revealed significant correlations between the number of adult females and group reproductive output (weighted mean r_s (16) = 0.185, $P < 0.028$), and between group size and group reproductive output (weighted mean r_s (17) = 0.252, $P < 0.003$) (Fig. 2). The numbers of adult males (weighted mean r_s (17) = 0.147, $P < 0.150$) and subadults of either sex (females: weighted mean r_s (14) = 0.058, $P < 0.579$; males: weighted mean r_s (16) = 0.076, $P < 0.484$) were not significantly correlated with group reproductive output across studies. These results remain unchanged when we excluded our study from the analysis.

Study Group Demographics

We observed 21 groups across 63 group-years (40 group-years for *Leontocebus weddelli* and 23 group-years for *Saguinus imperator*) during which they could have reproduced, including 14 groups of *L. weddelli* sampled for a mean of

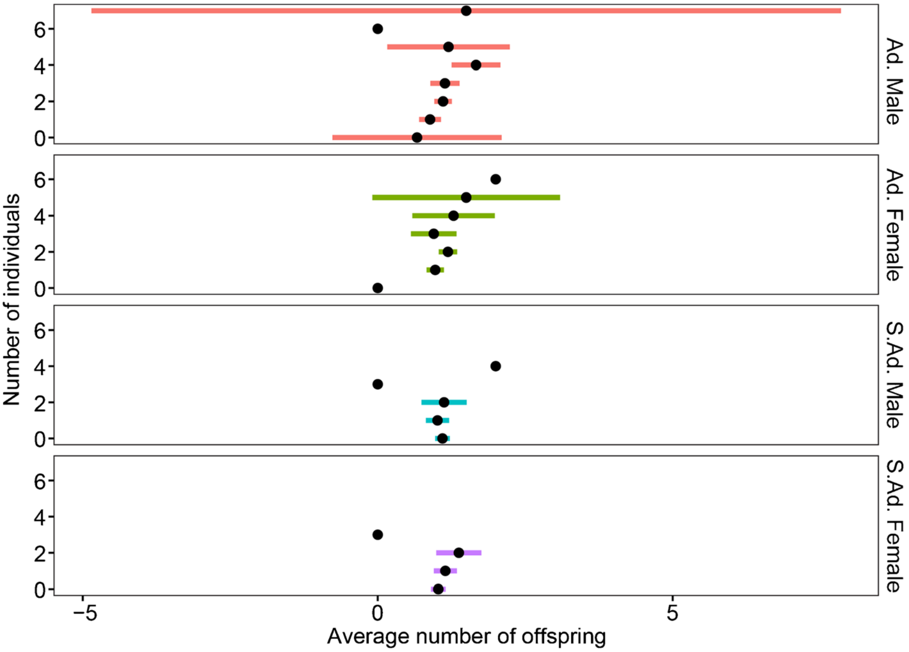
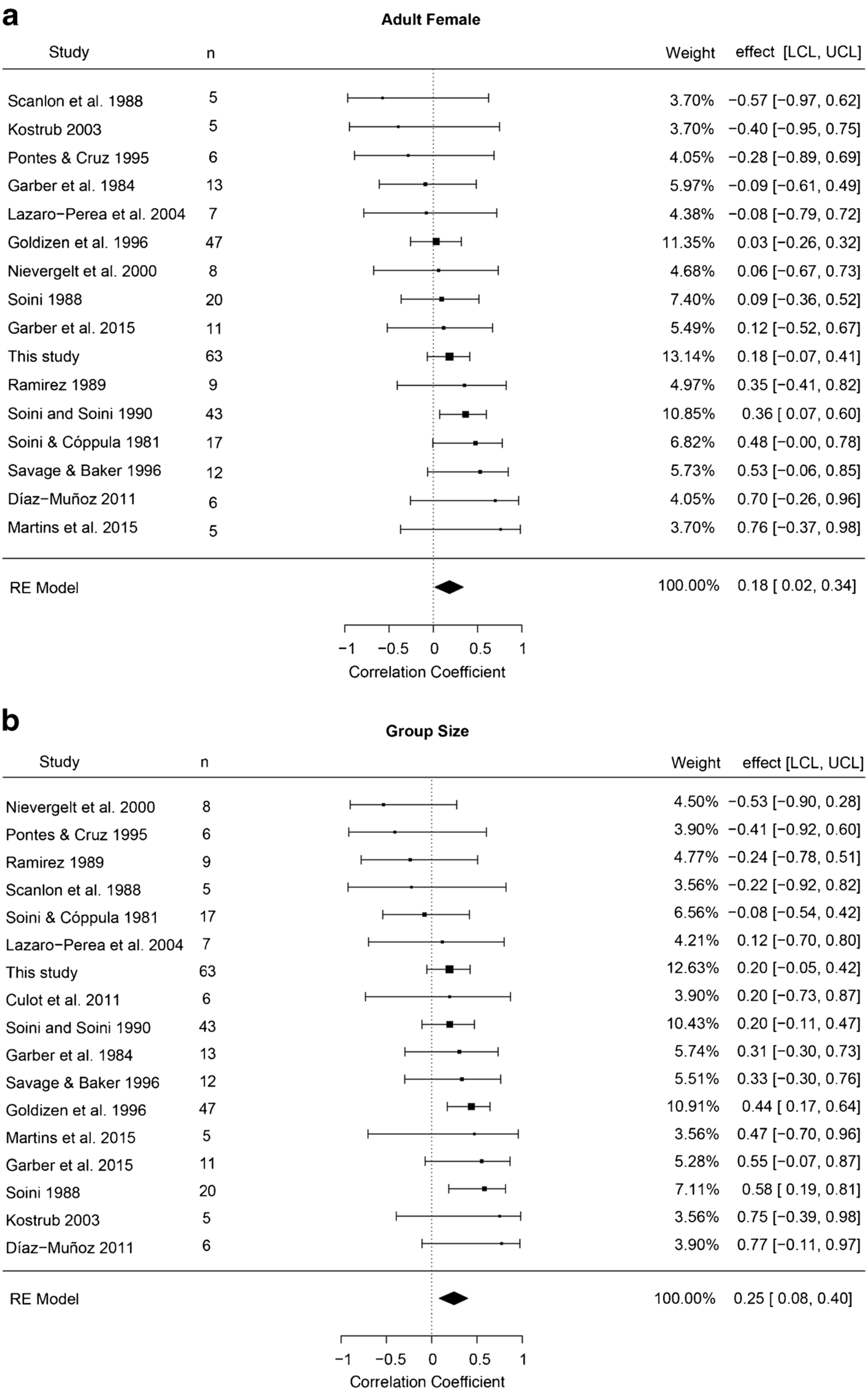


Fig. 1 Mean number of infants (dots), with 95% confidence intervals (lines) depending on the number of individuals from each age–sex class. The species represented in this dataset compiled from past studies are *Saguinus mystax* (Culot *et al*. 2011; Garber *et al*. 1984; Ramirez 1989; Soini and de Soini 1990), *S. weddelli* (Garber *et al*. 2015; Goldizen *et al*. 1996), *S. geoffroyi* (Díaz-Muñoz 2011), *Callithrix jacchus* (Lazaro-Perea *et al*. 2004; Nievergelt *et al*. 2000; Pontes and da Cruz 1995; Scanlon *et al*. 1988), *S. tripartitus* (Kostrub 2003), *S. oedipus* (Savage and Baker 1996), *S. fuscicollis illigeri* (Soini and Cóppula 1981), *Leontopithecus caissara* (Martins *et al*. 2015), and *Cebuella pygmaea* (Soini 1988; Heymann and Soini 1999).

2.9 ± SD 1.4 yrs. and 7 groups of *S. imperator* sampled for a mean of 3.4 ± SD 1.3 years. We found no significant difference between species in mean group sizes (Table I) (exact Wilcoxon Mann-Whitney test: $z = -1.067$, $P = 0.292$), mean adult group sex ratios (males:females) (*L. weddelli*: 1.23 ± SD 0.63; *S. imperator*: 1.65 ± SD 1.34) (Welch's two-sample *t*-test: $t = -0.979$, $P = 0.335$), and mean group reproductive outputs (Welch's two-sample *t*-test: $t = 0.300$, $P = 0.766$) (Table I). Of all captured individuals, 8.7% were infants, with one to two offspring per group and only one instance of three offspring in a single group. We also observed seven instances of two primary breeding females present in one group – four cases of *L. weddelli* and three of *S. imperator*.

Fig. 2 Forest plots with bars representing the 95% confidence interval around the correlation coefficient between group reproductive output and **(a)** number of adult females; **(b)** group size and **(c)** number of adult males, for each study in the dataset compiled from past studies. Data were compiled from *Saguinus mystax* (Culot *et al*. 2011; Garber *et al*. 1984; Ramirez 1989; Soini and de Soini 1990), *S. weddelli* (Garber *et al*. 2015; Goldizen *et al*. 1996), *S. geoffroyi* (Díaz-Muñoz 2011), *Callithrix jacchus* (Lazaro-Perea *et al*. 2004; Nievergelt *et al*. 2000; Pontes and da Cruz 1995; Scanlon *et al*. 1988), *S. tripartitus* (Kostrub 2003), *S. oedipus* (Savage and Baker 1996), *S. fuscicollis illigeri* (Soini and Cóppula 1981), *Leontopithecus caissara* (Martins *et al*. 2015), and *Cebuella pygmaea* (Soini 1988; Heymann and Soini 1999). LCL = lower confidence limit; UCL = upper confidence limit.

▶


a
Adult Female
Study
n
Weight
effect [LCL, UCL]
Scanlon et al. 1988 5 3.70% −0.57 [−0.97, 0.62]
Kostrub 2003 5 3.70% −0.40 [−0.95, 0.75]
Pontes & Cruz 1995 6 4.05% −0.28 [−0.89, 0.69]
Garber et al. 1984 13 5.97% −0.09 [−0.61, 0.49]
Lazaro−Perea et al. 2004 7 4.38% −0.08 [−0.79, 0.72]
Goldizen et al. 1996 47 11.35% 0.03 [−0.26, 0.32]
Nievergelt et al. 2000 8 4.68% 0.06 [−0.67, 0.73]
Soini 1988 20 7.40% 0.09 [−0.36, 0.52]
Garber et al. 2015 11 5.49% 0.12 [−0.52, 0.67]
This study 63 13.14% 0.18 [−0.07, 0.41]
Ramirez 1989 9 4.97% 0.35 [−0.41, 0.82]
Soini and Soini 1990 43 10.85% 0.36 [0.07, 0.60]
Soini & Cóppula 1981 17 6.82% 0.48 [−0.00, 0.78]
Savage & Baker 1996 12 5.73% 0.53 [−0.06, 0.85]
Díaz−Muñoz 2011 6 4.05% 0.70 [−0.26, 0.96]
Martins et al. 2015 5 3.70% 0.76 [−0.37, 0.98]
RE Model 100.00% 0.18 [0.02, 0.34]
−1
−0.5
0
0.5
1
Correlation Coefficient
b
Group Size
Study
n
Weight
effect [LCL, UCL]
Nievergelt et al. 2000 8 4.50% −0.53 [−0.90, 0.28]
Pontes & Cruz 1995 6 3.90% −0.41 [−0.92, 0.60]
Ramirez 1989 9 4.77% −0.24 [−0.78, 0.51]
Scanlon et al. 1988 5 3.56% −0.22 [−0.92, 0.82]
Soini & Cóppula 1981 17 6.56% −0.08 [−0.54, 0.42]
Lazaro−Perea et al. 2004 7 4.21% 0.12 [−0.70, 0.80]
This study 63 12.63% 0.20 [−0.05, 0.42]
Culot et al. 2011 6 3.90% 0.20 [−0.73, 0.87]
Soini and Soini 1990 43 10.43% 0.20 [−0.11, 0.47]
Garber et al. 1984 13 5.74% 0.31 [−0.30, 0.73]
Savage & Baker 1996 12 5.51% 0.33 [−0.30, 0.76]
Goldizen et al. 1996 47 10.91% 0.44 [0.17, 0.64]
Martins et al. 2015 5 3.56% 0.47 [−0.70, 0.96]
Garber et al. 2015 11 5.28% 0.55 [−0.07, 0.87]
Soini 1988 20 7.11% 0.58 [0.19, 0.81]
Kostrub 2003 5 3.56% 0.75 [−0.39, 0.98]
Díaz−Muñoz 2011 6 3.90% 0.77 [−0.11, 0.97]
RE Model 100.00% 0.25 [0.08, 0.40]
−1
−0.5
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1
Correlation Coefficient

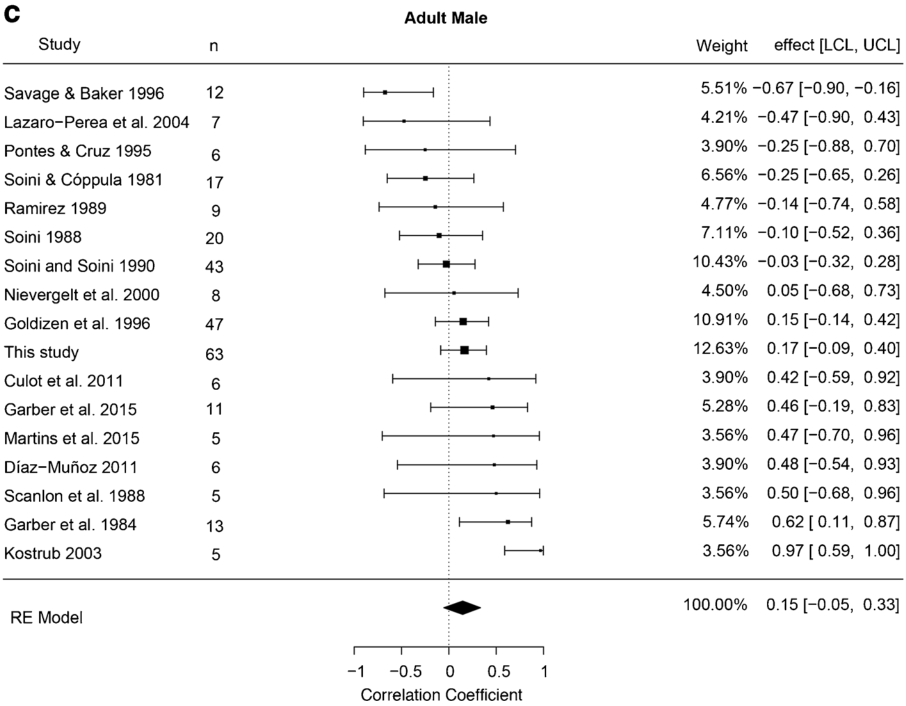

Fig. 2 (continued).

The Developmental Class Model

Our model satisfied the minimum requirements for factor analyses, with a mean of 19 samples per variable for the females and 23 for males. The first two dimensions represented a mean of 86% (range: 82–90%) of total group variation. For all species–sex classes, Principal Components Analysis dimension 1 was determined by all morphological variables and Principal Components Analysis dimension 2 was determined primarily by nipple length in females and suprapubic area and body mass in males (Tables SI and SII in ESM Appendix 1).

The LDA correctly assigned 98% of female *Leontocebus weddelli*, 100% of female *Saguinus imperator*, 77% of male *L. weddelli*, and 88% of male *S. imperator* of known developmental class (Fig. 3, Table II). The LDA mismatched one secondary breeding female to the nonbreeding class (*L. weddelli*), four primary breeding males as secondary breeding males, three secondary breeding males as primary breeding males (*L. weddelli*), and two primary breeding males as secondary breeding males (*S. imperator*). The LDA distinguished between developmental classes for females and males of both species (MANOVA $P < 0.0001$, Table III), and we calculated mean values and ranges of morphological variables per species-sex group (Table IV). We observed variation in developmental classes in all age classes except among infants in both species (Fig. 4).

Table I Group compositions based on developmental class

Species	N	Group Size	Primary Breeding Females	Secondary Breeding Females	Primary Breeding Males	Secondary Breeding Males	All Females	All Males	All Infants (nonbreeders)
Leontocebus weddelli	14	4.95 ± 1.63 (3–8)	0.95 ± 0.50 (0–2)	0.90 ± 0.78 (0–3)	1.40 ± 0.98 (0–3)	0.65 ± 0.74 (0–2)	1.88 ± 0.69 (1–4)	2.05 ± 0.90 (0–5)	1.03 ± 0.86 (0–3)
Saguinus imperator	7	5.21 ± 1.41 (3–8)	1.08 ± 0.41 (0–2)	0.67 ± 0.96 (0–3)	1.71 ± 1.23 (0–4)	0.63 ± 0.77 (0–2)	1.96 ± 1.00 (1–4)	2.33 ± 1.20 (0–6)	0.92 ± 0.88 (0–2)

All figures are provided as mean number of individuals ± standard deviation (range). *N* = Number of unique groups. We obtained all data from *Leontocebus weddelli* and *Saguinus imperator* studied at the Estación Biológica Río Los Amigos in Peru (2010–2015)

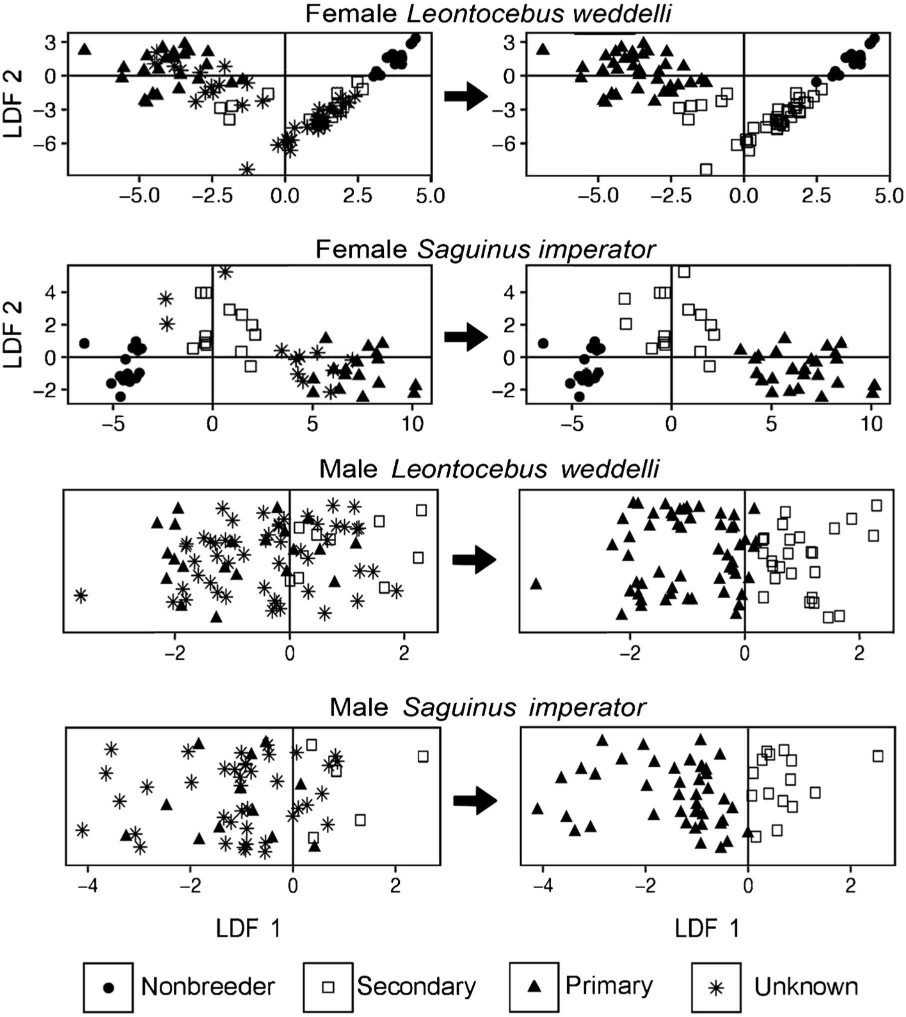

Fig. 3 Developmental class by species and sex before (left) and after (right) implementing the PCA–DFA assignment model and classifying all individuals of uncertain developmental class (star symbol) to a developmental class based on reproductive morphology and mass. Female categories are differentiated by discriminant functions 1 and 2 (DF1 and DF2), while primary breeding and secondary breeding males are differentiated by DF1 only. All data were obtained from *Leontocebus weddelli* and *Saguinus imperator* studied at the Estación Biológica Río Los Amigos in Peru (2010–2015).

Group Reproductive Output in the Los Amigos Dataset

We excluded the proportion of secondary breeding males (maximum likelihood logistic regression: $B = 0.395$, SE = 5.088, $\chi^2 = 0.006$, $P = 0.938$), which was the least significant factor in the saturated logistic model to predict presence of infants (group reproductive output either 0 or 1), from subsequent models. The minimal model selected after the elimination of this factor revealed that the proportion of primary breeding males, the proportion of primary breeding females, and group size were significant factors in predicting the presence of offspring in a group (Table V). The

Table II Sample sizes of developmental classes before and after the Linear Discriminant Functional Analysis model was applied

	Known developmental class	Full dataset	% correctly classified by LDA (%)	Known developmental class	Full dataset	% correctly classified by LDA (%)
	Leontocebus weddelli			*Saguinus imperator*		
Primary breeding females	24	36	100	17	26	100
Secondary breeding females	17	41	94	12	15	100
Nonbreeding females	18	19	100	17	17	100
Primary breeding males	21	55	81	12	42	83
Secondary breeding males	9	26	67	5	15	100
Nonbreeding males	28	28	NA	11	11	NA

We obtained all data from *Leontocebus weddelli* and *Saguinus imperator* studied at the Estación Biológica Río Los Amigos in Peru (2010–2015)

mean proportion of primary breeding males in groups with no offspring (0.27 ± SD 0.23, $N = 22$) was significantly lower than in groups with one or more offspring (0.41 ± SD 0.23, $N = 41$) (exact Wilcoxon–Mann–Whitney test: $z = -2.351$, $P = 0.018$), a but this was not the case for the proportion of primary breeding females ($z = -1.919$, $P = 0.054$) or group size ($z = -1.817$, $P = 0.068$) (Fig. 5).

A GLMM with offspring number as a discrete numerical response variable revealed that the proportion of secondary breeding males ($B = -0.131$, SE = 2.265, $\chi^2 = 0.003$, $P = 0.954$) was the least significant factor in the saturated model. After eliminating this factor, the GLMM indicated that the proportion of primary breeding females in a group ($B = 3.559$, SE = 0.962, $\chi^2 = 13.69$, $P < 0.001$) and group size ($B = 0.343$, SE = 0.128, $\chi^2 = 7.15$, $P = 0.008$) were the only two significant factors predicting group reproductive output. Removing the seven group-years in which there were multiple primary breeding females in a group did not alter the outcome of this GLMM.

Table III For each sex in both species, a MANOVA of the principal components of the LDA shows significant clustering of the three breeding classes: primary breeders, secondary breeders, and nonbreeders

Species–sex class	Wilks' λ	F	df	*P*-value
Female *Leontocebus weddelli*	0.0461	82.35	2	<0.0001
Female *Saguinus imperator*	00348	56.67	2	<0.0001
Male *Leontocebus weddelli*	0.3722	43.29	1	<0.0001
Male *Saguinus imperator*	0.4756	19.48	1	<0.0001

Female assessment included all three developmental classes (df = 2), and males included two (df = 1); nonbreeders were excluded. We obtained all data from *Leontocebus weddelli* and *Saguinus imperator* studied at the Estación Biológica Río Los Amigos in Peru (2010–2015)

Table IV Morphological variables by developmental class

Sex and species	Developmental class	Nipple length (mm)	Suprapubic area (mm^2)	Vulva index (mm) or Testes volume (mm^3)	Mass (g)	Number of samples	Number of unique individuals
Female *Leontocebus weddelli*	Nonbreeder	0.00	22.30 ± 32.52 (0.00–104.28)	10.98 ± 2.05 (7.90–16.15)	230 ± 47.55 (135–330)	19	14
	Secondary breeder	0.24 ± 0.58 (0.00–1.91)	251.27 ± 101.29 (75.36–483.48)	19.11 ± 3.26 (13.50–28.10)	394.59 ± 34.08 (305–475)	41	29
	Primary breeder	3.41 ± 0.79 (2.15–5.60)	276.32 ± 86.21 (103.14–522.21)	21.74 ± 2.52 (17.40–29.40)	401.11 ± 31.96 (340–490)	36	21
Male *Leontocebus weddelli*	Nonbreeder	NA	8.09 ± 22.05 (0.00–101.99)	106.37 ± 45.48 (42.60–243.39)	219.82 ± 34.52 (160–285)	28	27
	Secondary breeder	NA	83.25 ± 49.00 (0.00–174.03)	671.33 ± 146.03 (321.88–953.17)	363.15 ± 24.94 (310–430)	26	21
	Primary breeder	NA	148.54 ± 69.11 (0.00–323.22)	1029.13 ± 248.34 (579.83–1986.27)	396.91 ± 23.52 (350–460)	55	30
Female *Saguinus imperator*	Nonbreeder	0	0.79 ± 3.25 (0.00–13.41)	12.64 ± 3.72 (0.00–16.55)	318.24 ± 73.06 (200–460)	17	11
	Secondary breeder	1.21 ± 1.00 (0.00–3.000)	151.51 ± 88.09 (0.00–295.22)	20.67 ± 2.95 (13.38–24.70)	518.33 ± 43.33 (455–595)	15	12
	Primary breeder	5.15 ± 0.94 (3.65–7.45)	232.02 ± 67.37 (91.08–364.00)	25.59 ± 3.55 (19.88–32.65)	572.50 ± 52.20 (465–645)	26	10
Male *Saguinus imperator*	Nonbreeder	NA	0	122.06 ± 36.82 (56.16–175.11)	258.18 ± 51.73 (150–320)	11	11
	Secondary breeder	NA	15.43 ± 35.45 (0.00–122.20)	518.24 ± 104.06 (298.30–722.06)	453.93 ± 42.46 (360–520)	15	13
	Primary breeder	NA	69.51 ± 90.96 (0.00–300.83)	832.76 ± 189.08 (417.14–1150.34)	517.02 ± 52.66 (420–645)	42	18

All values are expressed as mean ± SD (range). The vulvar index is provided for females and testes volume for males. We obtained all data from *Leontocebus weddelli* and *Saguinus imperator* studied at the Estación Biológica Río Los Amigos in Peru (2010–2015)

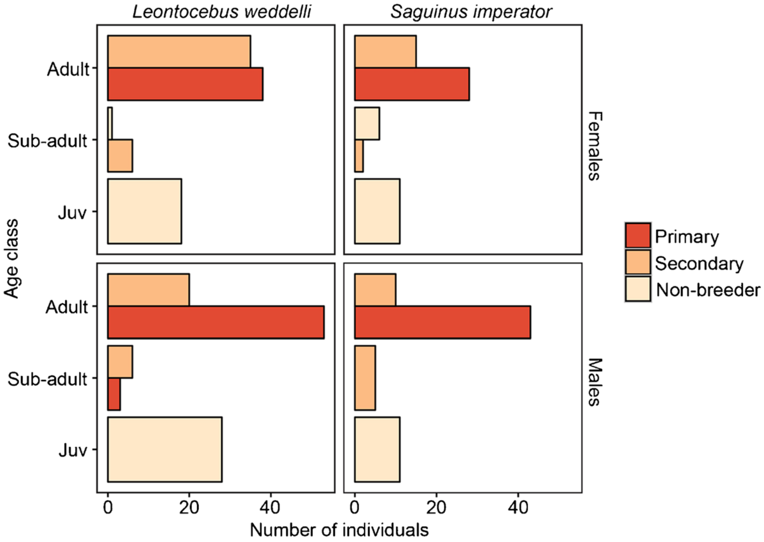

Fig. 4 The distribution of developmental classes (primary breeder, secondary breeder, and nonbreeder) between age classes (adult, subadult, and juvenile) for males and females of both *Leontocebus weddelli* and *Saguinus imperator* at the Estación Biológica Río Los Amigos in Peru (2010–2015).

Discussion

We showed that adult male numbers are unequally distributed over groups in the dataset compiled from past studies, which means that correlational studies between group reproductive output and adult male numbers may be biased by the rarity of observing groups with high numbers of males. A meta-analysis revealed that adult males were not correlated with group reproductive output, but that adult females and group size play a significant role in this respect. By exploring in greater detail similar data at a long-term field site on two callitrichine species, we created a model based on morphology to assign developmental class to the animals in this population. When we included the proportions of individuals in various developmental classes in logistic models of group reproductive output and the proportion of various classes of adults and subadults in a group, we found that primary breeding males, primary breeding females and group size, were the strongest predictors of the presence of weaned infants, but only primary breeding females and group size predicted the number of offspring that survived to weaning.

Our developmental class model assigned females more reliably to the correct class than males, likely owing to the availability of better external indicators of developmental class in females, such as observed nursing and nipple lengths (Soini and de Soini 1990). Higher resolution of male developmental class would require the inclusion of all or most copulation records, which is not feasible as copulation is cryptic in arboreal primates (Campbell 2006) and short (1–12 s) in tamarins (Watsa 2013). Nevertheless, our model successfully discriminated between developmental categories for all sex classes, and revealed that animals in particular age–sex classes have different reproductive capabilities. This method allowed us to reexamine how group composition influences group reproductive output, by discriminating based on developmental class, in addition to age–sex class.

Table V Results of a) Maximum likelihood logistic regression examining the effects of the proportions of primary breeding females, primary breeding males, secondary breeding females, group size, and species on the presence or absence of infants in a group and b) a generalized linear mixed-model examining the effects of the proportions of primary breeding males and females, secondary breeding females, group size, and species on group reproductive output among saddleback and emperor tamarins in Peru

Factor	Estimate	SE	χ^2	*P*
a: Logistic regression	AIC = 58.887, df = 57			
Intercept	−18.675	9.322		
Primary breeding females	31.619	17.222	22.204	**<0.001**
Primary breeding males	4.376	1.942	6.037	**0.014**
Secondary breeding females	2.116	2.934	0.543	0.461
Group size	2.418	1.264	15.340	**<0.001**
Species	−1.215	0.798	2.483	0.115
Minimal model	AIC = 58.532, df = 59			
Intercept	−17.590	8.959		
Primary breeding females	29.765	16.455	23.529	**<0.001**
Primary breeding males	3.248	1.507	5.297	**0.021**
Group size	2.336	1.177	14.444	**<0.001**
b: GLMM	AIC = 151.45, df = 57			
Intercept	−3.033	0.993		
Primary breeding females	4.139	1.247	10.756	**0.001**
Primary breeding males	1.156	0.749	2.559	0.110
Secondary breeding females	0.533	1.137	0.219	0.640
Group size	0.331	0.128	6.612	**0.010**
Species	−0.177	0.269	0.439	0.508
Minimal model	AIC = 148.77, df = 60			
Intercept	−2.443	0.763		
Primary breeding females	3.559	0.962	13.339	**<0.001**
Group size	0.343	0.128	7.090	**0.008**

The minimal models include only factors with significant effects on the response variables ($\alpha = 0.05$). Significant *P*-values are in bold. AIC = Akaike Information Criterion (Akaike 1994); GLMM = general linear mixed model. We obtained all data from *Leontocebus weddelli* and *Saguinus imperator* studied at the Estación Biológica Río Los Amigos in Peru (2010–2015)

The meta-analysis did not support the prediction that the number of males would positively influence group reproductive output across the Callitrichidae. Instead, group size and the number of adult females were positively correlated with group reproductive output across five callitrichine genera for which data were available. This does not necessarily imply that adult males have a negligible effect on infant survival. Our meta-analysis was restricted to correlations with the number of infants in a group, but logistic regression based on the Los Amigos dataset showed that groups with high proportions of primary breeding adult males are most likely to have one or more infants present. This finding supports a study of factors explaining infant survival to three months of age in *Saguinus mystax*

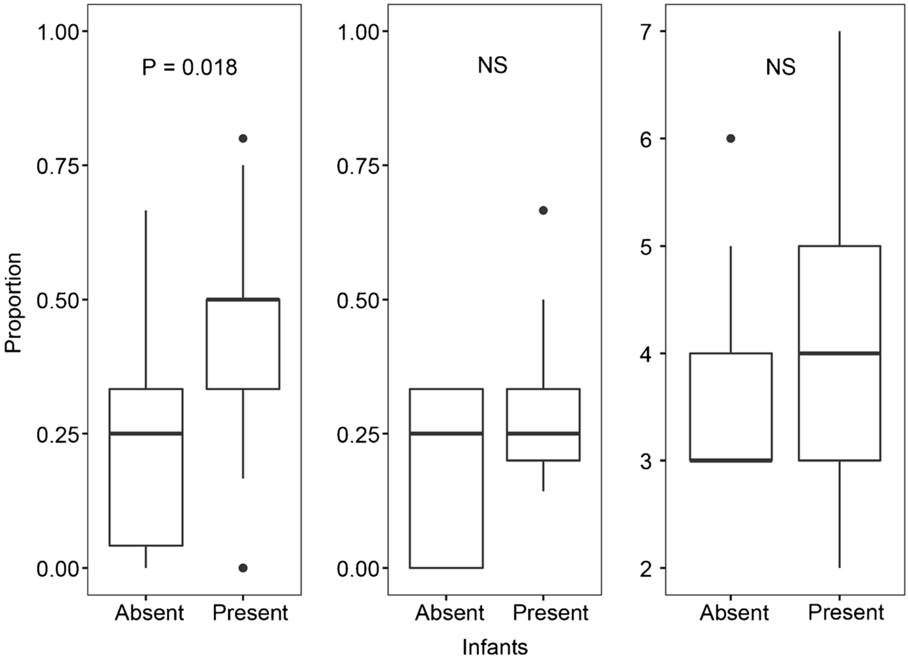

Fig. 5 Boxplots of the proportion of primary breeding males, proportion of primary breeding females, and group size compared across group-years when infants were either absent or present. The mean proportion of breeding males, unlike the proportion of primary breeding females and group size, was significantly higher when infants were present than absent (exact Wilcoxon–Mann–Whitney test). All data were obtained from *Leontocebus weddelli* and *Saguinus imperator* studied at the Estación Biológica Río Los Amigos in Peru (2010–2015). Dark lines indicate median values, boxes indicate the interquartile range (IQR) between the first and third quartiles, dots indicate outliers (3 × IQR above the third quartile or below the first quartile), and ns = nonsignificant difference ($P > 0.05$) between group size in the presence or absence of infants.

using similar methodology (Culot *et al.* 2011). These results show that males influence the likelihood that infants are present in a group, but are not indicative of higher group reproductive output per se among these callitrichids.

Although females are not usually identified as playing a significant role in determining group reproductive output, a study of the most comprehensive dataset on a wild callitrichine population to date (*Leontopithecus rosalia* from Poço das Antas Reserve in Brazil) did highlight the importance of many female factors to reproductive success (Bales *et al.* 2001). Our analyses indicate that, after controlling for group size, the proportion of primary breeding adult females in a group is the chief determinant of group reproductive output. Our results remained the same even when seven instances of multiple primary breeding females in a single group were excluded from the analysis. Thus we consider the circumstances under which the proportion of primary breeding adult females could contribute to increased group reproductive output, given numerous observations of adults and subadults of both sexes actively participating in alloparenting (Erb and Porter 2017). We posit three possible scenarios for high proportions of primary breeding adult females in a group: 1) a single primary breeding female present in a relatively small group, 2) multiple primary breeding females present in a relatively small group, or 3) multiple primary breeding females present in an average-sized group.

In the first scenario, a single primary breeding female forms a large proportion of a small group and remains reproductively dominant, without any female challengers. The proportion of primary breeding females would be maximized at 0.5 if only one primary breeding adult male comprised the rest of the group. A recent review of a range of wild tamarin studies (*N* = 183 groups and an additional 66 resampled cases) reported this group composition in only 9.4% of cases, and these single breeding pairs invariably failed to raise infants in the wild (Garber *et al.* 2015). Before our study, there was only one reported exception to this trend, in *Saguinus imperator* at Cocha Cashu (Windfelder 2000). However, we report mixed reproductive success from our smallest groups, i.e., those that contained a single pair of primary breeding adults and one secondary breeding subadult. In three cases of *Leontocebus weddelli* and one of *Saguinus imperator* there were no living infants at the time of evaluation, either because the female did not give birth or the male–female pair was unable to raise offspring to the age of weaning. In contrast, we observed two groups of *L. weddelli* where one infant survived successfully to weaning age. In one of these groups, this occurred in two consecutive years, and the infant from the first year was still present in the second year as a secondary breeding subadult. Thus, of seven group-years of a single pair of primary breeding adults, we observed a *ca.* 43% success rate in raising infants to weaning, which is more common than in the remaining callitrichine data.

In scenarios 2 and 3, multiple primary breeding adult females coexist in a single group of small or average size and could enhance infant survival in several ways. If only one female breeds successfully, i.e., there is high female reproductive skew, then the second female can enhance infant survival indirectly by increasing vigilance and foraging efficiency, or directly by alloparenting in an equivalent manner to a primary or secondary male breeder. This in turn could be beneficial to this second female in a variety of ways (parenting experience, future reproductive opportunities, or via kin selection if she is the breeder's sibling or close relative) (Erb and Porter 2017). In a study of 12 groups of *Leontocebus weddelli* in Bolivia (Garber *et al.* 2015), 25% of the groups contained two parous females (determined by nipple length), and the majority of these pairs were genetically verified to be likely mother–daughter pairs. Unfortunately, none of the groups contained infants at the time of assessment, so whether both females bred simultaneously is unknown. In the longest running study to date on *L. weddelli*, spanning 13 years at Cocha Cashu, female reproductive skew was high, with a suspected 50% of females never breeding (Goldizen *et al.* 1996), although how the reproduction of these females was limited is not known precisely. However, a broader review of all callitrichine studies to date (Garber *et al.* 2015) reveals that groups with multiparous females see low frequencies (6.3% or 18 of 287 group-years) of both females breeding in tamarins (genera *Saguinus* and *Leontopithecus*) but a higher tendency for this to occur (41.7% or 25 of 60 group-years) in the marmoset genus *Callithrix* (Garber *et al.* 2015). Owing to marmoset propensities to carry multiple litters in a year, there are more breeding opportunities available to primary breeding females, groups are larger, and in several of these cases females gave birth several months apart (Garber *et al.* 2015).

At least 10 cases of infanticide by females have been reported in the wild for both marmosets and tamarins together, including some involving cannibalism (Arruda *et al.* 2005; Bezerra *et al.* 2007; Ferrari and Digby 1996). Though infanticide could reduce group reproductive output in groups with multiple primary breeding females that have offspring, it does not necessarily result in reduced group reproductive output relative to the rest of the population. For example, we observed a case of allonursing of infants by a primary breeding female *Leontocebus weddelli* who most likely lost her own infants at birth either to predation, infanticide, or other injury. This permitted a pair of twin offspring to nurse until 6 mo of age on two females, their mother and subsequently the second female that lost her infants, whereas they would normally be weaned around three months (full account in Watsa 2013). This pair of infants survived for >3 yr. in their natal group before dispersing. Allomaternal care such as this can be greatly beneficial to the survival of offspring across primate species (Fedigan and Jack 2011; Isler and van Schaik 2012; Smith *et al.* 2001) and also occurs commonly in cooperatively breeding meerkats (*Suricata suricatta*) as well (MacLeod 2013). Multiple females breeding in a group a few months apart might also enhance group reproductive output, if these separated births reduce conflicts related to infant care. We observed multiple breeding females in a group of *L. weddelli* in which a pair of infants differed in age by approximately two months based on timings of tooth eruption, indicating that only one infant from each female survived. Offspring survival from both females has been observed in at least two cases in the genus *Saguinus* (Calegaro-Marques and Bicca-Marques 1995; Garber *et al.* 1993) and in multiple cases of *Callithrix* (Digby 1994; Digby and Ferrari 1994; Ferrari and Digby 1996; Roda 1989). We also report a case in which a group of two adult male and two adult female *L. weddelli* raised three offspring of approximately the same age, implying that the females had produced offspring simultaneously. This group composition of adults is a common minimum among callitrichines; for example, 32% of groups assessed in the longest study of *L. weddelli* (Goldizen *et al.* 1996) and 66.7% of groups of the same species assessed recently in Bolivia (Garber *et al.* 2015) had at least two adult males and females, although morphological data used to determine the precise developmental classes of the adults is not reported in these studies.

Our data emphasize the value of long-term, individual-based field studies in which morphology described via mark-recapture programs can be utilised in evaluating overall patterns of reproductive output, a view shared by others in primatology (Clutton-Brock 2012; Clutton-Brock and Sheldon 2010; Robbins 2010). Many other valuable characteristics of this study population are currently being evaluated to further inform these analyses. First, analyses of dental ecomorphology will allow us to fine-tune age classes and predict chronological age for identified individuals. With chronological age for each individual, we can explore how reproductive status changes over an individual's lifetime, monitor shifting population demographics in developmental class, and test for interspecific differences in development and reproductive behavior between *Saguinus* and *Leontocebus*. We can also use genetic sampling to determine paternity and relatedness to directly address the impacts of developmental class on the identities of biological parents in groups. Additional behavioral observations of actual infant care in this population could elaborate on the role of individuals of different developmental classes on group reproductive output. This study highlights the differences in the influences of primary breeding adult males and females on group reproductive output, which allows us to further understand the composition of groups capable of reproducing and contributing to population viability, which is an important consideration for the conservation of these primates. A recent assessment of the conservation status of the Callitrichidae revealed that of the 48 identified species, six remain data deficient and *ca.* 36% (15 species) of the remaining species are classified as threatened by the International Union for the Conservation of Nature (Estrada *et al.* 2017). Thus, these data will form an important benchmark against which future research can be compared for the monitoring of the long-term viability of these primates.

Data Availability

The datasets during and/or analysed during the current study available from the corresponding author on reasonable request.

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Compliance with Ethical Standards

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

References

Akaike, H. (1994). A new look at the statistical model identification. *IEEE Transactions on Automatic Control, 19*(6), 716–723.

Altmann, J. (1990). Primate males go where the females are. *Animal Behaviour, 39*(1), 193–195.

Arruda, M. F., Araújo, A., Sousa, M. B. C., Albuquerque, F. S., Albuquerque, A. C. S. R., & Yamamoto, M. E. (2005). Two breeding females within free-living groups may not always indicate polygyny: Alternative subordinate female strategies in common marmosets (*Callithrix jacchus*). *Folia Primatologica, 76*(1), 10–20.

Baker, A. J., Dietz, J. M., & Kleiman, D. G. (1993). Behavioural evidence for monopolization of paternity in multi-male groups of golden lion tamarins. *Animal Behaviour, 46*(6), 1091–1103.

Bales, K., Dietz, J., Baker, A., Miller, K., & Tardif, S. D. (2000). Effects of allocare-givers on fitness of infants and parents in callitrichid primates. *Folia Primatologica, 71*(1–2), 27–38.

Bales, K., O'Herron, M., Baker, A. J., & Dietz, J. M. (2001). Sources of variability in numbers of live births in wild golden lion tamarins (*Leontopithecus rosalia*). *American Journal of Primatology, 54*(4), 211–221.

Bales, K. L., French, J. A., McWilliams, J., Lake, R. A., & Dietz, J. M. (2006). Effects of social status, age, and season on androgen and cortisol levels in wild male golden lion tamarins (*Leontopithecus rosalia*). *Hormones and Behavior, 49*(1), 88–95.

Barrett, J., Abbott, D. H., & George, L. M. (1990). Extension of reproductive suppression by pheromonal cues in subordinate female marmoset monkeys, *Callithrix jacchus*. *Journal of Reproduction and Fertility, 90*(2), 411–418.

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2014). Fitting linear mixed-effects models using lme4. arXiv.org. doi:arXiv:1406.5823.

Beehner, J. C., & Lu, A. (2013). Reproductive suppression in female primates: A review. *Evolutionary Anthropology: Issues News and Reviews, 22*(5), 226–238.

Bezerra, B. M., Da Silva Souto, A., & Schiel, N. (2007). Infanticide and cannibalism in a free-ranging plurally breeding group of common marmosets (*Callithrix jacchus*). *American Journal of Primatology, 69*(8), 945–952.

Boulton, R. A., & Fletcher, A. W. (2015). Do mothers prefer helpers or smaller litters? Birth sex ratio and litter size adjustment in cotton-top tamarins (*Saguinus oedipus*). *Ecology and Evolution, 5*(3), 598–606.

Buckner, J. C., Lynch Alfaro, J. W., Rylands, A. B., & Alfaro, M. E. (2015). Biogeography of the marmosets and tamarins (Callitrichidae). *Molecular Phylogenetics and Evolution, 82*, 413–425.

Calegaro-Marques, C., & Bicca-Marques, J. C. (1995). Two breeding females in a *Saguinus fuscicollis weddelli* group. *Neotropical Primates, 3*(4), 183.

Campbell, C. J. (2006). Copulation in free-ranging black-handed spider monkeys (*Ateles geoffroyi*). *American Journal of Primatology, 68*(5), 507–511.

Carnes, L. M., Nunn, C. L., & Lewis, R. J. (2011). Effects of the distribution of female primates on the number of males. *PLoS One, 6*(5), e19853.

Clutton-Brock, T. (2012). Long-term, individual-based field studies. In P. M. Kappeler & D. P. Watts (Eds.), *Long-term field studies of primates* (pp. 437–449). Berlin and Heidelberg: Springer Verlag.

Clutton-Brock, T., & Sheldon, B. C. (2010). Individuals and populations: The role of long-term, individual-based studies of animals in ecology and evolutionary biology. *Trends in Ecology & Evolution, 25*(10), 562–573.

Culot, L., Lledo-Ferrer, Y., Hoelscher, O., Muñoz Lazo, F. J. J., Huynen, M.-C., & Heymann, E. W. (2011). Reproductive failure, possible maternal infanticide, and cannibalism in wild moustached tamarins, *Saguinus mystax*. *Primates, 52*(2), 179–186.

Díaz-Muñoz, S. L. (2011). Paternity and relatedness in a polyandrous nonhuman primate: Testing adaptive hypotheses of male reproductive cooperation. *Animal Behaviour, 82*, 563–571.

Díaz-Muñoz, S. L. (2015). Complex cooperative breeders: Using infant care costs to explain variability in callitrichine social and reproductive behavior. *American Journal of Primatology, 78*(3), 372–387.

Digby, L. J. (1994). *Social organization and reproductive strategies in a wild population of common marmosets* (*Callithrix jacchus*). Doctoral thesis, University of California, Davis.

Digby, L. (1995). Infant care, infanticide, and female reproductive strategies in polygynous groups of common marmosets (*Callithrix jacchus*). *Behavioral Ecology and Sociobiology, 37*(1), 51–61.

Digby, L. J., & Ferrari, S. F. (1994). Multiple breeding females in free-ranging groups of *Callithrix jacchus*. *International Journal of Primatology, 15*(3), 389–397.

Digby, L., & Saltzman, W. (2009). Balancing cooperation and competition in callitrichid primates: Examining the relative risk of infanticide across species. In S. M. Ford, L. M. Porter, & L. C. Davis (Eds.), *The smallest anthropoids*, 1st ed. (pp. 135–153). Developments in Primatology: Progress and Prospects. New York: Springer Science+Business Media.

Dunbar, R. I. M. (2000). Male mating strategies: A modeling approach. In *Primate males: Causes and consequences of variation in group composition* (pp. 259–268). Cambridge: Cambridge University Press.

Erb, W. M., & Porter, L. M. (2017). Mother's little helpers: What we know (and don't know) about cooperative infant care in callitrichines. *Evolutionary Anthropology, 26*(1), 25–37.

Estrada, A., Garber, P. A., Rylands, A. B., Roos, C., Fernandez-Duque, E., et al (2017). Impending extinction crisis of the world's primates: Why primates matter. *Science Advances, 3*(1), e1600946.

Fedigan, L. M., & Jack, K. M. (2011). Tracking Neotropical monkeys in Santa Rosa: Lessons from a regenerating Costa Rican dry forest. In P. M. Kappeler & D. P. Watts (Eds.), *Long-term field studies of primates* (pp. 165–184). Berlin and Heidelberg: Springer-Verlag.

Ferrari, S. F., & Digby, L. J. (1996). Wild *Callithrix* groups: Stable extended families?, *38*, 19–27.

French, J. A. (1997). Proximate regulation of singular breeding in callitrichid primates. In J. A. French & N. G. Solomon (Eds.), *Cooperative breeding in mammals* (pp. 34–75). New York: Cambridge University Press.

French, J. A., & Cleveland, J. (1984). Scent-marking in the tamarin, *Saguinus oedipus*: Sex differences and ontogeny. *Animal Behaviour, 32*(2), 615–623.

French, J. A., Bales, K. L., Baker, A. J., & Dietz, J. M. (2003). Endocrine monitoring of wild dominant and subordinate female *Leontopithecus rosalia*. *International Journal of Primatology, 24*(6), 1281–1300.

Garber, P. A. (1997). One for all and breeding for one: Cooperation and competition as a tamarin reproductive strategy. *Evolutionary Anthropology: Issues, News, and Reviews, 5*(6), 187–199.

Garber, P. A., Moya, L., & Malaga, C. (1984). A preliminary field study of the moustached tamarin monkey (*Saguinus mystax*) in northeastern Peru: Questions concerned with the evolution of a communal breeding system. *Folia Primatologica, 42*(1), 17–32.

Garber, P. A., Ón, F. E., Moya, L., & Pruetz, J. D. (1993). Demographic and reproductive patterns in moustached tamarin monkeys (*Saguinus mystax*): Implications for reconstructing platyrrhine mating systems. *American Journal of Primatology, 29*(4), 235–254.

Garber, P. A., Moya, L., Pruetz, J. D., & Ique, C. (1996). Social and seasonal influences on reproductive biology in male moustached tamarins (*Saguinus mystax*). *American Journal of Primatology, 38*(1), 29–46.

Garber, P. A., Porter, L. M., Spross, J., & Di Fiore, A. (2015). Tamarins: Insights into monogamous and non-monogamous single female social and breeding systems. *American Journal of Primatology, 78*(3), 298–314.

Ginther, A. J., Ziegler, T. E., & Snowdon, C. T. (2001). Reproductive biology of captive male cottontop tamarin monkeys as a function of social environment. *Animal Behaviour, 61*(1), 65–78.

Goldizen, A. (1988). Tamarin and marmoset mating systems: Unusual flexibility. *Trends in Ecology & Evolution, 3*(2), 36–40.

Goldizen, A. W., & Terborgh, J. (1986). Cooperative polyandry and helping behavior in saddle-backed tamarins (*Saguinus fuscicollis*). In J. G. Else & P. C. Lee (Eds.), *Proceedings of the Xth Congress of the International Primatological Society: Primate Ecology and Conservation* (pp. 191–198). Chicago: University of Chicago Press.

Goldizen, A. W., & Terborgh, J. (1989). Demography and dispersal patterns of a tamarin population: Possible causes of delayed breeding. *The American Naturalist, 134*(2), 208–224.

Goldizen, A. W., Mendelson, J., Van Vlaardingen, M., & Terborgh, J. (1996). Saddle-back tamarin (*Saguinus fuscicollis*) reproductive strategies: Evidence from a thirteen-year study of a marked population. *American Journal of Primatology, 38*(1), 57–83.

Gurevitch, J., Morrow, L. L., Wallace, A., & Walsh, J. S. (1992). A meta-analysis of competition in field experiments. *American Naturalist, 140*(4), 539–572.

Heymann, E. W. (2000). The number of adult males in callitrichine groups and its implications for callitrichine social evolution. In P. Kappeler (Ed.), *Primate males: Causes and consequences of variation in group composition* (pp. 64–71). Cambridge: Cambridge University Press.

Heymann, E. W., & Soini, P. (1999). Offspring number in pygmy marmosets. *Cebuella pygmaea, in relation to group size and the number of adult males, 46*(6), 400–404.

Huck, M., Lottker, P., & Heymann, E. W. (2004). The many faces of helping: Possible costs and benefits of infant carrying and food transfer in wild moustached tamarins (*Saguinus mystax*). *Behaviour, 141*(7), 915–934.

Huck, M., Löttker, P., Böhle, U.-R., & Heymann, E. W. (2005a). Paternity and kinship patterns in polyandrous moustached tamarins (*Saguinus mystax*). *American Journal of Physical Anthropology, 127*(4), 449–464.

Huck, M., Löttker, P., Heymann, E., & Heistermann, M. (2005b). Characterization and social correlates of fecal testosterone and cortisol excretion in wild male *Saguinus mystax*. *International Journal of Primatology, 26*(1), 159–179.

Huck, M., Roos, C., & Heymann, E. W. (2007). Spatio-genetic population structure in mustached tamarins, *Saguinus mystax*. *American Journal of Physical Anthropology, 132*(4), 576–583.

Isler, K., & van Schaik, C. P. (2012). Allomaternal care, life history and brain size evolution in mammals. *Journal of Human Evolution, 63*(1), 52–63.

Jennions, M. (1994). Cooperative breeding in mammals. *Trends in Ecology & Evolution, 9*(3), 89–93.

Kappeler, P. M. (2000). *Primate males: Causes and consequences of variation in group composition*. Cambridge: Cambridge University Press.

Kappeler, P., & van Schaik, C. (2002). Evolution of primate social systems. *International Journal of Primatology, 23*(4), 707–740.

Koenig, A. (1995). Group size, composition, and reproductive success in wild common marmosets (*Callithrix jacchus*). *American Journal of Primatology, 35*(4), 311–317.

Kostrub, C. E. (2003). *The social organization and behavior of golden-mantled tamarins, Saguinus tripartitus, in Eastern Ecuador*. Ph.D. thesis. University of California, Davis.

Lazaro-Perea, C., Arruda, M. d. F., & Snowdon, C. T. (2004). Grooming as a reward? Social function of grooming between females in cooperatively breeding marmosets. *Animal Behaviour, 67*(4), 627–636.

Löttker, P., Huck, M., Heymann, E., & Heistermann, M. (2004). Endocrine correlates of reproductive status in breeding and nonbreeding wild female moustached tamarins. *International Journal of Primatology, 25*(4), 919–937.

MacLeod, K. (2013). Factors predicting the frequency, likelihood and duration of allonursing in the cooperatively breeding meerkat. *Animal Behaviour, 86*(5), 1059–1067.

Martins, M. M., Nascimento, A., & Nali, C. (2015). A test for sex-biased dispersal in the black-faced lion tamarin (*Leontopithecus caissara*): Inferences from microsatellite markers. *Studies on Neotropical Fauna and Environment, 50*(1), 14–20.

Matauschek, C., Roos, C., & Heymann, E. W. (2010). Mitochondrial phylogeny of tamarins (*Saguinus*, Hoffmannsegg 1807) with taxonomic and biogeographic implications for the *S. nigricollis* species group. *American Journal of Physical Anthropology, 144*(4), 564–574.

Mitani, J. C., Gros-Louis, J., & Manson, J. H. (1996). Number of males in primate groups: Comparative tests of competing hypotheses. *American Journal of Primatology, 38*, 315–332.

Moreira, L. A. A., de Oliveira, D. G. R., de Sousa, M. B. C., & Pessoa, D. M. A. (2015). Parturition signaling by visual cues in female marmosets (*Callithrix jacchus*). *PLoS One, 10*(6), e0129319.

Moreno, P. G., Eberhardt, M. A. T., Lamattina, D., Previtali, M. A., & Beldomenico, P. M. (2013). Intra-phylum and inter-phyla associations among gastrointestinal parasites in two wild mammal species. *Parasitology Research, 112*(9), 3295–3304.

Nievergelt, C. M., Digby, L. J., Ramakrishnan, U., & Woodruff, D. S. (2000). Genetic analysis of group composition and breeding system in a wild common marmoset (*Callithrix jacchus*) population. *International Journal of Primatology, 21*(1), 1–20.

Nunn, C. L. (1999). The number of males in primate social groups: A comparative test of the socioecological model. *Behavioral Ecology and Sociobiology, 46*(1), 1–13.

Pontes, A., & da Cruz, M. (1995). Home range, intergroup transfers, and reproductive status of common marmosets *Callithrix jacchus* in a forest fragment in north-eastern Brazil. *Primates, 36*(3), 335–347.

Porter, L. M. (2001). Social organization, reproduction and rearing strategies of *Callimico goeldii*: New clues from the wild. *Folia Primatologica, 72*(2), 69–79.

Poulin, R. (1994). Meta-analysis of parasite-induced behavioural changes. *Animal Behaviour, 48*(1), 137–146.

R Development Core Team. (2015). R: A language and environment for statistical computing. Vienna, Austria. https://www.R-project.org/.

Ramirez, M. M. (1989). *Feeding ecology and demography of the moustached tamarin Saguinus mystax in northeastern Peru*. Ph.D. dissertation, The City University of New York.

Ridley, M. (1986). The number of males in a primate troop. *Animal Behaviour, 34*(6), 1848–1858.

Robbins, M. M. (2010). Long-term field studies of primates: Considering the past, present, and future. *Evolutionary Anthropology: Issues News and Reviews, 19*, 87–88.

Roda, S. A. (1989). Ocorrência de duas fêmeas reprodutivas em grupos selvagens de *Callithrix jacchus* (Primates, Callitrichidae). In M. L. Cristoffersen & D. S. Amorim (Eds.), *Resumos do XVI Congresso Brasileiro de Zoologia* (p. 122). Resumos do XVI congresso Brasileiro de zoologia.

Rollin, B. E., & Kessel, M. L. (2006). Guidelines for the treatment of animals in behavioural research and teaching. *Animal Behaviour, 71*, 245–253.

Savage, A., & Baker, A. J. (1996). Callitrichid social structure and mating system: Evidence from field studies. *American Journal of Primatology, 38*(1), 1–3.

Savage, A., Giraldo, L., Blumer, E., Soto, L., & Burger, W. (1993). Field techniques for monitoring cotton-top tamarins (*Saguinus oedipus oedipus*) in Colombia. *American Journal of Primatology, 31*(3), 189–196.

Savage, A., Snowdon, C. T., Giraldo, L. H., & Soto, L. H. (1996). Parental care patterns and vigilance in wild cotton-top tamarins (*Saguinus oedipus*). In M. A. Norconk, A. L. Rosenberger, & P. A. Garber (Eds.), *Adaptive radiations of Neotropical primates* (pp. 187–199). New York: Springer Science+Business Media.

Scanlon, C., Chalmers, N., & Monteiro Da Cruz, M. (1988). Changes in the size, composition, and reproductive condition of wild marmoset groups (*Callithrix jacchus jacchus*) in north east Brazil. *Primates, 29*(3), 295–305.

Scheiner, S. M., & Gurevitch, J. (2001). *Design and analysis of ecological experiments*. Oxford: Oxford University Press.

Sikes, R. S., & Gannon, W. L. (2011). Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy, 92*(1), 235–253.

Smith, A. C., Tirado Herrera, E., Buchanan-Smith, H. M., & Heymann, E. W. (2001). Multiple breeding females and allo-nursing in a wild group of moustached tamarins (*Saguinus mystax*). *Neotropical Primates, 9*(2), 67–69.

Soini, P. (1988). The pygmy marmoset, genus *Cebuella*. In R. A. Mittermeier, A. Rylands, A. Coimbra-Filho, & G. da Fonseca (Eds.), *Ecology and behavior of neotropical primates* (Vol. 2, pp. 79–129). Washington, DC: World Wildlife Fund.

Soini, P., & Cóppula, M. (1981). *Ecologia y dinamica poblacional del pichio Saguinus fuscicollis (Primates, Calltrichidae): Informe de Pacaya No. 4 (No. 4). Centro de Dators Para La conservación* (pp. 1–31). Direccion Regional de Agricultura.

Soini, P., & de Soini, M. (1990). Distribución geografica y ecologia poblacional de *Saguinus mystax*. In *La primatologia en el Peru: Proyecto Peruano de Primatología* "*Manuel Moro Sommo*" (pp. 1–31). Lima: Proyecto Peruana de Primatología.

Sousa, M. B. C., Albuquerque, A. C. S. D. R., Albuquerque, F. D. S., Araujo, A., Yamamoto, M. E., & Arruda, M. d. F. (2005). Behavioral strategies and hormonal profiles of dominant and subordinate common marmoset (*Callithrix jacchus*) females in wild monogamous groups. *American Journal of Primatology, 67*(1), 37–50.

Suárez, S. S. (2007). *Paternity, relatedness, and socio-reproductive behavior in a population of wild red-bellied tamarins* (*Saguinus labiatus*). Doctoral Dissertation, New York University. Retrieved from http://gradworks.umi.com/32/47/3247393.html.

Sussman, R. W., & Garber, P. A. (1987). A new interpretation of the social organization and mating system of the Callitrichidae. *International Journal of Primatology, 8*(1), 73–92.

Tardif, S. D. (1994). Relative energetic cost of infant care in small-bodied neotropical primates and its relation to infant-care patterns. *American Journal of Primatology, 34*(2), 133–143.

Tardif, S. D. (1997). The bioenergetics of parental behavior and the evolution of alloparental care in marmosets and tamarins. In N. G. Solomon & J. A. French (Eds.), *Cooperative breeding in mammals* (pp. 11–33). New York: Cambridge University Press.

Terborgh, J., & Goldizen, A. W. (1985). On the mating system of the cooperatively breeding saddle-backed tamarin (*Saguinus fuscicollis*). *Behavioral Ecology and Sociobiology, 16*, 293–299.

Tirado Herrera, E. R., Knogge, C., & Heymann, E. W. (2000). Infanticide in a group of wild saddle-back tamarins, *Saguinus fuscicollis*. *American Journal of Primatology, 50*(2), 153–157.

van Schaik, C. P., & Hörstermann, M. (1994). Predation risk and the number of adult males in a primate group: A comparative test. *Behavioral Ecology and Sociobiology, 35*(4), 261–272.

Venables, W. N., & Ripley, B. D. (2002). Modern applied statistics with S-plus, 4 ed. (pp. 1–498). New York: Springer Science+Business Media.

Watsa, M. (2013). *Growing up tamarin: Morphology, reproduction,* and population demography of sympatric free-ranging *Saguinus fuscicollis* and *S. imperator*. Doctoral thesis, Washington University in St. Louis. Retrieved from http://openscholarship.wustl.edu/etd/1046/.

Watsa, M., Erkenswick, G. A., Halloran, D., Kane, E. E., Poirier, A., et al (2015). A field protocol for the capture and release of callitrichids. *Neotropical Primates, 22*(2), 59–68.

Windfelder, T. L. (2000). Observations on the birth and subsequent care of twin offspring by a lone pair of wild emperor tamarins (*Saguinus imperator*). *American Journal of Primatology, 52*(2), 107–113.

Wislocki, G. B. (1939). Observations on twinning in marmosets. *American Journal of Anatomy, 64*(3), 445–483.

Zeller, U., Epple, G., Küderling, I., & Kuhn, H. (1988). The anatomy of the circumgenital scent gland of *Saguinus fuscicollis* (Callitrichidae, Primates). *Journal of Zoology, 214*(1), 141–156.

Ziegler, T. E., Savage, A., Scheffler, G., & Snowdon, C. T. (1987). The endocrinology of puberty and reproductive functioning in female cotton-top tamarins (*Saguinus oedipus*) under varying social conditions. *Biology of Reproduction, 37*(3), 618–627.

Ziegler, T. E., Epple, G., Snowdon, C. T., Porter, T. A., Belcher, A. M., & Kuderling, I. (1993). Detection of the chemical signals of ovulation in the cotton-top tamarin, *Saguinus oedipus*. *Animal Behaviour, 45*(2), 313–322.