

Two Girls for Every Boy: The Effects of Group Size and Composition on the Reproductive Success of Male and Female White-Faced Capuchins

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ABSTRACT Many factors have been hypothesized to affect the size and adult sex ratios of primate groups and these, in turn, have been argued to influence birth rates. Using park-wide census data collected on a population of capuchins over a 25-year period, we examined whether group size and adult sex ratio affect the per capita reproductive success of male and female white-faced capuchins (*Cebus capucinus*) in Santa Rosa National Park, Costa Rica. We found that the reproductive success of females (measured as the observed minus the expected ratio of immatures to adult females in the group) decreased with increasing group size, whereas that of males was independent of group size. The proportion of adult males residing in groups had significant, yet contrasting effects on males and females. Male reproductive success was negatively associ-

ated with the proportion of males residing in groups whereas female reproductive success increased with the proportion of males. The latter finding supports the intersexual conflict hypothesis, which suggests that a conflict of interest occurs between males and females over adult sex ratios. The effects of group size and composition on the reproductive success of capuchins, a male-dispersed omnivorous species, are similar to those reported for howlers, a bisexually-dispersed folivorous species. One common factor between these taxa is that groups with low ratios of males to females are at greater risk of takeovers and resultant infanticide. Our results suggest that regardless of dietary preference and dispersal pattern, the threat of infanticide can constrain primate group size and composition. *Am J Phys Anthropol* 144:317–326, 2011. © 2010 Wiley-Liss, Inc.

Many studies have examined and debated determinants of primate group size and composition. Because most primates are social, the issue is seldom whether or not they should live in groups but rather what sort of group they should live in to be maximally successful. Research and theory both suggest that the same factors that select for sociality (enhanced resource and predator detection/improved defense and security against conspecific threat) may also select for larger group size (Wrangham, 1980; Janson and van Schaik, 1988; Robinson, 1988a; Sterck et al., 1997). However, sociality is not without its costs. Thus, factors such as increased within-group competition for food and reproductive opportunities (Terborgh and Janson, 1986; Janson and Goldsmith, 1995), increased travel and energetic costs (Janson, 1988; Chapman and Chapman, 2000a,b; Majolo et al., 2008), increased exposure to disease and parasites (Freeland, 1976; Chapman et al., 2009), and increased risk of attracting nonresident male invaders (Crockett and Janson, 2000; Pope, 2000) have all been found or theorized to constrain group size.

Group size in turn may influence the reproductive success of both males and females and various models have been developed to explain how group size is related to birth rates and infant survivorship. For example, Wrangham (1980) suggested that females in both very small and very large groups would have lower reproductive success (due to between-group and within-group competitive pressures, respectively), resulting in an inverted U-shaped relationship between group size and reproductive success. On the other hand, van Schaik (1983) hypothesized that birth rates would decrease linearly

with increasing group size due to within-group feeding competition but infant survival would increase in larger groups because of enhanced predator defense. These two models stimulated a number of empirical studies that failed to clearly resolve the debate. For example, some researchers concluded that female reproductive success was higher in larger groups due to their increased success during intergroup resource competition (e.g., *Lemur catta*: Takahata et al., 2006; *Cebus olivaceus*: Robinson, 1988a,b; O'Brien, 1991; Miller, 1992; *Callithrix jacchus*: Koenig, 1995, 2002; *Macaca fuscata*: Suzuki et al., 1998). Others concluded that females in larger groups experienced lower birth rates and/or infant survival due to increased intragroup feeding competition and energetic costs (e.g., *Lemur catta*: Jolly et al., 2002; *Alouatta siniticus*: Crockett and Janson, 2000; *Presbytis entellus*: Treves and Chapman, 1996; *Trachypithecus phayrei*:

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Borries et al., 2008; *Macaca silenus*: Kumar, 1995; *Macaca fascicularis*: van Noordwijk and van Schaik, 1991; *Papio spp.*: Hill et al., 2000; Altmann and Alberts, 2003; Charpentier et al., 2008; and see Majolo et al.'s 2008 meta-analysis of 86 studies/44 primate species). Some studies found no relationship between group size and birth rates (e.g., *Macaca cyclopis*: Hsu et al., 2006; *Gorilla gorilla*: Robbins et al., 2007).

It is likely that no general consensus has been reached on the issue of group size and reproductive success for several reasons: 1) many different factors may play a role in determining optimal group size for each species in given environments; 2) different definitions and measures of reproductive success have been used in different studies; 3) male and female reproductive success may be differentially affected by group size (a form of intersexual conflict); and 4) because group composition may be as (or more) important to reproductive success as is the overall group size. In particular, the number and proportion of adult males and adult females in a group is theorized to be relevant to reproductive success. Too high a ratio of adult males to females is thought to be detrimental to male reproductive success because of increased within-group competition for fertile females (Bateman, 1948; Trivers, 1972; Dobson, 1982; Moore and Ali, 1984; Waser, 1985; Zhao, 1994; Morelli et al., 2009). Too many adult females or too low a ratio of adult males to females is theorized to be detrimental to female reproductive success because of increased female–female competition for resources (van Belle and Estrada, 2008), decreased ability to defend the group against conspecific threat (especially infanticide; Steenbeek, 2000), and increased attraction to invading males (Crockett and Janson, 2000).

Ryan et al. (2008) analyzed 23 years of group composition data on the howlers (*Alouatta palliata*) of Barro Colorado Island (BCI), Panama and found that both female and male per capita reproductive success decreased with increasing group size. However, the sexes differed in their responses to changing sex ratios within the group; female reproductive success increased whereas that of males decreased as groups exhibited increasingly male biased adult sex ratios. These authors concluded that a conflict of interest between the sexes over adult sex ratios play a key role in determining group size and composition in their study population. However, they stress that the applicability of their findings were uncertain until tested in other species via similar long-term demographic data. To date, the differential effect of group size and composition on male versus female reproductive success (which Ryan et al. referred to as the intersexual conflict hypothesis) has only been tested, to our knowledge, among howlers (Treves, 2001; Ryan et al., 2008; van Belle and Estrada, 2008).

In this article, we examine demographic data from park-wide censuses carried out over a 25-year period in Santa Rosa and analyze these data to address the question of how group size and composition are related to female and male reproductive success in white-faced capuchins (*Cebus capucinus*). Following Ryan et al. (2008), reproductive success is operationally defined in this study as the deviation from the population expectation for the number of infants (or immatures) per group, with respect to the number of adult females or males (see also Treves, 2001; van Belle and Estrada, 2008).

White-faced capuchins reside in groups that contain an average of 17 individuals and are comprised of multiple immigrant adult males, multiple natal adult females, and

their immature offspring (Fedigan and Jack, 2001). Male natal dispersal occurs around the time of sexual maturity (~4.5 years) and males continue to disperse throughout their lives (Jack and Fedigan, 2004a,b). Our study groups experience complete changeovers in male group membership at ~4-year intervals. These male changeovers generally involve coalitions of two or more males aggressively challenging residents. In successful takeovers, invading males almost always outnumber resident males, which highlight the importance of male coalitionary aggression for both gaining group membership and maintaining it (Fedigan and Jack, 2004). Aggressive takeovers are associated with the deaths and disappearances of both adult and immature group members and all changeovers in male group membership are associated with increased infant mortality (Fedigan, 2003; Fedigan and Jack, 2004). Dispersal is the primary means of rank increase for male white-faced capuchins in the Santa Rosa study population (Jack and Fedigan, 2004b), although a rank reversal was observed at the nearby site of Lomas Barbudal, Costa Rica, where male dispersal and group takeovers occur less frequently (Perry, 1998).

On the basis of these observations and an extensive review of the literature on this topic, we made three predictions regarding group size and composition in this species:

Prediction 1. As group size increases in the Santa Rosa population of white-faced capuchins, reproductive success for both females and males will decrease linearly. Rationale: Janson (1988) found that larger groups of *Cebus apella* had lower foraging efficiency than smaller groups in that they travelled farther and foraged longer to obtain the nutrients needed. Chapman (1987) and Chapman and Chapman, (2000a) found that capuchin groups at our site deplete food patches and move successively from one feeding tree to the next when the rate of food intake declines. This suggests that individuals in large groups must travel more and expend more energy to feed themselves. As originally argued by van Schaik (1983), increased intragroup feeding competition (both scramble and contest) in larger groups should lead linearly to lower birth rates.

Additionally, Vogel (2005) found that female capuchins at the neighboring site to our own in Costa Rica experience differential competitive success such that dominant individuals have higher nutrient/energy intake rates than do subordinates and the former are able to consistently supplant the latter from preferred food sources, water holes, and safe sleeping sites. Foraging competition such as this may constrain group membership and has the potential to negatively affect birth rates and infant survival in lower-ranked individuals.

Prediction 2. Groups with a higher proportion of adult males to females (an adult sex ratio skewed toward males) will exhibit greater female reproductive success than will groups with an adult sex ratio skewed toward females. Rationale: In several primate species invading/dispersing males are attracted to groups with a higher proportion of females to males (Isbell, 1991; Treves and Chapman, 1996; Crockett and Janson, 2000) and this is what we found in our study groups of white-faced capuchins (Fedigan and Jack, 2004; Jack and Fedigan, 2004b). This suggests that groups with too few males are at greater risk of being targeted for take-over attempts and resultant infanticide. Indeed the proportion of males in a group was the single significant variable predicting group takeovers in our study groups, with groups that

display low ratios of males to females being targeted (Fedigan and Jack, 2004). Furthermore, greater numbers of adult males can better protect the females and infants of a group, from both predators and would-be invaders (Baldellou and Henzi, 1992; Clutton-Brock and Parker, 1995; van Schaik and Kappeler, 1997; Borries et al., 1999; Treves, 2001; Ortega and Arita, 2002; Ostner and Kappeler, 2004).

Prediction 3. Groups with a higher proportion of adult males to females will exhibit lower per capita male reproductive success. Rationale: As noted by Ryan et al. (2008), there may be a conflict of interest between males and females in polygynandrous societies over the intra-group sex ratio. Although a higher proportion of adult males is beneficial to female reproductive success, a finite number of breeding opportunities are shared by all the males in the group and the higher the ratio of males to females, the lower their per capita reproductive success (see classic studies by Bateman, 1948; Trivers, 1972). Furthermore, in a mating system skewed toward breeding success for dominant males, subordinate males receive few opportunities to produce offspring. We found in our long-term study groups at Santa Rosa that subordinate males do mate with females but this occurs primarily when the females are pregnant or nonconceptive (Carnegie et al., 2006), which is probably why the alpha male sires the vast majority of the offspring (Jack and Fedigan, 2007). A similar finding has been reported for the neighboring population of *C. capucinus* at Lomas Barbudal (Perry, 2008). As noted above, groups (including the alpha male) need sufficient numbers of resident males to defend access to resources and also to defend the group from takeover attempts. Thus, the dilemma for males is that they need coresident males to gain and retain membership in groups, but these same coresident males also compete for reproductive success. This intragroup male–male competition for access to conceptive females is predicted to drive down the per capita reproductive success of males.

METHODS

Study site

Santa Rosa National Park (SRNP), established in 1971 in Costa Rica consists of 108 km² of tropical dry forest. In 1986, a project was begun to purchase the ranchlands surrounding SRNP and the result is a much enlarged megapark, known as “Area de Conservación Guanacaste” [ACG (Janzen, 2002)]. The core of ACG remains “Sector Santa Rosa,” and the original SRNP park boundaries form the borders of our census research, which began in 1983 and continues through to the present time.

There are three species of monkeys in SRNP: mantled howlers (*Alouatta palliata*), white-faced capuchins (*Cebus capucinus*), and black-handed spider monkeys (*Ateles geoffroyi*). Members of our research team have studied the density and distribution of the three primate species in the park since 1983 and many aspects of their population dynamics and life histories have now been described (e.g., Fedigan and Rose, 1995; Sorensen and Fedigan, 2000; Fedigan and Jack, 2001; Fragaszy et al., 2004; DeGama-Blanchet and Fedigan, 2006; Jack and Fedigan, 2007).

Census techniques and data collection

Our long-term research on the capuchins of Santa Rosa started with extensive censuses of the park-wide

population in 1983 and 1984. In 1984, we selected several “study groups” for intensive research and began to discriminate and habituate the individual monkeys in them. In 1985, we started to record births, deaths, and dispersals in our study groups, as well as details of foraging and social behavior on a regular biweekly basis, a practice that continues through to the present. The intensive biweekly data obtained from our study groups provide a detailed sample that helps us interpret larger demographic events in the park-wide population that we observe during our population censuses.

Between 1983 and 2007, we conducted 11 censuses of the capuchin monkeys located throughout SRNP. We use a modified quadrat technique that has proven useful in areas of fragmented forest patches (see Fedigan et al., 1996, 1998; Fedigan and Jack, 2001 for details). These censuses were almost always carried out in May and June, during which time we located and counted the capuchin groups in SRNP and recorded their locations.

We chose one area of the park at a time (usually a patch of forest) and walked either transects or all known trails and dry stream beds in the area to locate monkeys. We considered any individual monkey within 100–300 m of the group and consistently traveling in the same direction as the group (even if in a peripheral position) to be part of that group. We made use of unique markings and distinctive age/sex compositions to identify the same group on successive days for repeat counts. Multiple observers repeatedly counted a group until achieving a stable count and composition, and plotted its location on a map. After establishing a stable count on one group, we located its nearest neighbor group. Whenever possible, with the aid of two-way radios, we used simultaneous contact with neighboring groups by different observers to establish their independence. With many years of practice, it has become increasingly easy to relocate our census groups in successive years and to determine when new groups have appeared.

For the present analyses, we assigned each individual in a group to one of four age/sex classes: adult/subadult male (>6 years), adult female (>6 years), juvenile (1–6 years), and infant (capuchins: <1 year). Adult capuchins are easily sexed and the age classes of infants, juveniles, and adults are easily distinguished by size, shape, and fur patterns. Subadult males were included with adult males. For some of the analyses, we created a category called “immatures,” which we define for this study as all monkeys aged <6 years (i.e., juveniles + infants).

Data analysis

We conducted park-wide censuses of the capuchin groups in 1983, 1984, 1985, 1986, 1987, 1988, 1990, 1992, 1999, 2003, and 2007. Based on the extent and reliability of each census and the need to have censuses separated by at least 4 years (see below), we chose to analyze the censuses from 1984, 1992, 1999, 2003, and 2007. The numbers of groups for which we determined size and composition in these census years varied from 25 to 49 (Table 1). Choosing censuses separated by 4–8 years avoids the problem of repeated measures as far as infants are concerned and minimizes repeated measures on juveniles.

We first computed reproductive success of females for infants in group *i* and year *j* ($F_{INF ij}$) as the observed number of infants minus the expected number of infants, following the method of Ryan et al. (2008). To determine

TABLE 1. Means (ranges) of group size and composition for the five census years

	Year					
	1984	1992	1999	2003	2007	All Years
Number of groups	25	30	31	49	39	174
Group size	13.52 (6–26)	18.03 (6–31)	16.81 (7–40)	13.37 (4–28)	15.23 (3–32)	15.22 (3–40)
Number of adult males	2.16 (1–4)	4.20 (1–8)	4.00 (1–8)	4.12 (1–8)	4.36 (1–9)	3.89 (1–9)
Number of adult females	4.56 (2–10)	5.37 (1–10)	5.81 (2–18)	3.69 (1–8)	4.03 (0–9)	4.56 (0–18)
Number of immatures	6.20 (2–12)	7.43 (3–12)	6.10 (1–15)	5.53 (0–16)	6.13 (0–15)	6.19 (0–16)
Number of infants	1.49 (0–4)	3.17 (1–5)	1.77 (0–5)	0.96 (0–3)	1.90 (0–7)	1.77 (0–7)
Infants per adult female	0.33 (0–1)	0.69 (0.25–3)	0.33 (0–1)	0.29 (0–1)	0.53 (0–2)	0.42 (0–3)
Immatures per adult female	1.54 (0.66–5)	1.58 (0.37–6)	1.14 (0.25–4)	1.63 (0–7)	1.71 (0.42–5)	1.54 (0–7)
Infants per adult male	0.73 (0–2)	0.84 (0.4–2)	0.43 (0–1.25)	0.33 (0–2)	0.52 (0–2.33)	0.54 (0–2.33)
Immatures per adult male	3.09 (0.66–7)	1.94 (0.85–5)	1.58 (0.33–3)	1.61 (0–6)	1.56 (0–5)	1.86 (0–7)
Adult sex ratio (proportion males)	0.34 (0.16–0.6)	0.44 (0.2–0.87)	0.42 (0.25–0.7)	0.52 (0.22–0.83)	0.53 (0.25–1)	0.46 (0.16–1)

the expected number of infants for group i and year j , we first computed the overall ratio of infants per female within years, dividing the sum of all infants in all groups by the sum of all adult females in all groups for year j (IPAF(j)). This was then multiplied by the number of adult females in group i and year j (AF(ij)) to arrive at the expected number of infants for group i of year j . Therefore:

$$\begin{aligned}
 F_{INF}(ij) &= \text{Infants}(ij) - \text{ExpectedInfants}(ij) \\
 &= \text{Infants}(ij) - \text{IPAF}(j) \times \text{AF}(ij), \text{ where } ij \text{ refers} \\
 &\quad \text{to the } i\text{th group in the } j\text{th year.}
 \end{aligned}$$

To visualize this relationship for a given year, we plot the number of infants in a group as a function of the number of adult females in a group, and include a line drawn through the origin with a slope equal to the number of infants per female for all groups in that year combined. Reproductive success of females for a given group is then simply the difference in the number of infants observed in that group and the number from the expected line (Fig. 1 shows an example for 2007 census data). Points falling above the line represent groups with more infants than expected for that year, and points falling below the line represent groups with fewer than expected infants for that year. By computing reproductive success separately for each of the census years, we control for possible effects of differences among census years in resource levels and demographic/reproductive patterns.

We computed similar values for female reproductive success based upon “immatures” (all monkeys <6 years, infants and juveniles combined, F_{IMM}), and male reproductive success based on infants (M_{INF}) and immatures (M_{IMM}). We used each of these four measures of reproductive success as the dependent variable in a multiple regression with adjusted group size and adjusted (residual) adult sex ratio as the independent variables.

Adjusted group size was computed as total group size minus the number of infants (G_{INF}) or immatures (G_{IMM}) per group, which avoids the statistical problem of having infants (or immatures) represented in both the dependent and independent variables. This measure of adjusted group size differs from the measure used by Ryan et al. (2008), and van Belle and Estrada (2008). Their measure was the residual of the regression of total group size on the number of infants or immature. However, simulations indicate that their measure may be a biased estimator of reproductive success.

Adjusted adult sex ratio (S) was computed as the residual of the regression of number of adult males per group

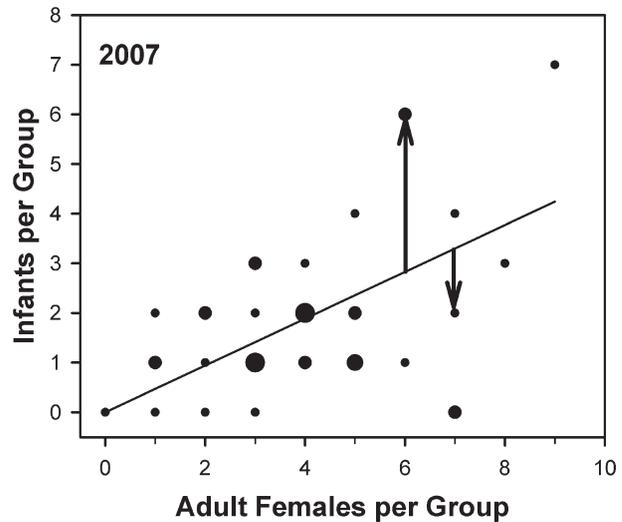


Fig. 1. Infants per group as a function of adult females per group for 2007. The solid line represents the predicted number of infants in a group, given the number of adult females per group. The slope of the line is the number of infants per adult female in the population as a whole, which was 0.471 in 2007. Per capita reproductive success of females (F_{INF}) is measured as the difference between the observed number of infants in a group and the predicted number of infants (solid line). Arrows illustrate two examples of these differences, one positive and one negative. Differences represent the degree to which groups have more or fewer than the expected number of infants based on the number of females in a group and the overall ratio of infants per female in the population. Symbol size is proportional to the number of groups with that ratio of infants to adult females per group.

on the number adult females per group (see Fig. 2). By using the adjusted (residual) sex ratio we avoid spurious relationships between independent and dependent variables that would arise through the use of sex ratio per se (Treves, 2001). The adjusted adult sex ratio represents the surplus or shortage of adult males in a group relative to the number of males expected for a given number of adult females. Thus, positive values represent groups with more males than expected and negative values represent groups with fewer males than expected.

Because we used the same data to analyze four different relationships (i.e. F_{INF} , F_{IMM} , M_{INF} , M_{IMM}), we applied a Bonferroni correction, such that our cut-off point for significant relationships was set to $P < 0.0125$. To represent the relationships of G to the dependent variables while controlling for S , and the relationships of S to the dependent variables while controlling for G , we present partial regression

leverage plots (see Ryan et al., 2008). Note that in partial regression leverage plots values are residuals and are therefore rescaled around zero. The Variance Inflation Factors of G and S in the four analyses were uniformly small (1.21 to 1.22), indicating that the effects of collinearity among independent variables were not affecting our interpretation of the models (Ryan et al., 2008). All analyses were conducted with PASW 17.0 (formerly SPSS).

RESULTS

Basic demographic parameters

The mean group size across all the census years was 15.2, with a range of 3–40 group members (Table 1), which corresponds closely to our previously reported average group sizes (Fedigan and Jack, 2001). The ratio of infants to adult females per group ranged from 0 to 3, with an overall mean of 0.42. Ratios greater than 1 occurred only twice. The ratio of immatures (juveniles plus infants) to adult females per group ranged from 0 to 7 with an overall mean of 1.54. Ratios such as 3:1 infants/female or 7:1 immatures/female are very rare, but possible given the combination of adult female mortality, alloparenting of orphans and small group sizes. There were on average 0.54 infants per adult male per group (range of 0–2.33) and 1.86 immatures per adult males per group (range of 0–7). There were usually fewer adult males than adult

females per group, with an overall mean proportion of adult males at 0.46 (range of 0.16–1.00).

Infants and females

F_{INF} showed a weak response to G_{INF} and S ($F_{2,171} = 2.96, P = 0.54, R^2 = 0.034, F_{INF} = 0.481 - 0.036 G_{INF} + 0.134 S$, Table 2). Although the relationships were in the predicted directions (see Fig. 3), after applying the Bonferroni correction (which requires a P value < 0.0125 to achieve significance) neither adjusted group size ($t = -1.96, P = 0.051$) (Fig. 3a) nor adjusted adult sex ratio ($t = 2.14, P = 0.034$) was a significant predictor of female per capita reproductive success (Fig. 3b).

Immatures and females

F_{IMM} showed a strong response to both G_{IMM} and S ($F_{2,171} = 20.4, P < 0.001, R^2 = 0.193, F_{IMM} = 2.41 - 0.267 G_{IMM} + 0.821 S$) (Table 2). Thus, as the adjusted group size increased, female reproductive success (measured via all the immatures in the group) decreased significantly ($t = -4.68, P < 0.001$), (Fig. 4a). Conversely, as the adjusted sex ratio became increasingly skewed in favor of adult males, female reproductive success increased significantly ($t = 5.90, P < 0.001$; Fig. 4b)

Infants and males

M_{INF} showed mixed results with G_{INF} and S ($F_{2,171} = 22.6, P < 0.001, R^2 = 0.209; M_{INF} = -0.512 + 0.038 G_{INF} - 0.400 S$) (Table 2). Thus, as adjusted group size increased, male per capita reproductive success increased ($t = 2.19, P = 0.028$), but not significantly so after the Bonferroni correction. On the other hand, as the adjusted sex ratio increased, male per capita reproductive success declined significantly ($t = -6.68, P < 0.001$), (Fig. 5a,b).

Immatures and males

M_{IMM} also showed mixed results with G_{IMM} and S ($F_{2,171} = 30.1, P < 0.001, R^2 = 0.260; M_{IMM} = -0.861 + 0.095 G_{IMM} - 1.04 S$; Table 2). When we used immatures as an indicator, male per capita reproductive success was independent of adjusted group size ($t = 1.68, P = 0.093$), but showed a marked decline with increase in the adjusted sex ratio ($t = -7.58, P < 0.001$; Fig. 6a,b).

Nonlinear effects

None of the four relationships between adjusted group size and per capita reproductive success (females and infants, females and immatures, males and infants, males and immatures) showed any statistical evidence of being nonlinear ($P = 0.302, 0.524, 0.095$, and 0.260 , respectively, for the second order terms). Moreover, visual inspection of

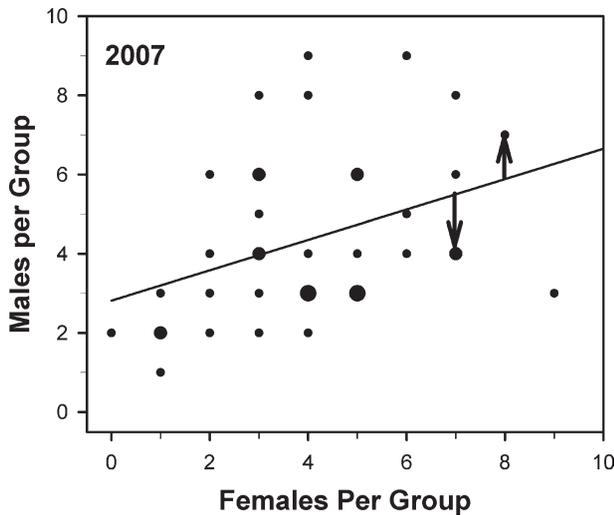


Fig. 2. Males per group as a function of females per group for 2007. Solid line is the regression of males per group on females per group. Residuals of the regression, as illustrated by the arrows, represent S , the degree to which groups have more or fewer males than expected based on the number of females in the group. Symbol size is proportional to the number of groups for each combination of the number of adult males and females per group.

TABLE 2. Statistical results of multiple regression analyses

Model	Intercept	Slope		R^2	$F_{2,171}$	t	
		GAdj	S			GAdj	S
F_{inf}	0.481	-0.036	0.134	0.034	2.966	-1.969	2.141
F_{imm}	2.415	-0.267	0.821	0.193	20.439***	-4.686***	5.097***
M_{inf}	-0.512	0.038	-0.400	0.209	22.605***	2.197	-6.682***
M_{imm}	-0.861	-0.095	-1.044	0.260	30.100***	1.688	-7.588***

*** $P < 0.001$.

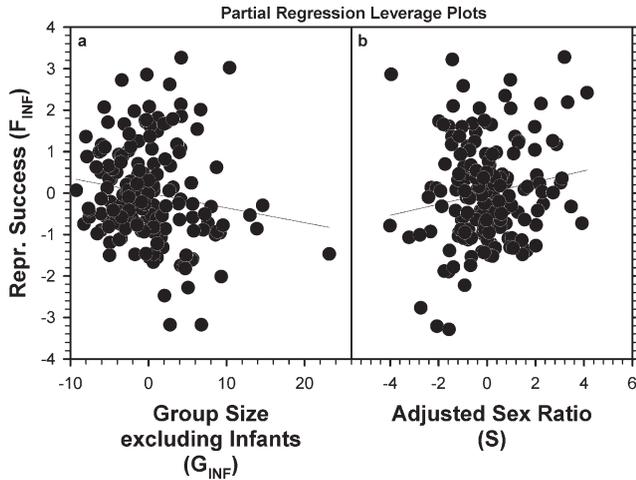


Fig. 3. Partial regression leverage plots of reproductive success of females based upon infants (F_{INF}) as a function of (a) group size minus infants (G_{INF}) and (b) sex ratio adjusted for the number of females (S). In these and all subsequent partial regression leverage plots the values are rescaled as residuals accounting for the independent variables not shown in the plots. So for example, G_{INF} , which varies from 3 to 36 in the original data, varies from -9.24 to 23.3 when rescaled.

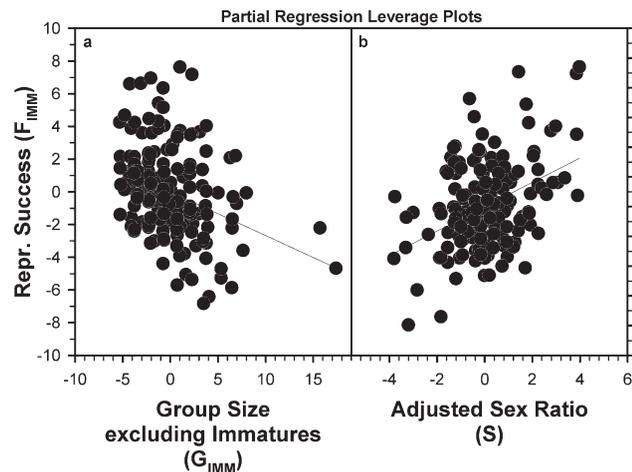


Fig. 4. Partial regression leverage plots of reproductive success of females based upon immatures (F_{IMM}) as a function of (a) group size minus immatures (G_{IMM}) and (b) sex ratio adjusted for the number of females (S).

Figures 3–6 shows no reason to suspect that nonlinear effects are an important part of the response in our system.

DISCUSSION

We found only mixed support for the idea that reproductive success would decrease with increasing group size (Prediction 1). Although per capita female reproductive success declined with increasing group size, this was not a significant pattern for our first of two measures (F_{INF}), which examined infants only. When all immatures are included (F_{IMM}), the per capita reproductive success of females did decline significantly with increasing group size. The per capita reproductive success of males was independent of group size whether we include only infants (M_{INF}) or all immatures

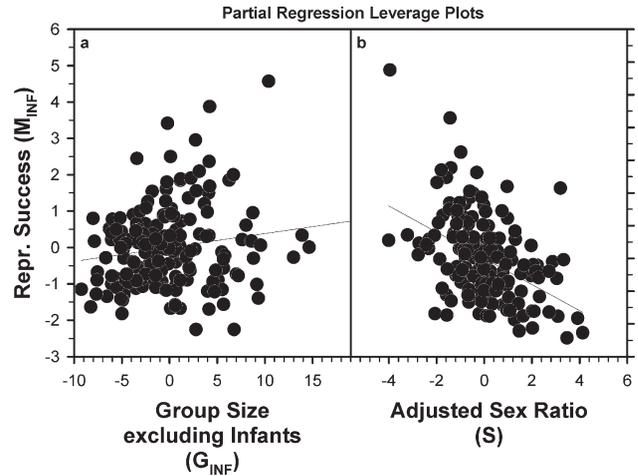


Fig. 5. Partial regression leverage plots of reproductive success of males based upon infants (M_{INF}) as a function of (a) group size minus infants (G_{INF}) and (b) sex ratio adjusted for the number of females (S).

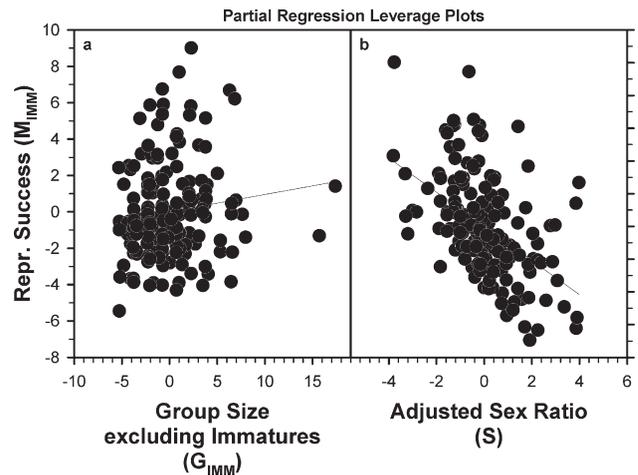


Fig. 6. Partial regression leverage plots of reproductive success of males based upon immatures (M_{IMM}) as a function of (a) group size minus immatures (G_{IMM}) and (b) sex ratio adjusted for the number of females (S).

(M_{IMM}). Although we have limited ability to comment on the debate between Wrangham (1980) and van Schaik (1983) as to the shape of the relationship between group size and reproductive success, none of the relationships in our study were other than linear. In so far as group size does penalize female reproductive success (F_{IMM}) in our study animals, it does so monotonically, which suggests that van Schaik's predation/infanticide-driven model better describes sociality in our population than does Wrangham's food competition-driven model.

The proportion of males residing in groups had significant, yet contrasting effects on both male and female reproductive success. We found a positive association between female reproductive success measured via immatures (F_{IMM}) and the proportion of males residing in the group (Prediction 2), whereas male reproductive success (both M_{INF} and M_{IMM}) was negatively associated with the proportion of males residing in groups (Prediction 3).

On the basis of these findings we can conclude that, like howler monkeys (Treves, 2001; Ryan et al., 2008; van Belle and Estrada, 2008), the reproductive strategies of male and female white-faced capuchins are at odds. Whereas per capita male reproductive success suffers with an increasing proportion of same-sex competitors in the group, it appears that female capuchins experience reproductive benefits from residing in groups with sex ratios skewed toward males.

We have previously shown that aggressive male takeovers are more likely to occur in groups with lower proportions of males (whereas group size, number of adult females, and number of adult males were not significant predictors of group takeovers; Fedigan and Jack, 2004). Given that infant deaths significantly increase in years following aggressive group takeovers (Fedigan, 2003), it makes sense that female reproductive success should be higher in groups with a greater proportion of males residing in them. Furthermore, residing with a relatively large number of adult males provides female capuchins with benefits additional to discouraging takeovers. For example, male capuchins are more vigilant and therefore better at detecting predators and extragroup conspecifics that may pose threats to females and their offspring (Rose and Fedigan, 1995). Males are also more active during encounters with predators and neighboring groups (Fedigan, 1993; Perry, 1996) and research on capuchins at other sites has shown that it is the number of males in a group (as well as the location of the intergroup encounter), rather than absolute group size, that dictates which groups gain access to critical resources like fruit trees and terrestrial water sources (Robinson, 1988a; Crofoot et al., 2008).

Given the significant impact of group composition on female reproductive success, Treves (2001) and Ryan et al. (2008) proposed that female howlers could maximize offspring survival by selectively joining and reproducing in groups containing large numbers of males relative to females. Female capuchins, however, appear to have relatively little control over the size and composition of the group in which they reside. Some female capuchins do disperse from their natal groups (~9% of adult females in our study groups have been immigrants) and this dispersal is intimately linked with the timing of takeovers and appears to be a strategy for avoiding infanticide (Jack and Fedigan, 2009). Female capuchins may also attempt to control group membership by using their knowledge of the home range to repeatedly "lose" new males; moving quickly around the range and failing to answer the lost calls of these males (usually this species exhibits "antiphonal" calling in which they respond to lost calls from group members, Digweed et al., 2007). However, most female capuchins eventually concede and new males join their groups.

Given that males are the dispersing sex, they should be selectively joining groups that serve to maximize their reproductive potential, and for the most part this is what they do. Our previous analysis (Jack and Fedigan, 2004b) of transferring males found that they preferentially move toward groups (usually via aggressive coalitionary takeovers) that afford them higher ratios of females to males ("two girls for every boy"). Male reproductive success is directly linked to their ability to gain access to mating opportunities and in some species it may also be related to the number of same-sexed competitors within a group.

One of the main predictions of the intersexual conflict hypothesis (Ryan et al., 2008: p 407) is that "male reproductive success per capita decreases with an increase in the propor-

tion of males within a group. . . . because a finite number of breeding opportunities is shared by all males in a group, so group males will want to keep male proportion limited." And we did find that per capita male reproductive success decreased with an increase in the proportion of males in the group. However, in species like white-faced capuchins that display high levels of reproductive skew (i.e., the alpha male sires the majority of the group's offspring; Jack and Fedigan, 2007; Muniz et al., 2010), and where the presence of subordinates provide benefits via increased infant survivorship (Fedigan, 2003; Fedigan and Jack, 2004), the alpha male may not "want" to keep male proportions limited. That is, if the alpha male is siring the majority of infants in a group, this should not change much regardless of how many coresident males there are. Indeed when we examined the number of infants per group (which can serve as an indicator of reproductive success for the alpha male), they increased with adjusted group size but were unaffected by adjusted sex ratio.

In fact, given the importance of male-male coalitions in gaining access to groups, retaining membership in them, and preventing conspecific attack, we might expect alpha males to preferentially seek out more subordinate males to join and remain in their group to help out with protection. Behavioral evidence shows this to be the case—alpha males sometimes travel away from their groups to locate subordinate males who have left the group's home range and then perform displays that are apparently designed to reinforce social bonds with these deserters (Perry, 1998; personal observations). Thus, it might be that in capuchins, it is mainly subordinate males that experience a decrease in their (admittedly already low) reproductive opportunities with any increase in the proportion of males in the group. Subordinate males may, however, offset the reproductive costs of residing in groups with high proportions of adult males by selectively residing with male kin. Although white-faced capuchins are a male-dispersed species, which does not generally lend itself to the maintenance of male kinship within groups, our study males often engage in parallel dispersal. We discovered that 74% of all dispersals by adult male capuchins were parallel in that males transferred between groups in small cohorts, or selectively dispersed into groups containing familiar males (Jack and Fedigan, 2004b). High rates of parallel dispersal such as those displayed in our study species (Jack and Fedigan, 2004b), have been suggested to lead to comparable levels of relatedness among the dispersing sex as those maintained through philopatry (Moore, 1992).

The effects of group size and composition on the reproductive success of male and female white-faced capuchins are similar to those reported for howler monkeys (Treves, 2001; Ryan et al., 2008), a bisexually dispersed folivorous species. The intersexual conflict hypothesis was originally suggested to explain why many folivorous species do not conform to the ecological constraints hypothesis (the "folivore paradox") in that they experience very low levels of resource competition but continue to reside in groups much smaller than predicted by socioecological models (Steenbeek et al., 1999). Several authors have suggested that group size in many female (or bisexually) dispersed folivorous species is limited by the threat of infanticide, rather than (or in some cases in addition to) predation pressure and intragroup foraging competition, (e.g.; Crockett and Janson, 2000; Steenbeek and Van Schaik, 2000; Koenig and Borries, 2002; Ryan et al., 2008; but see Treves and Chapman, 1996; Snaith and Chapman, 2007, 2008; Harris et al., 2010). Interest-

ingly, our results indicate that the threat of infanticide may also be posing constraints on group size in our study population of white-faced capuchins; a male dispersed omnivorous species.

We have often pondered why our capuchins do not form large extended social groups such as those seen in many cercopithecines that display similar polygynandrous social patterns with female philopatry and male dispersal (e.g., macaques and baboons) or even like those seen in their New World primate cousins, the squirrel monkeys, who often reside in groups containing well over 50 individuals (Boinski et al., 2003). While intragroup foraging competition (for females) and reproductive competition (for males) may play a role in overall group size, it does appear that group composition is strongly influenced by the threat of infanticide in white-faced capuchins. As demonstrated by Crockett and Janson (2000) for howlers, group composition is an important factor influencing the occurrence of group takeovers and subsequent infanticide in that groups with a greater number of females or low ratios of males to females are at higher risk of takeovers, which also appears to be the case in white-faced capuchins (Fedigan and Jack, 2004). Further comparative research is needed using these same measures of reproductive success to see if similar patterns hold in other nonfolivorous species that experience infanticide versus other species for which infanticide does not seriously influence male and female reproductive success. In their 1963 no. 1 hit song, "Surf City," Jan and Dean suggested that sex ratios skewed toward females (two girls for every boy) are preferred by at least some male primates and such a preference is indeed shown by our capuchin males. However, the present study, and other recent research into optimum group size and composition, suggests that this may not be the most beneficial arrangement for the reproductive success of female primates.

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