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ORIGINAL ARTICLE

Should I stay or should I go now: dispersal decisions and reproductive success in male white-faced capuchins (*Cebus imitator*)

Eva C. Wikberg[1,2] · **Katharine M. Jack**[3] · **Fernando A. Campos**[1] · **Mackenzie L. Bergstrom**[4] · **Shoji Kawamura**[2] · **Linda M. Fedigan**[4]

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Abstract

Although males often disperse to increase their immediate access to mates, it is unclear whether they also consider potential future reproductive opportunities. We investigated whether immediate or delayed reproductive opportunities predicted dispersal decisions and reproductive success of subordinate immigrant male white-faced capuchins in the Sector Santa Rosa, the Área de Conservación Guanacaste, Costa Rica. We collected genetic, behavioral, and demographic data from four social groups across 20 years. We genotyped individuals at up to 20 short tandem repeat loci to determine paternity. Having previously sired offspring in a group did not predict the subordinate immigrant male's likelihood of staying or dispersing. Instead, a male was more likely to remain in the group if he was younger and likely to benefit from queuing for future reproductive opportunities. Subordinate immigrant males were more likely to sire offspring if they resided with a long-term alpha male and his mature daughters, who avoid inbreeding. Reproductive output was similar among three categories of males: those that became alpha immediately after immigration, those that became alpha after queuing, and subordinate males that resided with a long-term alpha male and his mature daughters. These three categories of males had higher reproductive success than subordinates who did not reside with mature daughters of the alpha male. Waiting for reproductive opportunities can lead to high reproductive success and could be important in maintaining tolerant or cooperative male-male relationships in species with high reproductive skew, long alpha male tenures, and intense between-group mating competition requiring cooperative male group defense.

Significance statement

We used 20 years of data from white-faced capuchins to assess whether male dispersal decisions were predicted by actual reproduction, perceived reproductive opportunities, or future reproductive opportunities and whether male reproduction was predicted by demographic factors and the male's social position. Immigrant subordinate males were less likely to disperse from the group if they were younger and likely to benefit from queuing for future reproductive opportunities. Subordinate males residing in groups with a long-term alpha male and his mature daughters produced a similar number of offspring as did alpha males. Queuing for reproductive opportunities may maintain cooperative male-male relationships in populations with high reproductive skew and long alpha male tenures. Because these patterns only become apparent over time, our study highlights the importance of taking longitudinal paternity patterns into account to understand the evolution of dispersal and cooperation in long-lived species.

Keywords Capuchins · Dispersal · Reproductive success · Delayed direct benefits · Queuing

Introduction

Many mammalian populations show sex-biased dispersal in which males transfer from their natal social group to another group where they attempt to breed (Greenwood 1980). Male dispersal may increase reproductive opportunities with unrelated females, reduce reproductive competition

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Extended author information available on the last page of the article with kin, or both (Johnson and Gaines 1990; Perrin and Mazalov 2000; Lawson Handley and Perrin 2007; Li and Kokko 2019). However, dispersal can also impose considerable costs, including increased predation while moving between groups, aggression from conspecifics when trying to immigrate into a new group, reduced foraging efficiency, reduced body mass, and loss of allies (Isbell and Van Vuren 1996; Bonte et al. 2012; Maag et al. 2019; Woodroffe et al. 2020). Timing dispersal to maximize benefits while reducing costs is therefore key for achieving high Darwinian fitness (Jack and Isbell 2009).

In many group-living animal populations, males continue to transfer between groups throughout their lives (van Noordwijk and van Schaik 1985; Pusey and Packer 1987; Alberts and Altmann 1995; Jack and Fedigan 2004a; Borkowska 2011; Teichroeb et al. 2011; Marty et al. 2016). When males voluntarily engage in secondary dispersal (i.e., transfer from one non-natal group to another; also known as breeding dispersal), it is likely to increase their reproductive opportunities (Clobert et al. 2001). For example, males may increase their access to mates by dispersing to a group with a more-favorable sex ratio, as in ring-tailed lemurs (*Lemur catta*) (Sussman 1992; Parga and Lessnau 2008) and mantled howlers (*Alouatta palliata*) (Clarke and Glander 2010). In red deer (*Cervus elaphus*), male dispersal becomes less common as the ratio of females to young and adult males increases (Jack 2003a; Perez-Gonzalez and Carranza 2009). An individual's dominance status may also influence dispersal decisions: Higher-ranking individuals are less likely to disperse in African wild dogs (*Lycaon pictus*) (Behr et al. 2020) and vervet monkeys (*Chlorocebus pygerythrus*) (Young et al. 2019). Males often increase their dominance rank after secondary dispersal in several primate species, including white-faced capuchins (*Cebus imitator*) (Jack and Fedigan 2004a), yellow baboons (*Papio cynocephalus*) (Alberts and Altmann 1995), and white-thighed black-and-white colobus (*Colobus vellerosus*) (Teichroeb et al. 2011).

A male that increases his rank from subordinate to alpha status via secondary dispersal will likely gain immediate fitness benefits in populations in which the alpha male monopolizes reproduction (Pope 1990; Packer et al. 1991; McElligott and Hayden 2000; Roed et al. 2002; Krutzen et al. 2004; Krakauer 2005; Jack and Fedigan 2006; Kappeler and Schaeffler 2008; Muniz et al. 2010; Ridley 2012; Higham et al. 2021). However, for males that are unable to immigrate or take over a social group on their own, it may be advantageous to reside in a social group as a subordinate. These low-ranking males may be tolerated by a dominant male in exchange for their cooperation during group defense (Vehrencamp 1983; Pope 1990; Emlen 1995; Snyder-Mackler et al. 2012; Hatchwell et al. 2013; Riehl 2013). In addition, even in populations with high reproductive skew, subordinate males could occasionally gain reproductive opportunities when the alpha male is unable to completely monopolize reproduction. The alpha male may have reduced ability to monopolize reproduction because of female mate choice and sperm competition, social perturbations, and highly skewed sex ratios or because of the temporal and spatial distribution of fertile females associated with large group sizes, large group spread, and estrus synchrony (Ims 1988; Say et al. 2001; Roed et al. 2002; Alberts et al. 2003; Ostner et al. 2008; Muniz et al. 2010; McDonald et al. 2013; Bierbach et al. 2014; Schlicht et al. 2015; McDonald and Pizzari 2016; Kaiser et al. 2017; Montana et al. 2020). Subordinate males may also eventually gain alpha status in the group by outcompeting or outliving the former alpha male (Riehl 2013; Díaz-Muñoz et al. 2014). This "reproductive queuing" occurs in several taxa (DuVal 2007; Cockburn et al. 2008; Bro-Jørgensen 2011; Bang and Gadagkar 2012; Riehl 2013) and may be particularly beneficial for relatively young males with lower chances of immediately becoming an alpha male and greater chances of outliving the current alpha male (Kokko and Johnstone 1999; Ragsdale 1999). However, relatively few studies have detailed longitudinal data on male siring success to enable comparisons of long-term reproductive output between males who at least initially queue for alpha status and those who enter a group as an alpha.

Although theory predicts a strong effect of queuing on continued male co-residency (Kokko and Johnstone 1999; Ragsdale 1999) and queuing for reproductive opportunities has been reported from several taxa (DuVal 2007; Cockburn et al. 2008; Bro-Jørgensen 2011; Bang and Gadagkar 2012; Riehl 2013), the relative importance of immediate and delayed reproductive opportunities in shaping subordinate male dispersal decisions has not yet been examined. The detailed demographic and behavioral data that accompany our long-term analysis of paternity patterns in white-faced capuchins (*Cebus imitator*) can offer new insights on this topic. While female white-faced capuchins remain in their birth group for life, males leave their natal group when they are around 4 years old (Jack et al. 2012), and continue to transfer between breeding groups at approximately 4-year intervals on average, although there is considerable variation among individuals (Fedigan and Jack 2004; Jack and Fedigan 2004a). Most cases of secondary dispersal by subordinate males in our study population appear to be voluntary (Jack and Fedigan 2004a), though in some cases, males are forced to disperse due to aggression from one or more males, often in the context of an alpha male replacement (Fedigan and Jack 2004; Jack and Fedigan 2004a). Despite males transferring between groups repeatedly throughout their lives, male group composition is relatively stable with approximately 78% of the immigrant males remaining resident in any given year. Although male reproductive skew is high in this species (Jack and Fedigan 2006; Muniz et al. 2010; Godoy et al. 2016a; Wikberg et al. 2017), males nonetheless form affiliative within-group relationships and dispersal coalitions with other males (Jack 2003a; Jack and Fedigan 2004a, b; Perry 2012; Perry et al. 2012; Wikberg et al. 2018) that are more successful than single males in gaining access to groups of females and their offspring (Fedigan and Jack 2004). Cooperation between unrelated males in spite of the high reproductive skew is not explained by inclusive fitness benefits (Wikberg et al. 2017).

In this study, we investigated the relative importance of immediate and delayed reproductive opportunities in predicting the dispersal decisions and reproductive success of subordinate male white-faced capuchins. First, we assessed whether secondary dispersal decisions of subordinate males could be predicted by actual reproduction (offspring sired within the last 12 months), perceived current reproductive opportunities (adult female-to-immigrant male sex ratio), or perceived future reproductive opportunities (the subordinate male's age, and the number of years the male may have to wait until the alpha male's daughters mature). Actual reproduction is best represented by paternity patterns, because copulations and co-residency with females do not necessarily lead to siring offspring (Carnegie et al. 2006). However, it is unclear whether white-faced capuchins have the ability to recognize paternal kin (Perry et al. 2008; Godoy et al. 2016b; Sargeant et al. 2016), and they may instead use copulations or co-residency with a greater number females in relation to competitors to assess their chances of reproduction (aka reproductive opportunities). We are unable to include copulations as another measure for recent reproductive opportunities due to the lack of continuous observational data throughout the 20-year study period. Future reproductive opportunities, for which a subordinate male must wait or queue, would be greatest if (1) the male is young and therefore more likely to outlive the current alpha (Kokko and Johnstone 1999; Ragsdale 1999) and (2) the alpha male's daughters are close to reaching sexual maturity, because alpha males and their daughters avoid inbreeding (Muniz et al. 2006; Godoy et al. 2016a; Wikberg et al. 2017). Second, we analyzed the degree to which demographic factors (including the number of infants born, sex ratio, subordinate male's age, and the presence of the alpha male's mature daughters) predicted whether a subordinate immigrant male sired offspring during any given year. Third, we investigated whether the number of infants sired differed between the following four social categories of males: (1) alpha males who gained the alpha position immediately after entering the group, (2) alpha males who gained the alpha position by queuing for it until the old alpha male disappeared, (3) subordinate males residing in a group in which the alpha male has mature daughters, and (4) subordinate males residing in a group in which the alpha male does not have mature daughters.

Material and methods

Study population

This study focused on white-faced capuchins in the Sector Santa Rosa of the Área de Conservación Guanacaste, Costa Rica. The mean group size varies between years from 12 to 18 with the highest proportion of adult females (0.27–0.37) and juveniles (0.27–0.41) followed by adult males (0.17–0.25) and infants (0.10–0.18) (Fedigan and Jack 2001, 2012; Hogan et al. 2019). Virtually, all female white-faced capuchin remain philopatric, as only 5 instances of female transfer between groups have been observed over our nearly 40 years of long-term study on this population (Jack and Fedigan 2009). Females give birth for the first time when they are six to seven years old and produce one infant on average every 26.4 months (Melin et al. 2020). Males disperse from their natal group around four years of age (Jack and Fedigan 2004b). Subadult males (7–10 years) are capable of reproduction (Perry et al. 2012), but males do not reach full body size until they are 10 years old and do not acquire the full complement of secondary sexual characteristics unless they attain the alpha status (Jack et al. 2014). The alpha male of a social group is easily identified based on exaggerated secondary sexual characteristics, such as increased facial and shoulder breadth in comparison to subordinate males, and the direction of submissive interactions. However, it is often difficult to discern a rank order among subordinate males due to low rates of agonistic interactions (Perry 1998; Jack 2003b).

White-faced capuchins exhibit a polygynandrous mating pattern and females engage in proceptive behaviors and mate outside the fertile window (Carnegie et al. 2006). This may be the reason why reproduction is skewed towards the alpha male in most groups and time periods even though all males are observed to mate with females (Muniz et al. 2006; Schoof et al. 2014; Godoy et al. 2016a; Wikberg et al. 2017). Although sperm competition remains unstudied in this species, rates of male-male intragroup aggression for access to group membership and alpha male dominance of reproduction suggest the predominant mode of mating competition in this species is direct male-male contest competition rather than sperm competition (Perry 1998; Gros-Louis et al. 2003; Jack 2003b; Muniz et al. 2006; Schoof and Jack 2013; Godoy et al. 2016a; Wikberg et al. 2017). Because copulations and co-residency with females do not necessarily correlate with siring offspring, actual reproduction is best represented by paternity patterns. It is unclear whether or not white-faced capuchins are able to recognize paternal kin. In the absence of paternal kin recognition, males may assess their chances of reproduction based on opportunities to mate or co-residency with a greater number of females in relation to competitors.

Demographic and behavioral data collection

We collected data between 1993 and 2013 from 4 social groups, which included 2 to 11 adult females and 1 to 10 immigrant males (Table 1). During our study period, a total of 41 adult females, 60 immigrant males (31 adults, 19 subadults, and 10 juveniles at the time of immigration), and 152 offspring resided in these groups. We collected demographic and behavioral data to determine group compositions, ages of individuals with known birth dates, and mother–offspring relationships. Because our study involved focal animals in the field, we could not record data blind. About 22% (13/60) of the immigrant males in this study were born in another study group and their exact ages were known. For male immigrants that were born in non-study groups, experienced observers estimated their ages based on similarities in size and appearance with males of known age. We determined alpha male status based on submissive interactions (Perry 1998; Jack 2003b).

Parentage determination

We attempted to collect at least two fecal samples from offspring, mothers, and candidate sires (Wikberg et al. 2014, 2017). We performed DNA extractions, DNA quantification using real-time quantitative polymerase chain reactions (PCRs), and PCR amplifications of up to 20 short tandem repeat loci (Jack and Fedigan 2006; Wikberg et al. 2014, 2017). PCR products were capillary electrophoresed, and genotypes were confirmed as previously described (Jack and Fedigan 2006; Wikberg et al. 2014, 2017). We obtained genotypes for 110 of 152 offspring born in the groups. We did not obtain working samples of the remaining 48 offspring who died as infants ($N = 46$) or juveniles ($N = 2$). We also obtained genotypes for 42 adult females and 38 immigrant males (including all alpha males). We assigned sires at the 95% confidence interval using the software CERVUS (Marshall et al. 1998; Kalinowski et al. 2007) as previously described (Wikberg et al. 2017). We confirmed paternity for 105 genotyped infants born during the study period while the paternity for 5 genotyped infants remained unresolved due to limited genotyping of candidate sires.

Data analysis

We excluded all natal males from our analyses as they never sired offspring in their natal group. Of the 60 immigrant males that were observed in the study groups during the study periods, we excluded 5 males that remained juveniles throughout the study period and were too young to reproduce and 6 males that were only seen in the group temporarily (i.e., present during one group census) and may not have disperse voluntarily (i.e., suspected forced dispersal in association with takeovers). Of the 49 immigrant males included in our analyses, 7 males only occupied an alpha position, 7 males were both alpha and subordinate during the study, and 35 males only occupied a subordinate position.

We investigated whether subordinate immigrant males were more likely to remain in a group (not disperse) when they had recently reproduced (sired offspring during the past 12 months), had high perceived immediate reproductive opportunities (adult female-to-immigrant male ratio), or had high potential for gaining future reproductive opportunities (subordinate male age and time until the alpha male's oldest daughter would mature to adulthood). This analysis contained 38 subordinate immigrant males, because we excluded 4 subordinate males that we lacked exact ages for in addition to excluding 7 males that became alpha immediately upon entering the group and never occupied a subordinate position. We did not count cases when a male was temporarily missing from the group during one census record and later reappeared in the group as a dispersal event. The outcome variable in this analysis was whether or not the subordinate male emigrated a given month ($N = 1206$ male-month combinations). We created a generalized linear mixed model (GLMM) with a binomial distribution and a complementary log–log link function, which is more suitable than the logit link function for skewed outcome variables (Zuur et al. 2009) such as ours (i.e., each month, most subordinate males remained in the group). To represent actual reproduction, we included as a predictor variable whether the subordinate male sired any offspring during the year prior. As a proxy for perceived immediate reproductive opportunities, we used the ratio of adult females to immigrant males (i.e., any non-natal male regardless of when he immigrated to the group) present in the group during that month, because each male may be more likely to reproduce if there are relatively fewer competitors. To assess future reproductive opportunities, we included two variables: the age of the subordinate male and the time until the alpha male's oldest daughter would mature to adulthood (both these fixed effects were recorded as years and months). We also included an interaction effect between these two variables, because increasing male age might make it advantageous to disperse in general, unless the alpha's oldest daughter is about to reach maturity. We coded time until the alpha's oldest daughter reaches maturity as zero if that daughter was already 6 years old and thus considered adult. We coded time until the alpha's oldest daughter reaches maturity as 6 years if the alpha male did not have any daughters, as this would be the earliest that a daughter of the alpha male may become available as a mate. For males that dispersed, we calculated the fixed

Table 1 The number of study groups, infants conceived with confirmed paternity, and the mean number (with the range of numbers in parentheses) of adult females, immigrant adult males, immigrant subadult males, and immigrant juvenile males in each year

Year	Groups	Infants	Females		Adult males		Subadult males		Juvenile males	
1993	2	3	3.20	(3–5)	3.00	(2–4)	3.00	(3–3)	0.50	(0–1)
1994	2	0	3.67	(3–5)	3.13	(2–5)	1.75	(0–3)	0.67	(0–2)
1995	2	4	4.31	(2–6)	2.89	(2–3)	1.50	(0–2)	0.50	(0–1)
1996	2	0	2.94	(2–4)	2.75	(1–4)	0.69	(0–2)	0.06	(0–1)
1997	2	2	3.21	(2–6)	2.86	(1–4)	0.57	(0–2)	0.57	(0–2)
1998	2	3	3.21	(2–5)	2.08	(2–4)	0.54	(0–1)	0.81	(0–2)
1999	2	5	3.00	(4–4)	2.00	(2–2)	0.00	(0–0)	0.50	(0–1)
2000	2	5	4.00	(4–4)	2.57	(2–4)	0.43	(0–2)	0.21	(0–1)
2001	2	2	5.19	(4–8)	4.25	(2–10)	1.12	(0–4)	0.00	(0–0)
2002	2	4	6.57	(4–10)	4.24	(1–8)	0.58	(0–2)	0.00	(0–0)
2003	2	1	4.94	(3–5)	2.30	(1–4)	0.50	(0–1)	0.00	(0–0)
2004	2	6	4.33	(3–6)	3.88	(2–9)	1.06	(0–3)	0.00	(0–0)
2005	2	3	4.54	(4–5)	2.50	(2–3)	1.00	(0–2)	0.00	(0–0)
2006	3	13	4.96	(5–6)	1.77	(0–3)	0.73	(0–2)	0.00	(0–0)
2007	4	7	5.75	(3–9)	2.10	(1–3)	0.06	(0–1)	0.00	(0–0)
2008	4	17	6.38	(3–10)	2.22	(0–4)	1.00	(0–4)	0.23	(0–1)
2009	4	7	7.08	(4–11)	2.19	(1–4)	1.00	(0–4)	0.25	(0–1)
2010	4	7	6.92	(2–10)	2.00	(1–4)	1.58	(0–5)	0.04	(0–1)
2011	4	6	7.19	(3–10)	1.96	(1–3)	1.42	(0–4)	0.00	(0–0)
2012	4	14	6.77	(2–11)	1.85	(0–4)	1.06	(0–3)	0.32	(0–3)

effects using the demographic data from the monthly census prior to the dispersal event rather than data from the same month. All continuous fixed effects were standardized using the z-transformation (Schielzeth 2010). We included male identity and group identity as random effects because we had unbalanced, repeated observations from the same males and groups. Although we had only four groups, simulations indicate that inferences about fixed effects are not affected by including random effects with few levels and that doing so is acceptable when inferences about the grouping levels are not of interest (Gomes 2022).

To examine how social and demographic factors influence the likelihood that subordinate immigrant males sire offspring during a particular year ($N = 107$), we set up a GLMM with a binomial distribution and a complementary log–log link function. Three subordinate immigrant males were excluded because of paternity uncertainty. We retained 39 adult and subadult subordinate immigrant males in this analysis. Fixed effects included the adult female-to-immigrant male ratio, the number of genotyped infants born during that year in that group, whether the alpha male had at least one adult daughter in the group, and male age class (subadult or adult), as subadults (7 to < 10 years) are smaller than adults and may be less likely to gain reproductive opportunities. We included male identity and group identity as random effects.

To assess whether males who occupy different social categories experience different reproductive outputs, we created a GLMM with a Poisson distribution and a log link function in which the outcome variable was the total number of offspring that a male sired while occupying a particular social position ($N = 63$). Five immigrant males were excluded because of paternity uncertainty for their entire tenure. We retained 44 adult and subadult immigrant males in this analysis. As a fixed effect, we included male social position, which had four categories: alpha who gained this status immediately or shortly after entering the group, alpha via queuing, subordinate residing with mature daughters of the alpha male, and subordinate not residing with mature daughters of the alpha male. We also included mean number of adult females while the male occupied that social position, because male reproductive success is likely to increase with the number of potential mates. We used years of tenure in the social position as an offset to account for differences in the length of time that each male occupied a position. Because some immigrant males changed categories, leading to multiple observations for certain males in different social positions (e.g., a subordinate male gained the alpha position via queuing), we included male identity as a random effect. As in previous models, we also included group identity as a random effect. We used the R package emmeans (Lenth 2022) to carry out post-hoc comparisons of estimated marginal means and 95% highest posterior density intervals using Tukey contrasts to determine whether the reproductive outputs differed between any of the social categories of males.

We fit all models in a Bayesian framework using the R package rstanarm in R version 4.1.0 (Goodrich et al. 2020). There were no issues with collinearity based on low variance inflation factors (VIFs: 1.06- 1.71). To assess the proportion of variance explained, we calculated marginal and conditional Bayesian R^2 (Gelman et al. 2018) for the two binomial models using the R package performance (Lüdecke et al. 2021) (Bayesian R^2 methods were not available for the Poisson model). For each model, we used 4 Markov chains with 10,000 total iterations each, including 5000 warm-up iterations, no thinning, and default (weakly informative) priors. We assessed model fit and chain convergence using Rhat (all < 1.001 for all fixed effects) and effective sample size and by visually assessing trace plots for the model's parameters.

Results

The first analysis of subordinate male dispersal included 38 immigrant males that resided in the study groups as subordinate subadult (7–10 years) or adult males (10–19 years). Voluntary dispersals by subordinate immigrant males occurred after the males had resided in the group for a median of 1 year (mean 2.4, *SE* 0.51), although a few males did not disperse until their sixth year in the group ($N = 3$ males). The likelihood of subordinate male dispersal was not predicted by whether the male had recently produced offspring (i.e., actual reproduction), the female-to-male ratio (i.e., perceived immediate reproductive opportunities), or time until the alpha male's oldest daughter would mature to adulthood (i.e., future reproductive opportunities) (Table 2; Fig. 1). The likelihood of subordinate male dispersal increased with the subordinate male's age (which ranged from 7 to 18 years), as expected if younger males are more likely to benefit from remaining subordinate and queuing for future reproductive opportunities (Table 2; Fig. 1). The interaction between the subordinate male's age and the number of years until the alpha male's oldest daughter would mature was not significant (Table 1). The model explained 19% of the observed variation ($R^2_c = 0.19$, $R^2_m = 0.17$).

During the study period, only 20% (21/88) of the offspring with confirmed paternity were sired by a subordinate immigrant male. However, during periods when the alpha male's mature daughters were producing offspring in the same group, up to 52% of the offspring (born by the alpha male's daughters and non-daughters) were sired by a resident subordinate male rather than the alpha male. We did not detect any cases of extra-group paternity. Males never sired offspring in their natal group, and natal males were

Table 2 Generalized linear mixed models predicting subordinate male secondary dispersal, presence of subordinate male reproduction during any given year, or the total number of offspring during a particular position with the median, 95% confidence interval, Rhat, and explained sum of squares (ESS) for each fixed effect

Outcome variable	Fixed effect	Median	95% CI	Rhat	ESS
Dispersal	Sired offspring (yes)	−0.84	−4.06 to 1.05	1.00	11,974
	F:M ratio	−0.04	−0.56 to 0.38	1.00	16,869
	Male age	0.54	0.15 to 1.05	1.00	8476
	Years until alpha's daughter mature	0.22	−0.43 to 0. 49	1.00	12,845
	Male age × years until alpha's daughter mature	−0.27	−0.73– 0.13	1.00	15,211
Siring offspring	Number genotyped infants born	−0.70	−1.99 to 0.56	1.00	4396
	F:M ratio	1.35	0.26 to 2.60	1.00	4223
	Age class (subadult)	−0.54	−2.81 to 1.56	1.00	6443
	Alpha male has adult daughters (yes)	5.74	3.29 to 9.77	1.00	3244
Number of offspring	Number of adult females	0.13	−0.69 to 0.81	1.00	3116
	Subordinate with alpha's daughters	2.13	0.72 to 3.67	1.00	3032
	Alpha via queuing	2.69	1.40 to 4.16	1.00	3809
	Alpha immediately	3.09	1.50 to 4.81	1.00	2953

Fig. 1 Observed residency and dispersal of subordinate immigrant males (with the size of the dots representing sample size) and the predicted relationship between the likelihood of subordinate male secondary dispersal during a particular month (with shaded areas or error bars representing the 95% confidence interval) and (A) siring offspring during the past year; (B) adult female:immigrant male ratio; (C) male age; and (D) number of years until the alpha male's oldest daughter becomes adult, with the *y*-axis being square root transformed

therefore excluded from our analyses. The likelihood of a subordinate male siring infants increased with the presence of mature daughters of the alpha male and with the ratio of adult females to immigrant males (Table 2; Fig. 2). The likelihood of siring infants was not predicted by the subordinate male's age class (adult vs subadult) or by the number of genotyped infants that were born that year (Table 2; Fig. 2). The model explained 74% of the observed variation ($R^2_c = 0.74$, $R^2_m = 0.75$).

Each immigrant male produced between zero and five offspring during any given year. In the GLMM investigating whether different social categories of males were associated with differential reproductive output (using tenure as an offset), subordinate males residing in groups in which the alpha male did not have mature daughters sired fewer offspring compared to all other male social categories, including males who acquired the alpha position immediately after entering the group, males who acquired the alpha position

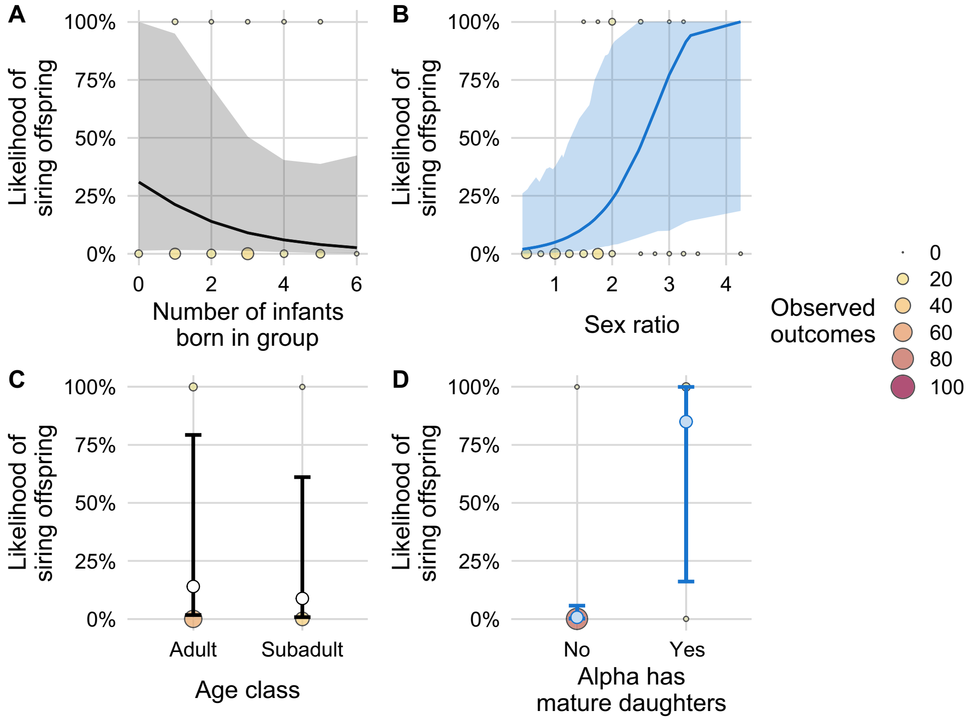

Fig. 2 Observed patterns of subordinate immigrant males siring offspring (with the size of the dots representing sample size) and the predicted relationship between the likelihood of a subordinate immigrant male siring offspring during a particular year (with shaded areas or error bars representing the 95% confidence interval) and (A) number of genotyped infants born that year; (B) adult female:immigrant male ratio; (C) male age category; and (D) presence of alpha's mature daughters, with the *y*-axis being square root transformed

via queuing, and subordinate males residing in a group in which the alpha male had mature daughters (Table 2; Fig. 3). There were no significant differences in number of offspring sired between the latter three social positions (a subordinate position with alpha's mature daughters vs. an alpha position acquired via queuing, coefficient estimate: 0.47, 95% CI: – 0.86 to 1.80; a subordinate position with alpha's mature daughters vs. an alpha position acquired immediately after entering the group, coefficient estimate: 0.96, 95% CI: – 0.77 to 2.68; an alpha position acquired via queuing

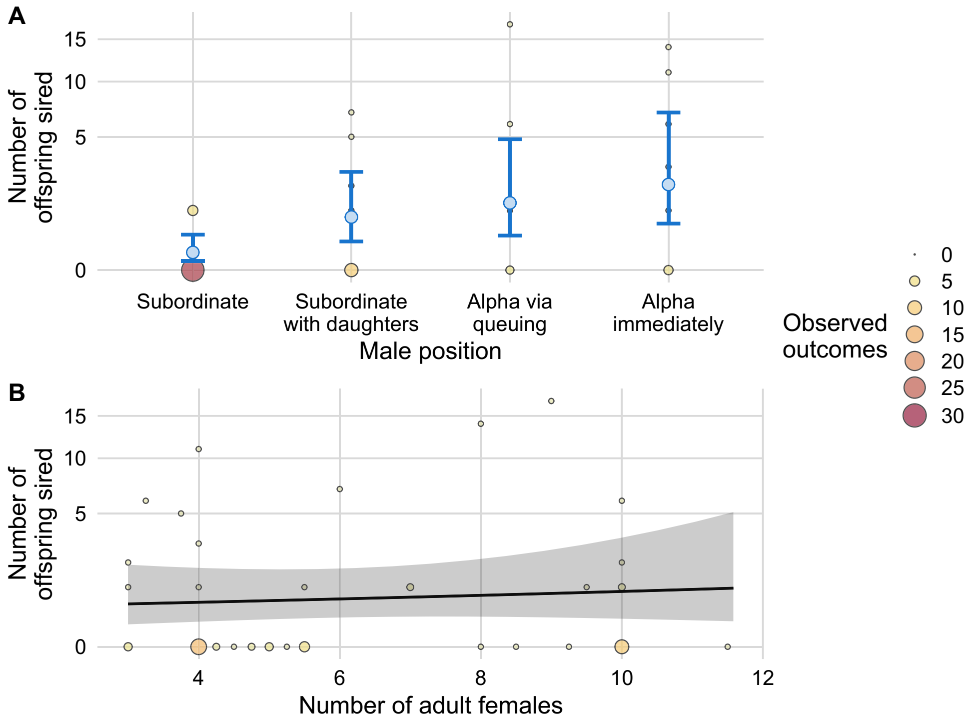

Fig. 3 Observed number of offspring produced by immigrant males (with the size of the dots representing sample size) and the predicted relationship between the total number of infants sired (with shaded areas or error bars representing the 95% confidence interval) and (A) male position and (B) number of adult females in the group, with the *y*-axis being square root transformed

vs. an alpha position acquired immediately after entering the group, coefficient estimate: 0.48, 95% CI: – 1.49 to 2.46). The number of offspring sired did not increase with the number of adult females in the group (Table 2; Fig. 3).

During the study period, each immigrant male produced between 0 and 25 offspring (Fig. 4). Subordinate males that did not reside in a group in which the alpha male had mature daughters produced a median of zero offspring (mean 0, *SE* 0.06, $N = 37$) during their tenures as subordinates. Subordinate males that resided with the mature daughters of the alpha male produced a median of one offspring (mean 2, *SE* 0.79, $N = 10$) during their tenures as subordinates. Alpha males that immediately gained the alpha position when entering the group produced a median of four offspring (mean 4, *SE* 1.52, $N = 10$) during their tenures as alpha males. Males that gained the alpha position by queuing for it until the previous alpha died or dispersed produced a median of five offspring (mean 4, *SE* 2.76, $N = 6$) during their tenures as alpha males.

Discussion

In this population of white-faced capuchins, the likelihood of subordinate male secondary dispersal increased with age, possibly because older males were less likely to benefit from remaining subordinate and queuing for reproductive opportunities. Residing with a long-term alpha male may be particularly beneficial because subordinate males often sire the offspring of the alpha male's mature daughters (Muniz et al. 2006; Godoy et al. 2016a; Wikberg et al. 2017). Subordinate males residing in groups with a long-term alpha male and his mature daughters produced a similar number of offspring as did alpha males. Thus, remaining subordinate can be a low-risk strategy that leads to relatively high reproductive success when the alpha male's tenure is long enough for his daughters to mature to adulthood or when the subordinate male can outlive or eventually outcompete the alpha.

Subordinate male secondary dispersal and reproductive opportunities

In white-faced capuchins, social bonds and coalitions among males are important for successfully taking over and defending social groups (Jack 2003b; Fedigan and Jack 2004; Jack and Fedigan 2004a, b; Perry 2012; Perry et al. 2012; Wikberg et al. 2018). Our previous research found that alpha males residing with one or two subordinate males have higher reproductive success than alpha males residing in uni-male groups in our study population (Wikberg et al. 2017). We may therefore expect alpha males to offer reproductive opportunities in exchange for continued coalitionary support from subordinate males (Emlen 1982; Stacey 1982; Vehrencamp 1983; Reeve and Ratnieks 1993), a pattern that has been reported in other primate species including geladas (*Theropithecus gelada*) (Snyder-Mackler et al. 2012) and chacma baboons (*Papio ursinus*) (Henzi et al. 2010). In contrast to this expectation, previous studies from the Santa Rosa and Lomas Barbudal populations of white-faced capuchins show that alpha males monopolize reproduction during most time periods (Jack and Fedigan 2006; Muniz et al. 2010; Godoy et al. 2016a; Wikberg et al. 2017). Alpha males do not appear to offer reproductive opportunities with unrelated females to subordinate males as staying incentives (Wikberg et al. 2017), similar to many other primates (Port et al. 2018). Even when subordinate immigrant males had produced offspring, often with the alpha male's mature daughters, it did not decrease their likelihood of dispersal. It is possible that it is not worth remaining as a subordinate in the group after recently producing offspring with the alpha's

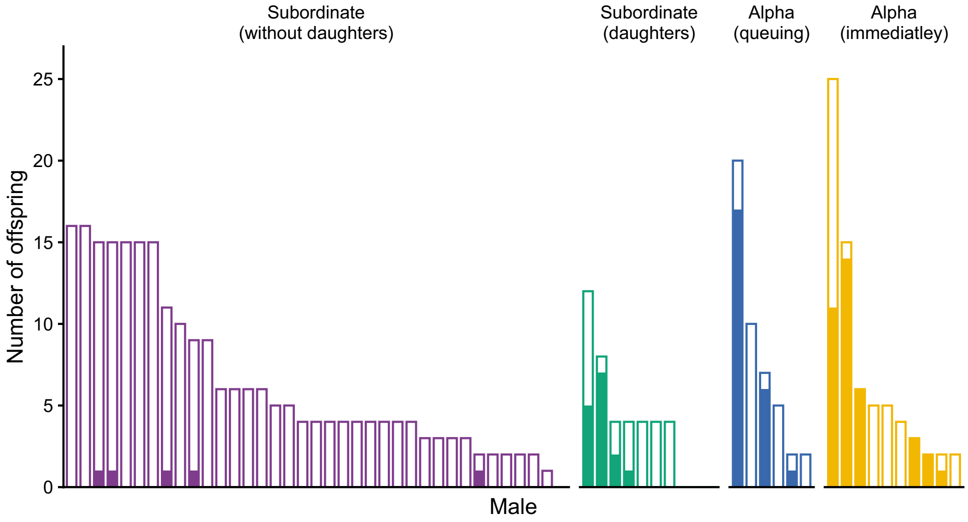

Fig. 4 Each bar represents an immigrant male with the solid part of the bar showing the number of offspring produced during his tenure in the position as follows: (1) a subordinate male in a group in which the alpha male did not have mature daughters; (2) a subordinate male with alpha's mature daughters; (3) an alpha via queuing and (4) an alpha who gained his position immediately or shortly after entering the group and the white part of the bar showing the total number of infants produced in the group during his tenure

mature daughter(s), because she will not produce another offspring until about two years later if her first infant survives (Fedigan et al. 2021). Alternatively, males may have a limited ability to assess parentage in groups where females mate promiscuously even after they become pregnant (Carnegie et al. 2006). White-faced capuchins appear to have limited ability to recognize paternal kin, as males do not bias affiliation towards their own offspring in this population (Sargeant et al. 2016) and white-faced capuchin females do not show paternal kin-bias (Perry et al. 2008; Sargeant et al. 2015). However, spatial proximity appears to offer clues to father-offspring relationships in the Lomas Barbudal capuchin population, which leaves open the possibility that individuals may recognize at least some types of paternal kin (Godoy et al. 2016b).

In contrast to capuchins, coresident males with cooperative relationships share reproduction relatively equitably in some groups of Geoffroy's tamarins (*Saguinus geoffroyi*) (Díaz-Muñoz 2011), northern muriquis (*Brachyteles hypoxanthus*) (Strier et al. 2011), chimpanzees (*Pan troglodytes schweinfurthii*) (Wroblewski et al. 2009), lions (*Panthera leo*) (Packer et al. 1991), and bottlenose dolphins (*Tursiops* sp.) (Wiszniewski et al. 2012). It is possible that alpha male capuchins do not need to offer reproductive opportunities as staying incentives if most subordinate males are unlikely to be able to reproduce elsewhere. In support of this notion, the best predictor of secondary dispersal by subordinate males was the male's age. The younger the males were, the less likely they were to engage in dispersal, perhaps because residing in a group provides a safe haven that increases survival while waiting for reproductive opportunities to arise (Kokko and Ekman 2002). These young males may benefit from remaining in a social group via reduced risk of predation or aggression from conspecifics (Isbell and Van Vuren 1996). Such a safe haven may be particularly beneficial for young males that have not yet reached full body size and are unable to outcompete adult males (van Noordwijk and van Schaik 2001). Once these young capuchin males attain full body size, they can attempt to gain reproductive opportunities by competing for an alpha position or by mating with the alpha male's mature daughters, if present. Queuing may also cease to be beneficial when the subordinate male is relatively old and unlikely to outlive the alpha male (Kokko and Johnstone 1999; Ragsdale 1999).

White-faced capuchin alpha males and their mature daughters avoid inbreeding, although it is not clear whether it is the alpha male, daughter, or both who actively avoid mating (Muniz et al. 2006; Godoy et al. 2016a; Wikberg et al. 2017). Because of this inbreeding avoidance, we also predicted that subordinate males would be more likely to remain if the alpha male's daughters were close to reaching adulthood and that the presence of mature daughters of the alpha male would increase the likelihood of subordinate males siring offspring. Although a subordinate male's likelihood of siring offspring increased when the alpha male had mature daughters, the number of years until the alpha male's oldest daughter reached adulthood did not increase the likelihood of subordinate male's dispersal. There was no significant interaction effect between male age and time until the alpha male's oldest daughter would reach adulthood. Thus, future reproductive opportunities with the alpha male's daughters do not seem to provide a strong incentive for remaining in the group as a subordinate. This may be because potential future reproductive opportunities are uncertain and may not outweigh the costs of remaining in the group if the subordinate male is likely to gain immediate reproductive opportunities in another group.

Males may instead use perceived short-term reproductive opportunities when determining whether to disperse. Subordinate immigrant males in our study population were less likely to sire offspring when adult female-to-immigrant male ratios were unfavorable. Thus, the sex ratio may provide a relatively good estimate of reproductive opportunities, and previous studies of our study population and other species have documented that males tend to disperse from groups or areas with relatively few females in relation to males, presumably to increase their potential reproductive opportunities (Sussman 1992; Jack and Fedigan 2004a; Parga and Lessnau 2008; Perez-Gonzalez and Carranza 2009; Clarke and Glander 2010; Steifetten and Dale 2012). However, the likelihood of secondary dispersal by subordinate males in this study was not predicted by the adult-female-to-immigrant-male ratio. The apparent lack of an effect of sex ratio on dispersal in this study may be due to our inability to account for the difference in sex ratios between the departing group and the receiving group.

Strategies to obtain high reproductive success

Although male reproduction is skewed towards alpha males in this species (Muniz et al. 2006; Godoy et al. 2016a; Wikberg et al. 2017), being an alpha male does not guarantee siring offspring, nor does being subordinate preclude reproduction. Some alpha males, particularly those that did not hold their alpha position for long, did not sire any offspring, likely because of a relatively low number of females in estrus at any given time (Carnegie et al. 2006). Some subordinate males sired as many offspring as the alpha male did or, for limited periods of time, sired even more offspring than the alpha male (Wikberg et al. 2018).

With that being said, the lowest long-term reproductive output was associated with the position of being subordinate in a group that did not contain mature daughters of the alpha male. Most subordinate males did not produce any offspring while occupying this social position. A similar low reproductive output by subordinate males has been documented in a large number of populations in which the alpha male monopolizes reproduction (Pope 1990; Packer et al. 1991; McElligott and Hayden 2000; Roed et al. 2002; Krutzen et al. 2004; Krakauer 2005; Kappeler and Schaeffler 2008; Muniz et al. 2010; Ridley 2012; Higham et al. 2021). Rather surprisingly, there was no significant difference in the long-term reproductive output of males occupying the other three types of social categories. Specifically, capuchin males that enter a group as an alpha male did not have higher long-term reproductive success than some of the other types of males. For example, subordinate males who successfully queued for the alpha position until the former alpha disappeared had similar reproductive output after attaining the alpha position as males who became the alpha male immediately after entering a new group. This may perhaps be explained by these two types of males having similar tenures once they achieve the alpha status (and we control for tenure length in our analysis). Some subordinate males were able to gain equally high reproductive success if they resided with a long-term alpha male whose daughters had matured to adulthood. This strategy may include staying subordinate and helping the alpha maintain his rank for up to six years, at which point the alpha's daughters reach sexual maturity. It is possible that a relatively high survival probability of subordinate male capuchins in combination with low direct fitness costs for young males (see previous section) makes queuing over long time periods a successful strategy. Similarly, potential future reproductive opportunities may be the reason why subordinate lance-tailed manakins (*Chiroxiphia lanceolata*) cooperate with an unrelated alpha, even when the latter does not offer immediate reproductive opportunities as staying incentives (DuVal 2007). In lance-tailed manakins, beta males that perform cooperative courtship displays are more likely than other males to gain future reproductive opportunities by inheriting the alpha position the following year (DuVal 2007). There are multiple alternative strategies to gain high reproductive success in other species of birds and mammals, some of which involve male-male cooperation (Packer et al. 1991; Krützen et al. 2003). These multiple routes to reproductive success may explain why males in some populations show a remarkable degree of cooperation despite reproduction being skewed towards the alpha male.

Our study is one of few that have compared the importance of actual reproduction, perceived reproductive opportunities, and delayed reproductive opportunities for secondary dispersal decisions. We conclude that low costs associated with remaining subordinate, possibly coupled with the potential for gaining future reproductive benefits, provided stronger staying incentives than do actual immediate reproductive opportunities, particularly for young males. Over time, queuing animals that eventually gained reproductive opportunities as an alpha male or as a subordinate male mating with the daughters of the alpha male were as successful as males that immediately took over the alpha position. Because these patterns only become apparent over time, our study highlights the importance of taking longitudinal paternity patterns into account to fully understand the evolution of dispersal and cooperation in long-lived species such as capuchins. Longitudinal data from individual males are thus necessary to investigate strategies for achieving a high long-term reproductive success, particularly when those strategies vary across individuals and time (Alberts et al. 2003; DuVal 2007; Dubuc et al. 2014; Milich et al. 2020). By considering such longitudinal patterns, our study and other long-term studies offer valuable insights into the apparent paradox of cooperation between unrelated males in populations with high reproductive skew.

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Author contribution The authors designed the study (ECW, KMJ, LMF, SK), genotyped the samples (ECW, FAC, AS, MLB, TH), analyzed the data (ECW, FAC), and/or wrote the manuscript (ECW, KMJ, LMF, FAC, MLB, SK).

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Data availability The data are available on figshare, https://figshare.com/s/c6a6cd40049fca9ff33b.

Declarations

Ethics approval The data collection methods followed the ABS/ASAB guidelines, and we obtained approval for this study from the University of Calgary's Life and Environmental Sciences Animal Care Committee (LESACC Protocol # AC2—0418) and Tulane University's Institutional Animal Care and Use Committee (IACUC Protocol #810). We also obtained permission to conduct this study from the Costa Rican Park Service and the administration of the Área de Conservación Guanacaste.

Competing interests The authors declare no competing interests.

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Authors and Affiliations

Eva C. Wikberg[1,2] · **Katharine M. Jack**[3] · **Fernando A. Campos**[1] · **Mackenzie L. Bergstrom**[4] · **Shoji Kawamura**[2] · **Linda M. Fedigan**[4]

✉ Eva C. Wikberg
eva.wikberg@utsa.edu

[1] Department of Anthropology, University of Texas at San Antonio, One UTSA Circle, MH 4.03.38, San Antonio, TX 78249, USA

[2] Department of Integrated Biosciences, University of Tokyo, Kashiwa, Chiba 277-8562, Japan

[3] Department of Anthropology, Tulane University, New Orleans, LA 70119, USA

[4] Department of Anthropology and Archaeology, University of Calgary, Calgary, AB T2N1N4, Canada