Inbreeding avoidance and female mate choice shape reproductive skew in capuchin monkeys (*Cebus capucinus imitator*)

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Abstract

Reproductive skew in multimale groups may be determined by the need for alpha males to offer reproductive opportunities as staying incentives to subordinate males (concessions), by the relative fighting ability of the alpha male (tug-of-war) or by how easily females can be monopolized (priority-of-access). These models have rarely been investigated in species with exceptionally long male tenures, such as white-faced capuchins, where female mate choice for novel unrelated males may be important in shaping reproductive skew. We investigated reproductive skew in white-faced capuchins at Sector Santa Rosa, Costa Rica, using 20 years of demographic, behavioural and genetic data. Infant survival and alpha male reproductive success were highest in small multimale groups, which suggests that the presence of subordinate males can be beneficial to the alpha male, in line with the concession model's assumptions. None of the skew models predicted the observed degree of reproductive sharing, and the probability of an alpha male producing offspring was not affected by his relatedness to subordinate males, whether he resided with older subordinate males, whether he was prime aged, the number of males or females in the group or the number of infants conceived within the same month. Instead, the alpha male's probability of producing offspring decreased when he was the sire of the mother, was weak and lacked a well-established position and had a longer tenure. Because our data best supported the inbreeding avoidance hypothesis and female choice for strong novel mates, these hypotheses should be taken into account in future skew models.

Keywords: animal mating/breeding systems, behavior/social evolution, inbreeding, mammals

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Introduction

Reproductive skew signifies unequal sharing of reproductive opportunities across same-sexed group members. The most extreme case occurs in some eusocial societies and cooperative breeders, in which only the alpha animal reproduces and subordinate animals help rear the young (Hymenoptera: Reeve & Keller 1995; African wild dogs, *Lycaon pictus*: Girman *et al.* 1997). In plural breeders, reproduction is skewed to the alpha male in some species (fallow deer, *Dama dama*: McElligott & Hayden 2000; mountain gorilla, *Gorilla beringei beringei*: Bradley *et al.* 2005; Verreaux's sifakas, *Propithecus verreauxi*: Kappeler & Schaeffler 2008), while male group members share reproductive opportunities relatively equally in other species (northern muriqui, *Brachyteles hypoxanthus*: Strier *et al.* 2011; Indo-Pacific

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bottlenose dolphins, *Tursiops aduncus*: Wiszniewski *et al.* 2012). The degree of reproductive skew can vary considerably within closely related taxa and even within the same species or population (Packer *et al.* 1991; Keller & Reeve 1994; Field *et al.* 1998; Ostner *et al.* 2008; Lucas *et al.* 2011). Several models have been proposed to explain the degree of reproductive skew (reviewed in Johnstone 2000; Port & Kappeler 2010). In this study, we evaluate which of the following models or hypotheses can best explain the degree of reproductive skew in a primate species (*Cebus capucinus imitator*) in which the degree of reproductive partitioning can vary from reproduction being completely dominated by the alpha male to being equally shared between alpha and subordinate males (Muniz *et al.* 2010).

The concession model suggests that the alpha male benefits from the presence of subordinate males and will offer them reproductive opportunities as staying or peace incentives (Emlen 1982; Stacey 1982; Vehrencamp 1983; Reeve & Ratnieks 1993). How large a share of the reproduction that the subordinate male will receive depends on his chances of breeding elsewhere or overtaking the alpha position in the current group (Vehrencamp 1983; Reeve & Ratnieks 1993). For example, the alpha male may not have to offer any reproductive opportunities if the constraints on breeding are severe and the subordinate male is unlikely to become an alpha male in his current group or elsewhere. In contrast, the alpha male will have to offer more reproductive opportunities as peace or staying incentive when his fighting ability is relatively low because the subordinate male may otherwise challenge him or when the subordinate male is likely to successfully breed elsewhere. Although each subordinate male requires a share of the reproduction, alpha male reproductive success can still increase with the number of subordinate males if groups with more males produce more infants. If the alpha is related to the subordinate male, the latter will gain inclusive fitness benefits from cooperating with the alpha male and will not require as large a share of the reproduction as unrelated males (Vehrencamp 1983; Reeve & Keller 1996).

The queuing model is a modified version of the concession model, which includes the possibility that subordinate males gain future direct fitness benefits by being in position to replace the alpha male when his tenure ends (Kokko & Johnstone 1999; Ragsdale 1999). The effect of queuing on reproductive skew can be so powerful that a young subordinate male that is likely to outlive the current alpha may not require any current reproductive opportunities regardless of relatedness and relative fighting abilities of subordinate and alpha males (Kokko & Johnstone 1999; Ragsdale 1999). In contrast, the alpha male will have to share reproduction with older subordinate males that are less likely to benefit from queuing.

The tug-of-war, or incomplete control, model proposes that alpha and subordinate males struggle to gain as many reproductive opportunities as possible. The alpha male will therefore lose more reproductive opportunities when he resides with relatively strong subordinate males (Reeve *et al.* 1998). This is similar to the concession model's prediction, even though the latter expects the alpha to willingly give up these reproductive opportunities. A key difference between the concession model and the tug-of-war model is the effect of relatedness on reproductive skew. Because competition between the alpha male and the subordinate male reduces group productivity, related males will invest less in reproductive competition to minimize reductions in inclusive fitness according to the tug-of-war model (Reeve *et al.* 1998). Therefore, group productivity will increase with male relatedness, although the degree of reproductive skew will remain relatively unaffected by male relatedness (but see Reeve *et al.* 1998; Johnstone 2000 for cases when skew may either increase or decrease with relatedness). The tug-of-war model does not predict reproductive skew to vary with group productivity or with constraints on solitary breeding, which is another difference from the concession model (Reeve *et al.* 1998).

Although not generally considered as a reproductive skew model, the priority-of-access model may also explain reproductive partitioning. The priority-of-access model suggests that the alpha male will be able to monopolize reproduction if breeding synchrony is low (Altmann 1962; Alberts *et al.* 2003, 2006). Thus, the degree of reproductive skew will decrease with the number of females exhibiting synchronous oestrus (e.g. Say *et al.* 2001; Ostner *et al.* 2008).

Finally, reproductive skew may depart from these predicted patterns due to mate choice for unrelated and novel partners (Magrath & Heinsohn 2000; Koenig & Haydock 2001). Breeding between close kin increases the degree of homozygosity in the offspring and may lead to the expression of recessive deleterious alleles in populations where inbreeding is rare and these alleles have not been purged (Keller & Waller 2002; Lehtonen & Kokko 2012). If the cost of inbreeding is relatively low, it may be offset by the increased reproductive success of the related mate (Bengtsson 1978; Waser *et al.* 1986; Kokko & Ots 2006; Szulkin *et al.* 2013). To reap such inclusive fitness benefits, relatives should prefer breeding with each other (Bengtsson 1978; Waser *et al.* 1986; Kokko & Ots 2006; Szulkin *et al.* 2013). In contrast, mechanisms for inbreeding avoidance should be under positive selection if inbreeding has a negative effect on offspring fitness (Bengtsson 1978; Waser *et al.* 1986;

Kokko & Ots 2006; Szulkin *et al.* 2013). Individuals can avoid inbreeding by dispersing from their natal group or natal home range, delaying maturation until related mates are replaced, or by exerting mate choice for unrelated mates (Blouin & Blouin 1988; Pusey & Wolf 1996). In mammals, females are expected to have stronger mate preferences than males because of a larger degree of female parental investment (Trivers 1972). Males may not avoid mating with related females if it does not affect their abilities to sire offspring with unrelated females, while females may show a strong mating preference for unrelated males (Waser *et al.* 1986; Blouin & Blouin 1988; Kokko & Ots 2006). In spotted hyenas (*Crocuta crocuta*), females prefer to mate with subordinate immigrants rather than natal alpha males (Engh *et al.* 2002). Although the effect of female mate choice on reproductive skew may be particularly strong in female-dominant species like hyenas, females in male-dominant primate species are still able to exert subtle preferences (Jack 2003b; Tennenhouse 2014). Female primates often show mate choice based on male strength, alpha status, relatedness and novelty (the latter may be used as a cue to assess relatedness) (Small 1989). However, female preferences may vary between periods of stable and unstable male dominance and group membership (Manson 1994). For example, when the alpha animals have tenures that exceed the age at which their offspring become mature, they often avoid breeding with them, which may give subordinate animals an opportunity to reproduce (Griffin *et al.* 2003; Muniz *et al.* 2006; Vigilant *et al.* 2015; Godoy *et al.* 2016a,b). Thus, mate choice for unrelated, novel males may lead to a lower reproductive skew in some populations.

Despite the long-held interest in the interplay between cooperation and competition in complex societies, debate continues over which of these hypotheses can best explain reproductive skew in different animal populations (Nonacs & Hager 2011; Arct *et al.* 2015 and comments). This lack of consensus is largely due to discrepancies between empirical and theoretical studies (Kokko & Ots 2006) and between different study populations, and some of these discrepancies may be caused by methodological issues (Wang 2010; Szulkin *et al.* 2013; Reid *et al.* 2015). Some studies of insects have been able to overcome these methodological issues by manipulating the environmental, genetic and social conditions (Langer *et al.* 2004). Such manipulations are impossible for many wild animals due to ethical concerns, and conclusive evidence in support of one hypothesis over another is therefore scant in many populations. This is particularly true for species with slow life histories where longitudinal data collection is necessary. In these species, limited reproductive opportunities for males constrain their potential for reproductive sharing (Port & Kappeler 2010). Thus, traditional skew models may need modifications to be applicable to a wider range of species, and detailed empirical data are necessary to build better theoretical models for these species (Port & Kappeler 2010).

Our study of paternity patterns in the white-faced capuchin (*Cebus capucinus imitator*) enables us to compare the explanatory power of the different hypotheses of reproductive partitioning. We have over 20 years of detailed demographic, behavioural and genetic data from several wild capuchin groups, which allowed us to circumvent methodological issues that have hampered conclusive findings in previous studies (see Methods and Supporting Information for further details). White-faced capuchin males form tolerant or affiliative social relationships (Perry 1998; Jack 2003a) and often disperse in parallel with related or unrelated males (Jack & Fedigan 2004a,b; Perry 2012; Perry *et al.* 2012; Wikberg *et al.* 2014). These male coalitions are better than single males at taking over social groups consisting of several breeding natal (i.e. born in the group) females (Fedigan & Jack 2004). Because males benefit from having coalitionary partners, they may share reproductive opportunities as predicted by the concession model. However, coresident males occasionally engage in aggressive interactions (Perry 1998) and kill off each other's offspring (Schoof *et al.* 2015). Such overt reproductive competition may be more in line with the tug-of-war model. There is no strict reproductive season in our study population (Carnegie *et al.* 2011), which presumably leads to relatively low oestrus synchrony and high potential for alpha male monopolization according to the priority-of-access model. The tenure of an alpha male can last up to 18 years (Perry 2012), whereas females typically produce their first offspring around the age of 6 years (Perry *et al.* 2012). Because females remain philopatric, alpha males with such long tenures reside with their mature daughters (Muniz *et al.* 2006; Godoy *et al.* 2016a). If alpha males and their mature daughters avoid inbreeding and/or females prefer to mate with novel males, male reproductive skew may be relatively low in groups with long-term alpha males.

Previous studies of white-faced capuchins focused on quantifying the degree of reproductive skew and evaluating which factors shape alpha male siring success (Jack & Fedigan 2006; Muniz *et al.* 2010). Here, we will further investigate male reproductive partitioning: first, by examining whether group productivity is positively correlated with the number of reproductively active males (as predicted by the concession model) or with male relatedness (as predicted by the tug-of-war model), and second, by formally evaluating the empirical support for the different reproductive skew models

(Table 1, Supporting Information) for the first time in this study species.

Methods

This study was conducted in Sector Santa Rosa of the Área de Conservación Guanacaste, Costa Rica. We collected data from four groups, Cerca de Piedra (CP), Exclosure (EX), Guanacaste (GN) and Los Valles (LV), between 1993 and 2013 (Table 2). Each group consisted of two or more natal adult females, one or more immigrant males (of which at least one was adult) and several natal immature males and females. Observers collected demographic data from each group at least once a month when present at the site ($N = 582$ group-months), and we used these data to determine group composition, immigration status, immigrant male tenure (mean: 4.5 years; range: 0–15 years), age of individuals and mother–offspring relationships. We also recorded submissive interactions (e.g. avoid, supplant, fear grin and flee) whenever we observed them (ad libitum sensu Altmann 1974) to determine alpha male status. Although alpha males can easily be distinguished based on the direction of these submissive interactions (Perry 1998; Jack 2003a; Jack *et al.* 2014), we were often unable to rank the subordinate males in relation to each other due to a limited number of observed submissive interactions. Resident males (i.e. all male group members) were categorized according to dominance rank (i.e. alpha or subordinate) and immigration status (i.e. natal or immigrant). Only immigrant males attained the alpha position during our study, whereas subordinate males were either immigrant or natal. Natal males were included as potential sires in our parentage analyses, but they were excluded from the analyses of group productivity and reproductive sharing because they never sired offspring in their natal group.

Table 2 Group composition during each study year

Group	Study years	Adult females	Immigrant males[†]	Infants
CP	1993–2012	2–10 (14/15)	1–6 (9/11)	0–7 (42/53)
EX	2006–2013	3–4 (4/4)	1–4 (6/6)	0–4 (10/16)
GN	1999–2013*	4–11 (12/12)	3–9 (9/13)	0–8 (36/46)
LV	1993–2013	4–6 (9/10)	2–10 (19/30)	0–4 (33/49)

The range represents the number of adult females, immigrant males and infants present in any year. The proportions of genotyped animals are indicated in parentheses.
*Group composition before 2006 is based on opportunistic encounters because it was not yet a behavioural study group.
[†]Some males resided in several groups during the study, and they are counted once in each group that they resided in.

Table 1 The alpha male's siring success is predicted to increase or decrease (indicated by arrows) with these predictor variables according to the hypotheses we investigated in this study

Hypothesis	Variables predicted to affect alpha siring success	Fixed effects in GLMM*	AICc	Δ	Weight
Null model	—	—	81.78	26.37	0.00

Concession	Alpha fighting potential (↑)
	  Alpha fighting potential (↑)
	  Alpha-subordinate relatedness (↑)
	  Number of individuals that needs
	    to be offered staying/peace incentives (↓)
		Alpha is prime age
		  Alpha is weak
		  Alpha-subordinate male R
		  Number of males
			73.69	18.29	0.00

Queuing	Subordinate's likelihood of not
	  benefiting from queuing (↓)
		Alpha resides with older
		  subordinate
			82.15	26.75	0.00

Tug-of-war	Alpha fighting potential (↑)
	  Alpha fighting potential (↑)
		Alpha is prime age
		  Alpha is weak
			70.68	15.28	0.00

Priority-of-access	Female breeding synchrony (↓)
	  Female breeding synchrony (↓)
		# of adult females
		  # of offspring conceived
			81.77	26.36	0.00

Mate choice (relatedness, strength)	**Alpha-mother relatedness (↓)**
	  Alpha is weak or low quality (↓)
		**Alpha is the sire of the
		  infant's mother**
		  Alpha is weak
			55.40	**0.00**	**0.87**

Mate choice (novelty, strength)	**Male familiarity (↓)**
	  Alpha is weak or low quality (↓)
		Alpha tenure
		  Alpha is weak
			59.28	**3.88**	**0.13**

We created a GLMM to investigate each hypothesis, and evaluated the support for each model based on AICc, delta (i.e. difference in AICc between the current model and the model with lowest AICc) and Akaike's weight (i.e. normalized model likelihood). The best supported hypotheses based on model AICc values and fixed effects' estimates (Fig. 3) are in boldface. All models contained group, mother identity and male identity as random effects.
*These fixed effects are used as proxies of the corresponding variables in the predictions column.

We attempted to collect at least two faecal samples from all capuchins in our study groups (Table 2). Of the 164 offspring born during the study period, we were unable to collect samples from 43 that died at an early age. The lack of samples due to early mortality was not biased to potentially inbred offspring produced by the alpha male's mature daughters (see Supplemental Information). We also lacked samples from 1 of 41 adult females that died in the beginning of this study and 14 of 43 immigrant males that dispersed before we started to collect samples for this study. Approximately 1 g of faeces was dissolved in 5 mL RNAlater (Life technologies, Tokyo, Japan) and stored in a freezer. From the faecal samples, we extracted DNA using the Qiamp stool kit (Qiagen, Crawley, UK) and determined the amount of genomic DNA using real-time quantitative polymerase chain reactions (Morin *et al.* 2001). The reactions were set up with 7.40 μL H_2O, 10.00 μL 2 × Premix Ex Taq buffer, 0.20 μL forward primer, 0.20 μL reverse primer, 0.20 μL Taq Man probe library (Takara Bio Inc.) and 2.00 μL template. The extracts contained a sufficient amount of DNA for subsequent genotyping for 121 offspring (which include 24 females that became breeding adults in their natal group and 4 males that remained in their natal group past subadulthood and were therefore considered as potential sires for offspring born during certain years), 40 adult females and 35 immigrant males (which include 9 alpha males, 20 subordinate males and 6 males that first held a subordinate position and later became alpha or vice versa).

We used polymerase chain reactions to amplify 20 short tandem repeat loci: Apm01, Ceb01, Ceb02, Ceb03, Ceb04, Ceb07, Ceb08, Ceb09, Ceb10, Ceb11, Ceb105, Ceb115, Ceb 199, Ceb120, Ceb127, Ceb128, Ceb130, d3s1210, d7s794 and pepl4 (see Jack & Fedigan 2006; Muniz & Vigilant 2008; Cortes-Ortiz *et al.* 2010 for details regarding primers and cycling protocol). We combined diluted PCR products and a size standard (Genescan 600 LIZ, Applied Biosystems, Tokyo, Japan) for capillary electrophoresis on an ABI PRISM3130 (Applied Biosystems, Tokyo, Japan). GENEMAPPER v3.7 (Applied Biosystems, Tokyo, Japan) automatically assigned allele sizes, which we confirmed and corrected when necessary by visually inspecting the electropherograms. Heterozygotes were confirmed using at least two replicates, while the number of replicates required to confirm homozygotes was calculated based on extract quality and locus-specific dropout rates (modified from Morin *et al.* 2001). We confirmed genotypes at a mean of 15 loci per study animal. We confirmed individual identities by genotyping two faecal samples collected at different times. For offspring from whom we lacked two well-amplifying samples, we confirmed their identities by checking that they shared at least one allele per locus with their mother (known from the demographic records).

We used the software CERVUS (Marshall *et al.* 1998; Kalinowski *et al.* 2007) to assign sires for all offspring and to assign mothers for offspring born in GN group between 1999 and 2006, as detailed demographic data were not collected from this group before 2006. Mothers were known from the demographic record for all other offspring. We considered all resident males (immigrant and natal) and females that were at least 6 years old at the time of conception as candidate parents. We calculated the proportion of genotyped candidate mothers (or sires) as the number of genotyped resident females (or males) divided by the total number of resident females (or males). However, we capped the maximum proportion of genotyped candidate parents to 0.90 to account for the possibility of extra-group paternity. The proportion of genotyped candidate sires ranged from 0.22 to 0.90, and we set the proportion of sampled candidate mothers in GN group to 0.90. We set the estimated rate of genotyping errors to 1% (Supporting Information). We used parentage analysis simulations with 10 000 iterations to find the critical delta scores to confirm parentage with 95% confidence given the observed allele frequencies in our population. We used these parentage assignments for determining whether the alpha male sired the offspring born in his group and for determining whether the alpha male and the mother should be classified as a sire–daughter dyad. We only investigate inbreeding avoidance between the alpha male and his mature daughters, because males never gained the alpha position in their natal group during our study and none of the alpha male–adult female dyads were categorized as close kin other than father–daughter dyads. Using the same set of markers to assess kinship between potential sires, mothers and offspring can in some cases bias parentage assignments to males that are less related to the mother and therefore seemingly support the inbreeding avoidance hypothesis (Wetzel & Westneat 2009; Wang 2010). However, our analysis is unlikely to suffer from such bias because our parentage assignments are reliable (Supporting Information).

We calculated estimated relatedness values (R) between alpha and subordinate males using the software ML-Relate (Kalinowski *et al.* 2006) because this method provided the most accurate relatedness estimates in our study population (Supporting Information). Such marker-based methods reflect genetic similarity more accurately than relatedness values calculated from shallow pedigrees according to recent studies (Forstmeier *et al.* 2012; Robinson *et al.* 2013). Due to these recent recommendations and a larger sample size, we use R-values rather than pedigree

relationships as our predictor variable for male relatedness in the analysis presented here.

Data analyses

Group productivity is affected by (i) whether each parous female reproduces annually and (ii) whether each infant survives to 1 year of age (i.e. the critical stage for offspring survival in this species). We investigated whether these two outcome variables were affected by either immigrant male group size as predicted by the concession model or the relatedness between the alpha and the subordinate immigrant males as predicted by the tug-of-war model (Tables S1 and S2, Supporting information). Group productivity can either increase linearly with male group size or be higher in small multimale groups than in unimale and large multimale groups (Port *et al.* 2010). Therefore, we used two alternative variables to represent group size: the number of immigrant males or a category that described immigrant male group size (unimale, small multimale with two to three males, or large multimale with >3 males). Because female capuchins only give birth to an infant every 2 years (if the infant survives), we included whether or not the female reproduced the previous year as a fixed effect in the models of female reproduction. In the models of infant survival, we included as a fixed effect whether there was a takeover (i.e. a change in alpha male status) during the 6 months before the infant was born (during female gestation) or the 12 months after the infant was born (during female lactation). If there is a takeover when the female is in gestation or lactation, her infant is vulnerable to infanticide by the new alpha male, and this is a major cause of infant mortality in our study population (Fedigan *et al.* 2008). For each outcome variable, we created a set of competing generalized linear mixed models (GLMMs) with binomial distribution and logit-link function: one

null model without any fixed effects and three alternative models (with one to two fixed effects) that each tested a particular hypothesis outlined in the introduction (Table 3, sensu Burnham & Anderson 2002). We included year, group identity and female identity as nested random effects in all models, because the reproductive potential may vary between females and also between groups and years due to environmental variation in food supply (Fedigan *et al.* 2008).

We compared the estimated reproductive success of alpha males in unimale and multimale groups based on mean values of alpha male tenure, access to females, interbirth interval and reproductive skew. We calculated estimated reproductive success using the following formula: [(mean alpha male tenure * mean number of adult females)/mean interbirth interval]* mean proportion of offspring sired by the alpha male (Snyder-Mackler *et al.* 2012). The interbirth interval during each alpha male's tenure was estimated from the total number of infants born in the group that survived until they were 1 year old, weighted by the number of female-years for that group (Snyder-Mackler *et al.* 2012). We used the same formula to calculate the minimum percentage of offspring that alpha males in multimale groups should sire and still have higher reproductive success than males in unimale groups. We only included alpha males with complete tenures.

We investigated male reproductive skew by asking whether an alpha male or a subordinate male sired a particular offspring. We chose to use this outcome variable rather than a skew index, because it is difficult to find a meaningful time period over which to calculate reproductive skew in species that lack strict reproductive seasons, with few offspring born each year and with exceptionally long alpha tenures (Port & Kappeler 2010). An additional benefit of analysing whether or not an alpha male sired a particular offspring rather than using a skew index is that it allowed us to investigate

Table 3 Models of annual group productivity and each model's outcome variable, fixed effects (with arrows indicating predicted effect on group productivity), AICc, delta and Akaike's weight

Outcome variables	Hypothesis	Fixed effects	AICc	Δ	Weight
Female reproduction	—	Reproduced previous year	219.15	0.00	0.34
	Concession	Reproduced previous year + male group size category (↑)	219.77	0.62	0.25
	Concession	Reproduced previous year + number of males (↑)	220.80	1.65	0.15
	Tug-of-war	Reproduced previous year + alpha-subordinate male R (↑)	220.90	1.75	0.14
	Null model	—	303.08	83.93	0.00
Infant survival	—	Takeover	141.27	0.00	0.36
	Concession	Takeover + male group size category (↑)	141.45	0.18	0.33
	Concession	Takeover + number of males (↑)	142.78	1.51	0.17
	Tug-of-war	Takeover + alpha-subordinate male R (↑)	143.35	2.08	0.13
	Null model	—	153.24	11.97	0.00

All models contained year, group and female/mother identity as random effects.

how male–female kinship shaped paternity patterns. We created a set of competing GLMMs with a binomial distribution and a complementary log–log function that is more suitable than the logit function for skewed outcome variables (Zuur *et al.* 2009) such as ours (i.e. the alpha male sires the majority of offspring). We created a null model that did not include any fixed effects and a set of alternative models (Table 1, Supporting Information) that each tested a particular hypothesis outlined in the introduction (sensu Burnham & Anderson 2002). To investigate the concession model, we included the following fixed effects: mean *R* between the alpha and the subordinate immigrant males, the number of immigrant males in the group, whether the alpha was prime aged (i.e. 11–16 years old: Jack 2003b) and whether the alpha male was strong and well established (as a proxy for fighting/resource holding potential) when the infant was conceived (Table S3, Supporting information). We determined that the alpha male was weak and had a low resource holding potential if he had a peripheral spatial position and ranged in the periphery rather than in the centre of the group (male spatial position is indicative of alpha status: Perry 1997), was wounded (which could possibly indicate within-group male conflicts), and if we observed him being challenged by other males and he did not have a well-established dominance position when the offspring was conceived. To investigate the queuing model, we included the fixed effect whether the alpha male resided with older subordinate males (Table S3, Supporting information). To investigate the tug-of-war model, we included the fixed effects whether the alpha was prime aged and whether he was weak (Table S3, Supporting information). To investigate the priority-of-access model, we included the fixed effects number of adult females (i.e. parous or pregnant nulliparous females) present when the focal offspring was conceived and the number of offspring conceived within a 30-day period of the focal offspring's estimated conception date (Table S3, Supporting information). The model investigating inbreeding avoidance (or mate choice for unrelated mates) contained the fixed effect whether the alpha male was the sire of the offspring's mother (i.e. a father–daughter dyad). We also included the fixed effect whether the alpha male was weak, because male strength often affects female mate choice (Small 1989; Table S3, Supporting information). The model investigating female mate choice contained the fixed effects alpha male tenure and whether he was weak (Table S3, Supporting information). We included year, mother identity and alpha male identity as random effects in all models (Table S3, Supporting information). We excluded offspring that were sired by the alpha male when he was the only immigrant male present in the group. We also excluded offspring that were sired during periods when the subordinate males remained unsampled, because we were unable to calculate male–male relatedness.

We standardized all numerical fixed effects using the z-score (Abdi 2007) following the recommendations by Schielzeth (2010). We computed the models with the package LME4 (Bates *et al.* 2014) in R version 3.1.0 (R Core Team 2014). We calculated variance inflation factors for the fixed effects included in the same model, and low values (VIF ≤2) indicated that the fixed effects were not multicollinear (Supporting Information). We evaluated the support for each model based on Akaike Information Criterion corrected for small sample sizes (AICc) (Akaike 1974). When several models received similar support, we took model selection uncertainly into account by averaging coefficients across models (Burnham & Anderson 2002) using the R package MUMIN (Barton 2013).

Results

The 20 loci had an exclusionary power of 0.99321 for assigning the first parent and 0.99991 for assigning the second parent. We determined parentage for 111 of 121 offspring via parentage assignments in this study. For the remaining 10 offspring genotyped in this study, we were unable to assign paternity most likely due to uncomplete sampling of their candidate sires. For seven of these 10 offspring, a previous study had sampled all their candidate sires and could resolve their parentage (Jack & Fedigan 2006). Of these offspring, alpha males sired 84% (99 of 118) and subordinate immigrant males sired 16% (19 of 118). Natal males did not sire any offspring. For the three remaining offspring whose parentage remained unresolved in our study and who were not part of Jack & Fedigan's (2006) study, the alpha male was not assigned as their sire and it is possible that they were sired by one of the subordinate immigrant males that we did not genotype. If we include these three offspring in our sample, alpha males sired 82% (99 of 121) of the genotyped offspring. However, there was considerable variation in the percentage of offspring sired by the alpha males (range: 48%–100%).

Group productivity

When analysing whether females reproduced annually (*N* = 216 female-years), the alternative models received stronger support than the null model that did not contain any fixed effects (Table 3). A female was less likely to reproduce if she had given birth to a surviving infant the previous year (estimate: −3.38, CI: −4.29 to −2.46). There was no consistent effect of immigrant male group

size category (small multimale groups, estimate: 0.80, CI: −0.34 to 1.94; large multimale groups, estimate: 0.00, CI: −1.08 to 1.09), the number of immigrant males (estimate: −0.13, CI: −0.49 to 0.24) or immigrant male–male relatedness on female reproduction (estimate: 0.11, CI: −0.25 to 0.47).

When analysing infant survival (N = 127 infants), the alternative models received stronger support than the null model (Table 3). Takeovers reduced the likelihood of infant survival (Fig. 1). Infants were more likely to survive in small multimale groups than in unimale groups (Fig. 1). There was no difference in infant survival between large multimale groups and the other group categories (unimale vs. large multimale: Fig. 1; small multimale vs. large multimale, estimate: −0.48, 95% CI: −1.63 to 0.65). There was no consistent effect of the number of immigrant males or immigrant male–male relatedness on infant survival (Fig. 1).

We calculated the estimated reproductive success for alpha males in unimale (N = 2 alpha males), small multimale (N = 4 alpha males) and large multimale groups (N = 6 alpha males). Alpha males in unimale groups sired a higher percentage of infants (100%), but had shorter tenures (4.0 years) and/or resided with fewer females (3.2) that had longer interbirth intervals (3.4 years) than did alpha males in small (percentage of infants sired: 85%, tenure: 5.6 years, the number of females: 4.3, interbirth interval: 2.4 years) and large multimale groups (percentage of infants sired: 79%, tenure: 2.8 years, the number of females: 5.5, interbirth interval: 3.2 years). As a result, the estimated reproductive success of alpha males is over twice as high in small multimale groups as in unimale and large multimale groups (Fig. 2). Even if alpha males in small multimale groups only sired 36% of the infants, they would still have higher estimated reproductive success than males in unimale groups.

Reproductive partitioning

We included 81 offspring sired during the tenure of eight alpha males in our analysis of reproductive partitioning because these were the only data points with complete information regarding relatedness between the alpha and the subordinate immigrant males. Four of the six alternative models (mate choice for strong unrelated mates, mate choice for strong novel mates, tug-of-war and concession) received stronger support than the null model (Table 1). The alpha male had a reduced probability of siring offspring born to his own daughters, with a longer alpha male tenure and when he was weak and lacked a well-established alpha position (Fig. 3). There was no significant effect of the number of immigrant males, the alpha male's mean relatedness with the immigrant males, whether the alpha was prime aged, whether the alpha male resided with older subordinate males, the number of adult females and the number of offspring conceived within the same 30-day period (Fig. 3).

Discussion

Longitudinal paternity patterns in four groups of white-faced capuchins revealed that alpha males sired the majority of offspring, although the degree of reproductive skew varied considerably (48%–100%), as previously reported from another population of white-faced capuchins (Muniz *et al.* 2010). Alpha males appear to benefit from the presence of subordinate males based on our analyses of annual group productivity and estimated alpha male reproductive success, which conforms to the concession model. However, the degree of reproductive skew was not predicted by any of the formal reproductive skew models. Instead, the degree of reproductive skew was best explained by mate choice for unrelated, novel and strong mates.
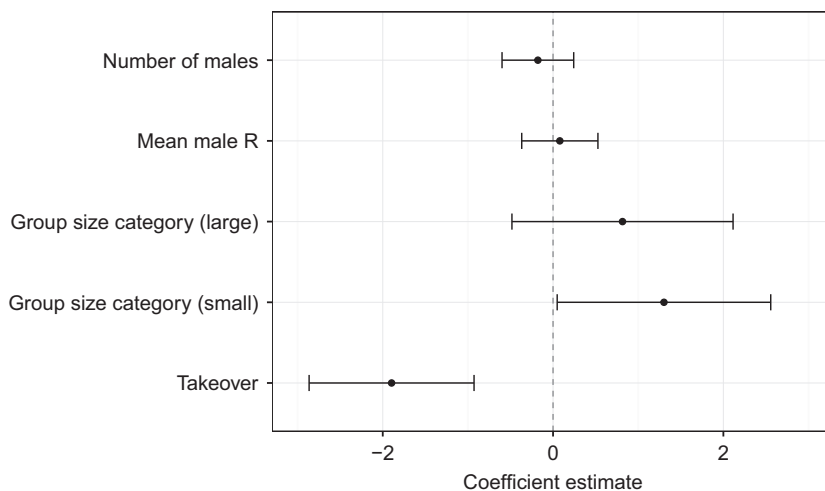

Fig. 1 Coefficient estimates with their 95% confidence interval for the models investigating infant survival. Immigrant male group size category is a factorial fixed effect, and its effect is evaluated against the baseline level unimale groups. The other fixed effects are binary (whether a takeover occurred) or continuous (number of immigrant males, mean alpha male—subordinate immigrant male R-value).
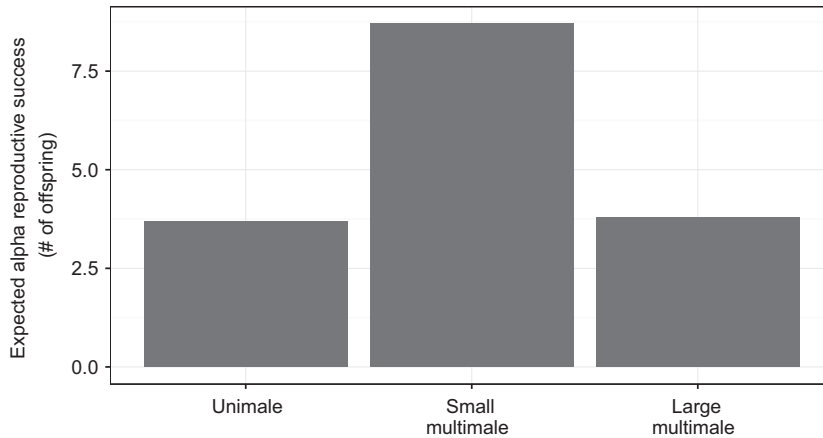
Fig. 2 Estimated alpha male reproductive success (i.e. number of offspring) in uni-male groups, small multimale groups (two to three males) and large multimale groups (>3 males).
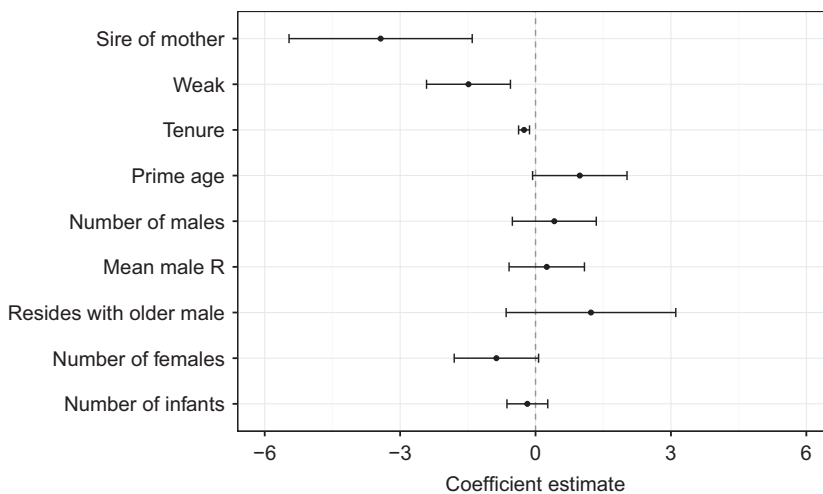
Fig. 3 Coefficient estimates for the models investigating alpha males' probability of siring a particular infant. Whether the alpha male is the sire of the mother, is weak, is prime aged and resides with older immigrant male are binary fixed effects, and the effect is evaluated against the baseline level (not sire of the mother, not weak, not prime aged and does not reside with older male). The other fixed effects are continuous (tenure, number of immigrant males, mean alpha male—subordinate immigrant male *R*-value, number of adult females, number of infants conceived within the same 30-day period).

Concession

Group productivity should increase with the number of males according to the concession model. Female reproduction was not affected by male group size, while infant survival was higher in small multimale groups than in unimale groups. The descriptive data we present also suggest that estimated alpha male reproductive success is highest in small multimale groups. Part of the reason why alpha males in small multimale groups have such high reproductive success is lower frequencies of male takeovers and infanticide, which enhances infant survival (Fedigan & Jack 2004; Jack & Fedigan 2004b). In contrast to bottlenose dolphins (Wiszniewski *et al.* 2012) and lions (*Panthera leo*: Bygott *et al.* 1979), alpha male reproductive success in our study population did not continue to increase with the number of males. Instead, our findings suggest that there may be an upper limit to the number of subordinate males beyond which additional males no longer provide benefits to the alpha male, similar to the pattern observed in redfronted lemurs (*Eulemur fulvus*

rufus: Port *et al.* 2010). A possible explanation is that groups with a large number of males consist of a high proportion of subadult males that may not be as effective coalitionary partners as fully grown adult males, which is the case in black howler monkeys (*Alouatta pigra*: Van Belle *et al.* 2014). Alternatively, our finding may be due to larger groups containing more free riders that do not participate in potentially costly cooperative activities, and such collective action problem occurs in human societies (Olson 1965), nonhuman primates (Willems *et al.* 2013) and other social animals such as lions (Heinsohn & Packer 1995).

Admittedly, our current analysis of estimated alpha male reproductive success was hampered by small sample size, particularly of unimale groups. The rarity of unimale groups in the entire Santa Rosa capuchin population (Fedigan & Jack 2012) indicates that this is an unstable group composition over time, either because the alpha male is unable to maintain exclusive group membership for long time periods (Fedigan & Jack 2004) or because he willingly accepts immigrant males when the conditions favour helping (Reyer 1980). The

fact that it is rare for our study groups to contain a single male for long time periods makes it difficult to evaluate whether alpha male reproductive success is lower in unimale than in multimale groups. However, a previous study using a large data set consisting of longitudinal observations of the entire Santa Rosa capuchin population revealed that group productivity increased with the male-to-female sex ratio (Fedigan & Jack 2011). This should translate into higher alpha male reproductive success in groups with more males, because reproduction is highly skewed towards the alpha male in most of our study groups (Jack & Fedigan 2006; this study). Based on these findings, we cautiously suggest that alpha males benefit from the presence of subordinate males in accordance with the underlying assumptions of the concession model.

Also in accordance with the underlying assumptions of the concession model, there are ecological constraints on independent breeding due to environmental stressors that the Santa Rosa tropical dry forest imposes on the capuchins (Fedigan *et al.* 1996). To cope with very hot and arid environmental conditions of the dry season, the capuchins adopt several behavioural strategies including prolonged resting periods and decreased home range sizes centred around water sources (Campos & Fedigan 2009, 2013; Campos *et al.* 2014). There are a limited number of water sources during the dry season (Fedigan *et al.* 1996; Campos & Fedigan 2009; Campos *et al.* 2014), and the capuchins aggressively defend these against intruding groups and extra-group males (Rose & Fedigan 1995; Childers 2008). The scarcity of water may set an upper limit on the number of groups that the habitat can support (Fedigan *et al.* 1996). It is therefore possible that the survival of subordinate males depends strongly on simply having a social group in which to reside and that these males do not require reproductive opportunities in exchange for their coalitionary support.

Even though some of the underlying assumptions of the concession model appear to be true in our study population, the degree of reproductive skew did not conform to the predictions of the concession model (Table 1), similar to the findings from wasps (Nonacs *et al.* 2006). This discrepancy between observed and expected degrees of reproductive skew may be due to predictions that are difficult to test in wild populations or due to animals being unable to make fine-scaled adjustments of the reproductive partitioning when kin recognition abilities are limited and when there are only a few reproductive opportunities to be shared (Field *et al.* 1998; Port & Kappeler 2010; Nonacs & Hager 2011). Thus, there is a current gap between theory and the animal societies in which these theories are being tested that needs to be overcome in order to increase

our understanding of reproductive skew in wild populations (Nonacs & Hager 2011).

Queuing

The alpha male's likelihood of siring offspring was not affected by the relative age of the subordinate male. Thus, the alpha male did not appear to concede reproductive opportunities to older subordinate males that are less likely to outlive the alpha and benefit from queuing. Even if the alpha male never willingly gives up reproductive opportunities, regardless of the individual male characteristics, some subordinate males may still gain future direct fitness benefits from cooperating with an alpha male. For example, subordinate lance-tailed manakins (*Chiroxiphia lanceolata*) rarely reproduce, but subordinate males that had engaged in cooperative courtship displays were more likely to become dominant than other subordinate males after experimental removal of the dominant male (DuVal 2007). It is possible that subordinate male capuchins also gain delayed direct fitness benefits if their support helps the alpha retain his tenure past the maturation of his daughters because the alpha and his daughters avoid inbreeding (Muniz *et al.* 2006; this study). An important topic for increasing our understanding of the evolution of male cooperation in this species is to investigate whether these future fitness benefits outweigh the costs of cooperating with a dominant male as suggested by the queuing model (Kokko & Johnstone 1999; Ragsdale 1999).

Tug-of-war

The tug-of-war model has received convincing support in a wide range of other species, such as Australian allodapine bees (*Exoneura nigrescens*) (Langer *et al.* 2004), meerkats (Clutton-Brock *et al.* 2001) and mountain gorillas (Bradley *et al.* 2005). Although our male reproductive partitioning data supported some of its predictions, the tug-of-war model was not well supported in comparison with the mate choice models (Table 1). Furthermore, our findings regarding group productivity did not support the tug-of-war model (Table 3). It is not too surprising that reproductive partitioning in capuchin groups did not conform to the tug-of-war model. Coresident capuchin males rarely engage in aggressive conflicts over access to females, and their relationships are best characterized as affiliative or tolerant, regardless of their relatedness (Perry 1998; Jack 2003a). These observations suggest that alpha and subordinate males do not usually compete overtly to gain as many reproductive opportunities as possible. It is still possible that male capuchins experience tug-of-

war during certain circumstances that we did not directly investigate, such as when the alpha male is under severe energetic constraints leading to a reduced fighting potential. Comparing biomarkers indicative of energy status when the alpha versus a subordinate male sires offspring may help to further investigate this possibility.

Priority-of-access

Failing to offer support to the priority-of-access model, the alpha male's probability of siring offspring was not affected by the number of females or by the number of offspring conceived at the same time, in contrast to the findings from other primates (Ostner *et al.* 2008) and feral cats (*Felis catus*: Say *et al.* 2001). The deviations from the priority-of-access model may be explained by female mate choice (spotted hyena: Engh *et al.* 2002). However, it is unclear why our results contrast to the findings from a nearby population of white-faced capuchins in which the number of females reduced the alpha male's probability of siring offspring (Muniz *et al.* 2010). It may be that the priority-of-access model is very sensitive to the exact number of females and their oestrus synchrony in combination with other factors such as group spread. To fully evaluate this hypothesis, future studies should monitor female reproductive cycles to more precisely determine how many females are in oestrus at the same time.

Inbreeding avoidance and mate choice

How inbreeding avoidance affects reproductive skew varies between populations in which alpha animals occasionally reside with mature, opposite-sex kin (Keane *et al.* 1996; Cooney & Bennett 2000; Griffin *et al.* 2003; Bradley *et al.* 2005; Muniz *et al.* 2006; Kappeler & Schaeffler 2008). Inbreeding avoidance reinforces high reproductive skew in several cooperative breeders where mature offspring rarely have access to unrelated mating partners in the group (Cooney & Bennett 2000; Clutton-Brock *et al.* 2001; Griffin *et al.* 2003; Nelson-Flower *et al.* 2011). In contrast, inbreeding avoidance can decrease the reproductive skew in pair-living or group-living animals if females can mate with less-related extra-group males or within-group subordinate males (plural breeding primates: Altmann *et al.* 1996; Muniz *et al.* 2006; Godoy *et al.* 2016a; pair-living birds: Arct *et al.* 2015; but see Reid 2015). Our study population appears to fall into this latter category of populations with active inbreeding avoidance leading to decreased reproductive skew, because the alpha male's probability of siring a particular offspring decreased when he was the sire of the offspring's mother. It is

important to note that such pattern of inbreeding avoidance may arise when animals mate randomly in regard to kinship, if kinship is correlated with a trait that is selected for in the opposite sex (black grouse, *Tetrao tetrix*: Soulsbury *et al.* 2012). We were unable to distinguish whether this pattern was due to inbreeding avoidance or due to female mate choice for novel and young adult males, because only old alpha males with long tenures reside with their adult daughters.

In addition to sire–daughter kinship and alpha male tenure, alpha strength also affected the alpha male's likelihood of siring offspring. Our results based on paternity data conform to behavioural data from several primate species—females choose mates based on alpha status, strength and novelty (reviewed in Small 1989). It is possible that the pattern we observed here is due to female mate choice for strong, unrelated and/or novel males (primates: Small 1989; hyenas: Engh *et al.* 2002). Another possibility is that the alpha male willingly gives up mating opportunities due to energetic constraints when he is wounded or when he lacks a well-established dominance position because he gains other benefits from doing so. In banded mongooses (*Mungos mungo*), the alpha male willingly gives up reproductive opportunities with female kin if it interferes with his ability to reproduce with the unrelated females in his group (Sanderson *et al.* 2015). It may also be particularly beneficial for the alpha male to concede reproductive opportunities to subordinate males during the late stage of the alpha male's tenure if it increases subordinate male tenure, reduces the risk of takeovers and decreases the risk of infanticide after takeovers (Henzi *et al.* 2010). Further analyses are required to determine whether mate choice of male and/or female capuchins is driving the observed pattern of reduced siring success of alpha males with long tenures, mature daughters and a temporarily reduced resource holding potential.

The sample size limitation ($N = 81$ offspring) typical of studies investigating reproductive patterns in animals with slow life histories (Muniz *et al.* 2006; Vigilant *et al.* 2015) begs the question as to whether our results are replicable. We would only be able to answer this question confidently with continued longitudinal sampling from our study groups or additional sampling from surrounding social groups. However, we cautiously suggest that inbreeding avoidance between alpha males and their mature daughters is typical of white-faced capuchins in this area based on similar patterns reported from a near-by population (Muniz *et al.* 2006; Godoy *et al.* 2016a).

Despite a long-held empirical and theoretical interest in investigating inbreeding, its effect on mating patterns is still under debate, partly due to a number of

methodological issues yielding mixed results from similar study systems (Wang 2010; Szulkin *et al.* 2013; Reid *et al.* 2015). We followed recently published guidelines (Wang 2010; Szulkin *et al.* 2013; Reid *et al.* 2015) for how to prevent misinterpretations of the data in favour of the inbreeding avoidance hypothesis, for example by using accurate methods to determine kinship, and continuously collected demographic data to assess the potential sampling bias (Supporting Information). Thus, our study is one of the first to show convincing evidence for inbreeding avoidance in a wild population. We encourage other researcher to adhere to these methodological guidelines so that we can gain a better understanding of the distribution of inbreeding avoidance across populations. It is not until then that we will be able to fully evaluate the importance of inbreeding in shaping mating patterns.

Conclusions

The unique degree of male cooperation despite high reproductive skew in white-faced capuchins may be explained by the concession model, because alpha males appear to benefit from the support of subordinate males that may not be able to breed independently due to severe ecological constraints. However, the exact degree of reproductive partitioning did not conform to any of the reproductive skew models. The discrepancy between observed and expected degrees of reproductive skew in our study may be due to extremely long male tenures, making inbreeding avoidance and female mate choice for novel males important factors in shaping the degree of male reproductive skew. Although our study is one of the first to follow recently published guidelines to circumvent methodological issues that can lead to a bias in favour of the inbreeding hypothesis, it is likely that inbreeding avoidance and female mate choice affect male reproductive skew in other species as well (Engh *et al.* 2002; Haydock & Koenig 2003; Townsend *et al.* 2009). Thus, incorporating inbreeding avoidance and female mate choice in future skew models may increase their predictive power. Studies such as ours, highlighting factors that may explain deviations from the skew models, offer valuable insights on how to bridge the gap between theoretical models and wild populations in which these models are being tested.

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Data accessibility

Genotypes and data files with outcome and predictor variables are uploaded on the University of Calgary's digital repository PRISM and on Dryad doi: 10.5061/dryad.3jd08.

Supporting information

Additional supporting information may be found in the online version of this article.

Table S1 Outcome variable and fixed effects in the first set of group productivity models.

Table S2 Outcome variable and fixed effects in the second set of group productivity models.

Table S3 Outcome variable and fixed effects in the reproductive skew models.

Table S4 VIF for the fixed effects in the models investigating group productivity.

Table S5 VIF for the fixed effects in each reproductive skew model.