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Sex differences in the drivers of reproductive skew in a cooperative breeder

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Running head: Sex differences in skew

ABSTRACT

Many cooperatively breeding societies are characterized by high reproductive skew, such that some socially dominant individuals breed, while socially subordinate individuals provide help. Inbreeding avoidance serves as a source of reproductive skew in many high-skew societies, but few empirical studies have examined sources of skew operating alongside inbreeding avoidance, or compared individual *attempts* to reproduce (reproductive competition) with individual reproductive success. Here we use long-term genetic and observational data to examine factors affecting reproductive skew in the high-skew cooperatively breeding southern pied babbler (*Turdoides bicolor*). When subordinates can breed, skew remains high, suggesting factors additional to inbreeding avoidance drive skew. Subordinate females are more likely to compete to breed when older or when ecological constraints on dispersal are high, but heavy subordinate females are more likely to successfully breed. Subordinate males are more likely to compete when they are older, during high ecological constraints, or when they are related to the dominant male, but only the presence of within-group unrelated subordinate females predicts subordinate male breeding success. Reproductive skew is not driven by reproductive effort, but by forces such as intrinsic physical limitations and intra-sexual conflict (for females), or female mate choice, male mate-guarding and potentially reproductive restraint (for males). Ecological conditions or ‘outside options’ affect the occurrence of reproductive conflict, supporting predictions of recent synthetic skew models. Inbreeding avoidance together with competition for access to reproduction may generate high skew in animal societies, and disparate processes may be operating to maintain male vs. female reproductive skew in the same species.

Keywords: reproductive skew, cooperative breeding, kin competition, reproductive conflict, subordinate breeding, mate choice.

INTRODUCTION

In many animal societies, socially dominant individuals reproduce more successfully than subordinates, a pattern termed reproductive skew (Koenig et al., 1992; Vehrencamp, 1983). Understanding what processes generate reproductive skew is one of the most intriguing problems in the study of social behavior in animals, and is of particular importance in elucidating the selective forces at work in the evolution of cooperative breeding (Keller and Reeve, 1994; Riehl, 2017). Reproductive skew is central to the structure of many cooperatively breeding societies, and an extensive theoretical framework has been developed to describe it (Reeve and Shen, 2013). However, empirical investigations of the specific factors affecting skew in cooperative societies are rare, especially in vertebrates, and further empirical research is therefore essential (Hodge, 2009). Such work provides insight into what factors generate skew, and how the resulting selection pressures shape individual behavior and morphology in cooperatively breeding species and animal societies more generally.

Reproductive skew can be affected by a range of environmental and social factors, making it difficult to disentangle which factors are most influential and to what extent. Inbreeding avoidance is known to play a major role in shaping skew in cooperatively breeding species, especially those in which nuclear families are common and extra-group breeding is rare (Faulkes and Bennett, 2001; Koenig et al., 2009; Nichols, 2017; Pusey and Wolf, 1996; Riehl, 2017). However, inbreeding avoidance behavior can mask other factors affecting reproductive skew. Subordinate reproductive success may be limited by extrinsic factors such as climatic variation in food resources (Clutton-Brock et al., 2001; Curry, 1988; Faulkes and Bennett, 2001; Nichols et al., 2012; Williams, 2004). Additionally, subordinates may be restricted because of intrinsic factors; for example, subordinates may be younger, smaller, or in poorer condition compared with dominant individuals (Clutton-Brock et al., 2008; Dierkes et al., 1999). Reproductive skew may also be maintained through social competition, either through mate choice or mate-guarding (Kokko and Morrell, 2005; Piper and Slater, 1993), or as a result of reproductive suppression of subordinates by dominant individuals (Young, 2009). Factors such as group size and the genetic relationship with the competing dominant may also affect skew, often interacting with other social factors (Clutton-Brock et al., 2008; Hellmann et al., 2016; Lu et al., 2011). Notably, while previous studies have considered some of these factors, few have considered the factors affecting reproductive skew once the influence of inbreeding avoidance has been removed.

Comparisons of when subordinates attempt to breed versus when they are successful can illustrate what mechanisms constrain subordinate reproduction. For example, in some species, subordinates do not attempt to breed (e.g., naked mole-rats *Heterocephalus glaber*, Jarvis, 1981; some honey bees, vespine wasps and ants, Bourke, 1988). These subordinates may be physiologically suppressed early in the breeding cycle by the presence or behavior of dominants (reviewed by Bourke, 1988; Young, 2009). In other species, subordinates frequently try to gain a share of reproduction, though they may be successful only rarely (e.g., cichlid fish *Neolaprologus pulcher,* Dierkes et al., 1999; meerkats *Suricata suricatta*, Clutton-Brock et al., 2001; southern pied babblers *Turdoides bicolor,* Nelson-Flower et al., 2013). Finally, in some species, subordinate attempts to breed are common or dominance hierarchies are poorly developed and reproductive skew is low (e.g. banded mongooses *Mungos mungo,* Cant et al., 2010, and acorn woodpeckers *Melanerpes formicivorus,* Haydock and Koenig, 2002). Whether subordinates attempt to breed, and the circumstances in which such attempts are made or are successful can reveal the proximate mechanisms of reproductive skew, and contribute to our understanding of the ultimate causes of skew in cooperative societies (Saltzman et al., 2009).

Advances in reproductive skew theory may help to explain the factors generating patterns of reproductive skew in cooperatively breeding species. Although some previous theoretical models incorporated biologically improbable assumptions (see critiques by Hodge, 2009; Magrath et al., 2004; Reeve and Shen, 2013), recent ‘synthesis’ or ‘generalized’ skew models more accurately reflect biological reality, or do away with assumptions altogether (Buston and Zink, 2009; Cant and Johnstone, 2009; Shen and Reeve, 2010). Additionally, they unite the previous smaller models (e.g., the ‘concessions’ or ‘tug-of-war’ models), combining their predictions to offer a more powerful perspective on the forces governing reproductive skew under different circumstances. Marrying empirical results with theoretical predictions can provide an opportunity to gain explanatory insight into patterns of reproductive skew.

In this study we examine reproductive skew in a cooperatively breeding African bird, the southern pied babbler. These birds live in year-round groups which are typically nuclear family units (61.9% of groups each year); in such groups, only the dominant male and female breed, while 2-3 adult subordinates of both sexes (mean number 2.4, range 0-10) help raise chicks (Nelson-Flower et al., 2011). Inbreeding avoidance appears to be an important influence on reproductive skew, with nuclear family groups exhibiting 100% skew. However, immigration of foreign dominant males and females means 34.1% of subordinates have access to unrelated within-group potential breeding partners; this is the only opportunity for subordinates to breed because extra-group parentage has never been observed (Nelson-Flower et al., 2011, 2012). Some subordinates are unrelated to both dominants, which can occur when the original dominant pair of the group have both been replaced or if the subordinate is itself an immigrant (though subordinate immigration is comparatively rare; Nelson-Flower et al., 2011). Subordinates with unrelated potential breeding partners in the group often attempt to breed, sometimes gaining a proportion of parentage in broods initiated by the socially dominant pair (Nelson-Flower and Ridley, 2015;

Nelson-Flower et al., 2011, 2013). Southern pied babbler groups build a single nest per breeding attempt, and subordinate female babblers breed only by laying fertilized eggs in the clutch of the dominant pair, while subordinate males breed with a group dominant or subordinate female that subsequently successfully lays in this nest. Female competition for reproduction within groups is costly and can involve the repeated destruction of eggs by competitors, resulting in a decrease in group productivity (Nelson-Flower et al., 2013). In contrast to females, competition by subordinate males does not affect group productivity, though subordinate males gain large shares of paternity on the rare occasions when they do successfully breed (Nelson-Flower and Ridley, 2015). Within groups, age-based hierarchies or queues exist for each sex, such that the eldest subordinate inherits the dominance position in the group when it becomes vacant and if the current opposite-sex dominant is unrelated (Nelson-Flower et al., 2012). Position in the social queue for dominance is particularly important for male acquisition of dominance in non-natal groups and affects the timing of male dispersal (Nelson-Flower et al., 2018).

Sex differences in reproductive skew and the factors shaping reproductive skew are common in many species (Hodge et al., 2008; Spong et al., 2008; Williams, 2004). This could generate important differences in social dynamics and life history strategies for males and females in group-living societies. As a result, we examine reproductive skew separately for male and female southern pied babblers. Furthermore, to understand reproductive skew independent of inbreeding avoidance, we focus on those adult subordinates with unrelated potential breeding partners in the group (Koenig et al., 2009; Riehl, 2017). We first use behavioral and life-history data to ask what factors (both social and environmental) affect the likelihood of reproductive competition by subordinates. We then use genetic data to examine the factors affecting the likelihood of reproductive success by subordinates to better understand the mechanisms underlying the high reproductive skew observed in this species.

METHODS

Study population

Data were collected from 2003 – 2014 from a habituated, color-ringed population of 45 groups of southern pied babblers at the Kuruman River Reserve (26°58’S; 21°49’E) in the Kalahari Desert, South Africa (habituation details: Ridley and Raihani, 2007a). Groups were visited at minimum 2-3 times per week for 2-4 hours of observation. Dominance status within groups was determined using behavioral cues and, for females, vocalizations during inter-group conflicts (Golabek and Radford, 2013). Mean group size (± standard error) was 4.4 ± 0.1 adults (range: 2-12 adults). When birds from outside the study area immigrated into groups, they were assumed to be a minimum of one year old if they had adult plumage, or six months old if they had juvenile plumage (Ridley, 2016). Body mass was measured at first light (before foraging began) during each observation session using a digital scale (weighing protocol: Ridley and Raihani, 2007a). The population pedigree was generated from microsatellite genotyping and life-history data and was used to assess relatedness between group members (Nelson-Flower et al., 2011). Subordinate males often live with dominant males that are brothers or fathers but are likely to disperse when unrelated dominant males enter their groups (Nelson-Flower and Ridley, 2016). Conversely, females readily live with mothers or unrelated dominant females, but rarely live with sisters (M. Nelson-Flower, unpublished data). Male and female subordinates were each ranked by age to determine their position in the social queue for dominance, sharing the same rank as same-sex broodmates (Nelson-Flower et al., 2018).

Most subordinates appeared to disperse voluntarily but eviction by dominants was also observed. Eviction of a subordinate by a dominant (N = 8 over 11 years) always occurred between members of the same sex, with no sex bias (5 female, 3 male; binomial test: p = 0.727). Most evictions by dominants, especially those among females, resulted in permanent departures by subordinates (5/5 female evictions; 1/3 male evictions); evictees were adults (aged 727.5 ± 137.3 days old) and most were reproductive competitors of the evictor (7/8 evictees: 5/5 female and 2/3 males).

Statistical analyses

All statistical analyses were performed within R v. 3.4.0 (R Core Team, 2017). R package 'lme4' v. 1.1.13 (Bates et al., 2015) was used to construct generalized linear mixed models (GLMMs; see below for specific details of analyses). We specified a binomial error structure and assessed model fit using Akaike's information criterion adjusted for small sample sizes (AICc; Burnham and Anderson, 2002). For each analysis, we first specified a global model including all terms of interest; submodels were then derived from this (Grueber et al., 2011). When one or more submodels scored within two AICc units of the best submodel, we employed model averaging using 'MuMIn' v.1.15.6 (Bartoń, 2016) after excluding 'nested' models (Arnold, 2010). All continuous variables were centered and scaled to facilitate model comparisons (Grueber et al., 2011). Correlated terms of interest should not be used in a submodel together, but comparisons of different submodels containing correlated terms is possible if they are drawn from the same dataset and have the same number of observations (Freckleton, 2011). Correlated terms are reported in the Electronic Supplementary Material (ESM). Tables present all models in the Δ2 AICc set, the full model (including correlated terms) and the null model. When model averaging was employed, confidence intervals are reported, and when a single top model was identified, the z-value is reported. Model estimates and standard errors were calculated using the full model average (Arnold, 2010). Means and standard errors presented in figures were generated from minimal models identified through AICc comparison or through multi-model averaging.

Subordinate reproductive competition

To investigate subordinate reproductive competition, we considered all breeding attempts for which we observed nest-building or courtship behavior by any group member during the fertile period (the seven days before incubation), and at which a potentially breeding subordinate was present. In this species, many subordinates attempt to breed but few succeed, hence subordinate reproductive success does not provide a complete picture of reproductive competition. For example, competition by subordinate females causes many breeding attempts to fail before incubation begins (Nelson-Flower et al., 2013). Previous work has identified subordinate nest-building and initiation of courtship as behaviors that indicate reproductive competition (and not cooperation) in both sexes; adult subordinates demonstrate these behaviors from the age of 11 months old only when their groups contain unrelated potential breeding partners (Nelson-Flower and Ridley, 2015; Nelson-Flower et al., 2013). We excluded nests built during winter months (7 of 215 nests observed) because for most years observers were not present during winter months, and winter conditions vary markedly from breeding season conditions.

For each breeding attempt we observed, we defined subordinate male competition as occurring when males were seen to engage in courtship, nest-building, or copulation (Nelson-Flower and Ridley, 2015). Subordinate female competition was similarly defined as occurring when females engaged in courtship, nest-building, copulation, or infanticide (Nelson-Flower et al., 2013). For both sexes, we also used genetically determined reproductive success as an indicator of competition. A breakdown of the relative frequencies of each type of evidence used for competition for each sex is found in Table 1.

For each subordinate, participation in the breeding attempt (competition) was set as the response variable in a binomial GLMM, and separate analyses were performed by sex. Explanatory variables included rainfall (mm) during the 30 days prior to the initiation of the nesting attempt as well as the seven days following initiation date (fertile period), mean group size (adults) over the fertile period, the individual's age (days) on the date of the competition, the presence of an additional unrelated subordinate breeding partner, the relationship between the subordinate and the same-sex dominant (sibling, parent or unrelated), and position in the social queue for dominance. Subordinate and group identity were included as random terms in both analyses. The dataset of observed nests for subordinates with unrelated potential breeding partners included 95 nests for 31 females at 17 groups, and 113 nests for 29 males at 20 groups.

We then investigated the relative importance of mass and age (which are highly correlated) on subordinate male and female reproductive competition. We calculated mean pre-forage body mass during the 37-day period prior to incubation, but several individuals were not weighed at least once at first light in this period, resulting in a smaller dataset. For this reason, we included only subordinate mass and age as explanatory variables, allowing the full dataset for each sex (including age) to be used for other factors of interest. Participation in the breeding attempt (competition) was again set as the response variable in a binomial GLMM. Subordinate and group identity were included as random terms. We excluded one outlier female whose mass was considerably lower than the others (60.0 g; average female mass = 77.3 ± 0.7 g; inclusion of this female did not quantitatively affect results). The dataset included 64 nests observed for 23 females at 12 groups and 86 nests observed for 21 males at 16 groups.

Subordinate reproductive success

To investigate subordinate success, we considered all breeding attempts which had been investigated using microsatellite genotyping, where we understood the social and genetic relationships between all group members, and at which a potentially-breeding subordinate was present. This approach excluded groups comprising nuclear families, in which skew is total (only the dominant pair breeds; Nelson-Flower et al., 2011). We genotyped individuals at nine microsatellite loci, and expanded the parentage analysis from five to 11 years following previously developed protocols (Nelson-Flower et al., 2011). Some elements of the parentage analysis were modified; please see the ESM for details.

We determined what factors affect reproduction per breeding opportunity by subordinate potential breeders. Whether the subordinate successfully bred (yes/no) was the response in a binomial GLMM, with separate analyses for males and females. We examined environmental and social factors that could potentially affect subordinate breeding success during the fertile period (the 7 days before incubation began; Nelson-Flower et al., 2013), as suggested by reproductive skew models (Magrath et al., 2004). As a proxy for food availability, we measured rainfall (mm) over the 37-day period before incubation began (the 30 days prior to the fertile period (Wiley and Ridley, 2016) and the seven days of the fertile period). Explanatory variables were mean group size (adults) over the fertile period, rainfall (mm), subordinate age (days) at incubation, the relationship between the subordinate and the same-sex dominant competitor (offspring, sibling or unrelated), and whether unrelated subordinate potential partners were present. Subordinate males living with unrelated dominant males never successfully bred; to aid model convergence we therefore excluded these clutches (N = 5/66) from the analysis and investigated whether living with a brother vs. a father affected adult male subordinate reproductive success. In addition, only those subordinates at the head-of-queue position bred, so queue position could not be included in the model. Subordinate and group identity were included as random terms. The datasets of genotyped clutches in groups where subordinates had unrelated potential breeding partners included 50 determinations of parentage for 22 females in 13 groups, and 61 determinations of parentage for 22 subordinate males in 15 groups.

As above, subsets of data were analysed for both sexes to compare the effects of mass and age on subordinate reproductive success. We again set success in breeding as the response variable in a binomial GLMM. Subordinate and group identity were set as random terms and the dataset included 29 determinations of parentage in genotyped clutches for 17 subordinate females in 9 groups, and 40 determinations of parentage for 17 subordinate males in 12 groups.

RESULTS

Reproductive skew due to inbreeding avoidance

Overall, reproductive skew in this long-term sample of 11 years was high, with 466 of 505 or 92.3% of chicks identified as the offspring of the dominant pair, and similar to that found in previous work with a smaller dataset of five years (95.2%, Nelson-Flower et al., 2011). Groups comprising nuclear families in which skew was 100% (i.e., only the dominant pair reproduced) produced 126 clutches (57.3%) including 286 chicks (56.6%). In addition to the complete skew, subordinate competition to breed was almost never observed in nuclear families (Nelson-Flower et al., 2013; Nelson-Flower and Ridley, 2015). Therefore, it appears that inbreeding avoidance is responsible for nearly 60% of the reproductive skew observed in the population overall.

Subordinate reproductive competition

Subordinates attempted to breed in 122 of a total of 208 observed breeding attempts (58.7%) in which they had an unrelated potential breeding partner. There was no sex difference in the likelihood of these attempts (N = 57/95 attempts by females (60.0%); 65/113 attempts by males (57.5%); proportion test: $\chi^2 = 0.048$, df = 1, $p = 0.823$). Females were more likely to attempt to breed when they were older and during periods of low rainfall

(Fig. 1, Table 2a). Female reproductive competition was not affected by queue position, relatedness to the dominant female, presence of unrelated subordinate males or group size (Table 2a). When we analysed the restricted dataset containing body mass, we found that age remained the best predictor of the likelihood of investing in reproductive competition (Table 2b).

Males were more likely to engage in reproductive competition when they were older, when there had been less rainfall, and when they were the dominant male's brother (Fig. 2, Table 3a). However, group size, the presence of unrelated subordinate females and queue position did not affect male investment in reproductive competition (Table 3a). The restricted dataset revealed no impact of body mass on male competitive behavior (Table 3b).

Subordinate reproductive success

When subordinates had unrelated potential breeding partners, they reproduced in 25 of 94 broods (26.6%), with 39 of 219 chicks having a subordinate parent (17.8%), leading to overall skew of 82.2%. There were no significant sex differences in the likelihood of breeding (N = 17 successful occurrences of breeding by subordinate females when living with unrelated potential partners of 50 opportunities (34.0%); 13 successful occurrences of breeding by subordinate males when living with unrelated potential partners of 61 opportunities (21.3%); proportion test: χ^2= 1.646, df = 1, p = 0.200). However, subordinate females produced a significantly greater proportion of offspring hatched than did subordinate males (N = 29 offspring with subordinate mothers of 113 chicks produced in groups where subordinate females could breed (25.7%); 19 offspring with subordinate fathers of 134 chicks produced in groups where subordinate males could breed (14.2%); proportion test: χ^2= 4.457, df = 1, p = 0.035).

For subordinate females, the only factor predicting success in breeding was age, with older females more likely to successfully breed (Fig. 3a, Table 4a). When we restricted the dataset to include only those females for which we had body mass measures, we found that higher mass was a better predictor of breeding success than age (Fig. 3b, Table 4b). Overall, it appears that female skew is best predicted by body mass and that results from the first analysis with the larger sample size (Table 4a) reflect the close correlation between mass and age.

For subordinate males, the presence of subordinate female unrelated potential partners predicted reproductive success, but no other variables had an effect (Fig. 4, Table 5a). In the restricted dataset, mass did not predict the breeding success of subordinate males (Table 5b). Few clutches were genotyped from groups containing subordinate males that lived with unrelated dominant males (N = 5 clutches of 69 hatched in groups with male competitors), as expected due to the short time periods that males tend to live with such dominant males (Nelson-Flower and Ridley, 2016, Nelson-Flower et al., 2018). None of the subordinate males bred in these five attempts, suggesting that nepotism could affect skew, but the sample size was insufficient for analysis.

A total of 12 broods (12.8%) occurred in groups where there were unrelated potential breeding partners for both male and female subordinates; this was usually a result of related males (brothers or a father and son) forming a group with related females (often a mother and daughter). When subordinates could breed together, they often did so (9/28 or 32.1% of chicks produced in such groups had subordinate parents). The low reproductive skew for males in these groups appears due entirely to subordinate males breeding with subordinate females, as there was no significant change in the number of chicks produced by dominant females and subordinate males (2/28 or 7.1% chicks with subordinate fathers and dominant mothers when subordinate female unrelated potential partners were present, 8/106 or 7.5% chicks with subordinate fathers and dominant mothers when subordinate female unrelated potential partners were absent; proportion test: $\chi^2 < 0.001$, df = 1, $p = 1$). Notably, subordinates breeding together did not lay independent clutches, but rather joined the clutch produced by the dominant pair.

DISCUSSION

Reproductive skew in southern pied babblers is primarily driven by inbreeding avoidance, such that 56.5% of chicks are hatched into nuclear families where only the dominant pair breeds and thus skew is 100%. However, when subordinates have the opportunity to breed, skew remains high (74.3% of parentage was monopolized by the dominant individual in females and 85.8% in males), indicating the importance of other social and environmental factors. Subordinate males and females living with unrelated potential partners frequently attempt to breed; these attempts are more likely when subordinates are older and when rainfall has been low. Additionally, males living with brothers are more likely to compete to breed than those living with unrelated dominant males. Despite frequent and similar levels of competition, subordinate females and males rarely gain reproductive success, though subordinate females produce a greater proportion of young than do subordinate males, resulting in lower skew among females. Notably, heavy subordinate females are more likely to breed, suggesting that physiological condition and competitive ability constrain female breeding. Conversely, subordinate male breeding success is unaffected by mass or age, but increases when unrelated subordinate females are available as potential partners, suggesting that female mate choice and/or male mate-guarding constrain male breeding. Together, these findings support the vital role of inbreeding avoidance in determining skew as recently discussed in a meta-analysis by Riehl (2017); however, our results also indicate that social and environmental factors other than inbreeding avoidance are also likely to affect reproductive competition and success by subordinates.

Reproductive skew among females appears to be driven by the intrinsic limits of physical condition when females are young and/or small, and by overt conflict when females grow older or larger. Younger subordinate female babblers rarely attempt to compete, while old or heavy females are more likely to compete and to succeed in breeding, a similar pattern to that seen in other cooperative species (Clutton-Brock et al., 2008, 2001; Heg et al., 2006; Zöttl et al., 2013). Such reproduction carries costs for the dominant female (Nelson-Flower et al., 2013; M. Nelson-Flower, unpublished data), resulting in reproductive conflict that takes the form of egg destruction and/or aggressive attacks during the fertile period (Nelson-Flower et al., 2013), as well as eviction. Size likely plays an important role in determining subordinate female competitive ability in such conflict and therefore reproductive success, and is associated with earlier female acquisition of the dominant breeding role (Ridley and Raihani, 2007b). These findings corroborate research suggesting that sexual selection operates to increase female size or competitive ability in species where female access to breeding opportunities are constrained (Clutton-Brock, 2009, 2017; Holekamp and Engh, 2009; Sharpe et al., 2016).

Subordinate female competition to breed is perhaps surprising given that eviction by dominant females always serves to remove adult reproductive competitors from the group, as seen in banded mongoose (Thompson et al., 2016). Eviction of subordinates remains a useful threat even when rare (Cant, 2011), as living alone carries high costs in this species (Ridley et al., 2008). However, females may be less deterred by the threat of eviction than males because females (but not males) can gain dominance by aggressively overthrowing dominant females in non-natal groups (Raihani et al., 2010); females may therefore suffer lower eviction costs since they have better ‘outside options’ (opportunities for dispersal or independent breeding) (Cant, 2011; Vehrencamp, 1983). This may explain why skew is lower among females than males.

Female reproductive competition and success are costly to dominant females as outlined above (Nelson-Flower et al., 2013; M. Nelson-Flower, unpublished data). Therefore, we might expect that subordinate females would refrain from competing with close relatives (Cant, 1998). However, we found that relatedness to the dominant female had no effect on subordinate female competition or success. This suggests that, though a subordinate female’s indirect fitness benefits are decreased by her reproduction and/or competition, these losses are outweighed by the direct fitness benefits (however unlikely) of reproduction. This may explain our observation that females rarely live with their dominant sisters; such subordinate females are likely to have arrived in a coalition to aid their sister in gaining dominance in the group and these partnerships are often not stable in the long-term (A.R. Ridley, unpublished data).

Male reproductive skew appears to be driven by dominant female mate choice or male mate-guarding, because the presence of unrelated subordinate females in the group predicted subordinate male reproductive success. Dominant males may prioritize guarding dominant females or may not be able to efficiently guard two females. Changes in male skew were not due to variation in male effort, as the presence of subordinate partners did not affect male competition to breed. Female choice has been suggested theoretically to play an important role in male skew, but has rarely been demonstrated empirically (Cant and Reeve, 2002; Mumme et al., 1983; Piper and Slater, 1993). Interestingly, differences in subordinate male age and mass had no effect on male breeding success; rather than using such attributes as a basis for mate choice, dominant females may choose mates using status as a rule of thumb, thereby usually mating with dominant males. Male mate-guarding may also be at work, a process that is not mutually exclusive with female choice. Evidence suggests that these two processes work in tandem to generate patterns of skew in primate societies, where failure of male mate-guarding enables females to breed with lower-status males, potentially safeguarding the female's offspring from infanticide (reviewed by van Schaik et al., 2004). Similarly, in dunnocks (*Prunella modularis*), females actively escape alpha male mate-guarding and solicit matings from beta males, thereby increasing male investment in their offspring (Davies, 1986). Future work on female choice and male mate-guarding behavior in babblers and the consequences for both female and male reproductive success could shed light on how these processes affect reproductive skew.

Patterns of male reproductive skew may also be driven by the genetic relationship between the subordinate and dominant male. Subordinate males that are unrelated to dominant males are unlikely to compete to breed and never successfully breed, even when living with unrelated subordinate females, a situation which generally leads to lower male skew. Dominant males appear to be intolerant of unrelated subordinate males (Nelson-Flower et al., 2018; Nelson-Flower and Ridley, 2016). These subordinate males may exercise reproductive restraint in response to decreased tolerance by dominant males and the large benefits of group-living in this species (Cant et al., 2010; Ridley et al., 2008). That is, these subordinate males may decrease breeding activity to avoid eviction. Reproductive restraint has been inferred in only a few cooperative vertebrate societies because intensive behavioural observations and long-term pedigrees are necessary to establish reproductive opportunities and competition; however, reproductive restraint may be a common mechanism generating reproductive skew (Cant, 2011; Harrison et al., 2013; Jarvis, 1981; Saltzman et al., 2009).

If reproductive restraint is an option for subordinate males, why do dominant males tolerate reproductive activity by relatives? Dominant males should prefer to breed themselves, even if they do gain indirect benefits by allowing related males to breed. We suggest that the tolerance of reproductive activity by related males may be a by-product of queueing dynamics among males. Subordinate males at the head of the social queue for dominance are far more likely to become dominant males themselves from this social position, and if in the natal group enjoy higher survival (Nelson-Flower et al., 2018). Dominant males may gain greater indirect benefits from tolerance of reproductively active male relatives than they lose from decreased paternity (which is generally small). We suggest that nepotistic tolerance of closely related individuals (despite the threat of reproductive competition) may be an important factor affecting dispersal rates and therefore reproductive skew across many cooperatively breeding species.

Our results provide valuable empirical evidence in support of recent developments in reproductive skew theory, which synthesize previous theoretical models (e.g. ‘concession’ or ‘transactional’ models among others) (Buston and Zink, 2009; Cant and Johnstone, 2009; Shen and Reeve, 2010). While these three models have different assumptions about the nature of the negotiations or conflict through which skew is decided, they all explore whether ‘outside options’ can affect the occurrence of within-group conflict over reproduction. This has rarely been shown empirically. Dispersal among males in this species is constrained by low rainfall, and breeding without helpers is usually only possible in wetter conditions (Nelson-Flower et al., 2018; Ridley, 2016), demonstrating that outside options in this species are shaped by rainfall. Our result indicating that rainfall affects reproductive competition for males and females provides evidence that outside options can influence the occurrence of within-group conflict over skew, thus offering support for a main premise of all three synthetic models (Buston and Zink, 2009; Cant and Johnstone, 2009; Shen and Reeve, 2010).

In summary, we find that reproductive skew remains high among males and females even after accounting for inbreeding avoidance. This appears likely to result from dominant suppression of subordinate reproduction because it is costly in terms of impaired productivity (females) or lost parentage (males) (Nelson-Flower et al., 2013; Nelson-Flower and Ridley, 2015). Skew among females was lower (74.3%) than among males (85.7%), indicating that subordinate females are more able to resist dominant suppression than are subordinate males, or that the combination of dominant suppression and female mate choice has an additive effect in shaping male skew. Disparate processes may be operating to maintain male vs. female reproductive skew in the same species, providing insight into the mechanisms governing the sex-specific struggle for reproduction between dominants and subordinates in cooperatively breeding species and animal societies more generally.

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Data Accessibility

Data for this paper has been deposited in Dryad Data Repository under doi:10.5061/dryad.477dp5c.

Author Contributions

All authors contributed to data collection. MJNF conceived the study, carried out the genotyping, performed the analyses and wrote the paper. TPF helped design the analyses and critically contributed to paper drafts. ARR habituated the population, coordinated volunteers and data collection at the field site, and critically contributed to paper drafts.

References

Arnold, T.W., 2010. Uninformative parameters and model selection using Akaike's Information Criterion. J. Wildl. Manag. 74, 1175–1178.

Bartoń, K., 2016. MuMIn: multi-model inference.

Bates, D., Machler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67, 1–48. https://doi.org/10.18637/jss.v067.i01

Bourke, A.F.G., 1988. Worker reproduction in the higher eusocial Hymenoptera. Q. Rev. Biol. 63, 291–311.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference, 2nd ed. Springer, New York, USA.

Buston, P.M., Zink, A.G., 2009. Reproductive skew and the evolution of conflict resolution: a synthesis of transactional and tug-of-war models. Behav. Ecol. 20, 672–684. https://doi.org/10.1093/beheco/arp050

Cant, M.A., 2011. The role of threats in animal cooperation. Proc. R. Soc. B Biol. Sci. 278, 170–178. https://doi.org/10.1098/rspb.2010.1241

Cant, M.A., 1998. A model for the evolution of reproductive skew without reproductive suppression. Anim. Behav. 55, 163–169. https://doi.org/10.1006/anbe.1997.0589

Cant, M.A., Hodge, S.J., Bell, M.B.V., Gilchrist, J.S., Nichols, H.J., 2010. Reproductive control via eviction (but not the threat of eviction) in banded mongooses. Proc. R. Soc. B Biol. Sci. 277, 2219–2226. https://doi.org/10.1098/rspb.2009.2097

Cant, M.A., Johnstone, R.A., 2009. How threats influence the evolutionary resolution of within-group conflict. Am. Nat. 173, 759–771. https://doi.org/10.1086/598489

Cant, M.A., Reeve, H.K., 2002. Female control of the distribution of paternity in cooperative breeders. Am. Nat. 160, 602–611. https://doi.org/10.1086/342820

Clutton-Brock, T., 2017. Reproductive competition and sexual selection. Philos. Trans. R. Soc. B Biol. Sci. 372, 20160310. https://doi.org/10.1098/rstb.2016.0310

Clutton-Brock, T., 2009. Sexual selection in females. Anim. Behav. 77, 3–11. https://doi.org/10.1016/j.anbehav.2008.08.026

Clutton-Brock, T.H., Brotherton, P.N.M., Russell, A.F., O'Riain, M.J., Gaynor, D., Kansky, R., Griffin, A.S., Manser, M., Sharpe, L., McIlrath, G.M., Small, T., Moss, A., Monfort, S., 2001. Cooperation, control, and concession in meerkat groups. Science 291, 478–481. https://doi.org/10.1126/science.291.5503.478

Clutton-Brock, T.H., Hodge, S.J., Flower, T.P., 2008. Group size and the suppression of subordinate reproduction in Kalahari meerkats. Anim. Behav. 76, 689–700. https://doi.org/10.1016/j.anbehav.2008.03.015

Curry, R.L., 1988. Group structure, within-group conflict and reproductive tactics in cooperatively breeding Galápagos mockingbirds, Nesomimus parvulus. Anim. Behav. 36, 1708–1728. https://doi.org/10.1016/S0003-3472(88)80111-8

Davies, N.B., 1986. Reproductive success of dunnocks, Prunella modularis, in a variable mating system. I. Factors influencing provisioning rate, nestling weight and fledging success. J. Anim. Ecol. 55, 123. https://doi.org/10.2307/4697

Dierkes, P., Taborsky, M., Kohler, U., 1999. Reproductive parasitism of broodcare helpers in a cooperatively breeding fish. Behav. Ecol. 10, 510–515. https://doi.org/10.1093/beheco/10.5.510

Faulkes, C.G., Bennett, N.C., 2001. Family values: group dynamics and social control of reproduction in African mole-rats. Trends Ecol. Evol. 16, 184–190. https://doi.org/10.1016/S0169-5347(01)02116-4

Freckleton, R.P., 2011. Dealing with collinearity in behavioural and ecological data: model averaging and the problems of measurement error. Behav. Ecol. Sociobiol. 65, 91–101. https://doi.org/10.1007/s00265-010-1045-6

Golabek, K.A., Radford, A.N., 2013. Chorus-call classification in the southern pied babbler: multiple call types given in overlapping contexts. Behaviour 150, 691–712.

Grueber, C.E., Nakagawa, S., Laws, R.J., Jamieson, I.G., 2011. Multimodel inference in ecology and evolution: challenges and solutions: Multimodel inference. J. Evol. Biol. 24, 699–711. https://doi.org/10.1111/j.1420-9101.2010.02210.x

Harrison, X.A., York, J.E., Cram, D.L., Hares, M.C., Young, A.J., 2013. Complete reproductive skew within white-browed sparrow weaver groups despite outbreeding opportunities for subordinates of both sexes. Behav. Ecol. Sociobiol. 67, 1915–1929. https://doi.org/10.1007/s00265-013-1599-1

Haydock, J., Koenig, W.D., 2002. Reproductive skew in the polygynandrous acorn woodpecker. Proc. Natl. Acad. Sci. 99, 7178–7183. https://doi.org/10.1073/pnas.102624199

Heg, D., Bergmüller, R., Bonfils, D., Otti, O., Bachar, Z., Burri, R., Heckel, G., Taborsky, M., 2006. Cichlids do not adjust reproductive skew to the availability of independent breeding options. Behav. Ecol. 17, 419–429. https://doi.org/10.1093/beheco/arj056

Hellmann, J.K., Sovic, M.G., Gibbs, H.L., Reddon, A.R., O'Connor, C.M., Ligocki, I.Y., Marsh-Rollo, S., Balshine, S., Hamilton, I.M., 2016. Within-group relatedness is correlated with colony-level social structure and reproductive sharing in a social fish. Mol. Ecol. 25, 4001–4013. https://doi.org/10.1111/mec.13728

Hodge, S.J., 2009. Understanding variation in reproductive skew: directions for future empirical research, in: Reproductive Skew in Vertebrates: Proximate and Ultimate Causes. Cambridge University Press, Cambridge, UK, pp. 439–466.

Hodge, S.J., Manica, A., Flower, T.P., Clutton-Brock, T.H., 2008. Determinants of reproductive success in dominant female meerkats. J. Anim. Ecol. 77, 92–102. https://doi.org/10.1111/j.1365-2656.2007.01318.x

Holekamp, K.E., Engh, A.L., 2009. Reproductive skew in female-dominated mammalian societies, in: Hager, R., Jones, C.B. (Eds.), Reproductive Skew in Vertebrates: Proximate and Ultimate Causes. Cambridge University Press, Cambridge, UK, pp. 53–83.

Jarvis, J., 1981. Eusociality in a mammal: cooperative breeding in naked mole-rat colonies. Science 212, 571–573. https://doi.org/10.1126/science.7209555

Keller, L., Reeve, H.K., 1994. Partitioning of reproduction in animal societies. Trends Ecol. Evol. 9, 98–102. https://doi.org/10.1016/0169-5347(94)90204-6

Koenig, W.D., Pitelka, F.A., Carmen, W.J., Mumme, R.L., Stanback, M.T., 1992. The evolution of delayed dispersal in cooperative breeders. Q. Rev. Biol. 67, 111–150.

Koenig, W.D., Shen, S.-F., Krakauer, A.H., Haydock, J., 2009. Reproductive skew in avian societies, in: Hager, R., Jones, C.B. (Eds.), Reproductive Skew in Vertebrates: Proximate and Ultimate Causes. Cambridge University Press, Cambridge, UK, pp. 227–264.

Kokko, H., Morrell, L.J., 2005. Mate guarding, male attractiveness, and paternity under social monogamy. Behav. Ecol. 16, 724–731. https://doi.org/10.1093/beheco/ari050

Lu, X., Wang, C., Du, B., 2011. Reproductive skew in an avian cooperative breeder: an empirical test for theoretical models. Behav. Ecol. 23, 11–17. https://doi.org/10.1093/beheco/arr143

Magrath, R.D., Johnstone, R.A., Heinsohn, R.G., 2004. Reproductive skew, in: Koenig, W.D., Dickinson, J.L. (Eds.), Ecology and Evolution of Cooperative Breeding in Birds. Cambridge University Press, Cambridge, UK, pp. 157–176.

Mumme, R.L., Koenig, W.D., Pitelka, F.A., 1983. Mate guarding in the acorn woodpecker: within-group reproductive competition in a cooperative breeder. Anim. Behav. 31, 1094–1106. https://doi.org/10.1016/S0003-3472(83)80017-7

Nelson-Flower, M.J., Hockey, P.A.R., O'Ryan, C., English, S., Thompson, A.M., Bradley, K., Rose, R., Ridley, A.R., 2013. Costly reproductive competition between females in a monogamous cooperatively breeding bird. Proc. R. Soc. B Biol. Sci. 280, 20130728. https://doi.org/10.1098/rspb.2013.0728

Nelson-Flower, M.J., Hockey, P.A.R., O'Ryan, C., Raihani, N.J., du Plessis, M.A., Ridley, A.R., 2011. Monogamous dominant pairs monopolize reproduction in the cooperatively breeding pied babbler. Behav. Ecol. 22, 559–565. https://doi.org/10.1093/beheco/arr018

Nelson-Flower, M.J., Hockey, P.A.R., O'Ryan, C., Ridley, A.R., 2012. Inbreeding avoidance mechanisms: dispersal dynamics in cooperatively breeding southern pied babblers. J. Anim. Ecol. 81, 876–883. https://doi.org/10.1111/j.1365-2656.2012.01983.x

Nelson-Flower, M.J., Ridley, A.R., 2016. Nepotism and subordinate tenure in a cooperative breeder. Biol. Lett. 12, 20160365. https://doi.org/10.1098/rsbl.2016.0365

Nelson-Flower, M.J., Ridley, A.R., 2015. Male-male competition is not costly to dominant males in a cooperatively breeding bird. Behav. Ecol. Sociobiol. 69, 1997–2004. https://doi.org/10.1007/s00265-015-2011-0

Nelson-Flower, M.J., Wiley, E.M., Flower, T.P., Ridley, A.R., 2018. Individual dispersal delays in a cooperative breeder: ecological constraints, the benefits of philopatry and the social queue for dominance. J. Anim. Ecol. https://doi.org/10.1111/1365-2656.12814

Nichols, H.J., 2017. The causes and consequences of inbreeding avoidance and tolerance in cooperatively breeding vertebrates. J. Zool. 303, 1–14. https://doi.org/10.1111/jzo.12466

Nichols, H.J., Bell, M.B.V., Hodge, S.J., Cant, M.A., 2012. Resource limitation moderates the adaptive suppression of subordinate breeding in a cooperatively breeding mongoose. Behav. Ecol. 23, 635–642. https://doi.org/10.1093/beheco/ars008

Piper, W.H., Slater, G., 1993. Polyandry and incest avoidance in the cooperative stripe-backed wren of Venezuela. Behaviour 124, 227–247. https://doi.org/10.1163/156853993X00597

Pusey, A., Wolf, M., 1996. Inbreeding avoidance in animals. Trends Ecol. Evol. 11, 201–206. https://doi.org/10.1016/0169-5347(96)10028-8

R Core Team, 2017. R: A language and environment for statistical computing.

Reeve, H.K., Shen, S.-F., 2013. Unity and disunity in the search for a unified reproductive skew theory. Anim. Behav. 85, 1137–1144. https://doi.org/10.1016/j.anbehav.2013.04.007

Ridley, A.R., 2016. Southern pied babblers: the dynamics of conflict and cooperation in a group-living society, in: Koenig, W.D., Dickinson, J.L. (Eds.), Cooperative Breeding in Vertebrates: Studies of Ecology, Evolution and Behavior. Cambridge University Press, Cambridge, UK, pp. 115–132.

Ridley, A.R., Raihani, N., 2007a. Facultative response to a kleptoparasite by the cooperatively breeding pied babbler. Behav. Ecol. 18, 324–330. https://doi.org/10.1093/beheco/arl092

Ridley, A.R., Raihani, N.J., 2007b. Variable postfledging care in a cooperative bird: causes and consequences. Behav. Ecol. 18, 994–1000. https://doi.org/10.1093/beheco/arm074

Ridley, A.R., Raihani, N.J., Nelson-Flower, M.J., 2008. The cost of being alone: the fate of floaters in a population of cooperatively breeding pied babblers Turdoides bicolor. J. Avian Biol. 38, 384–392. https://doi.org/10.1111/j.0908-8857.2008.04479.x

Riehl, C., 2017. Kinship and incest avoidance drive patterns of reproductive skew in cooperatively breeding birds. Am. Nat. 190, 774–785. https://doi.org/10.1086/694411

Saltzman, W., Digby, L.J., Abbott, D.H., 2009. Reproductive skew in female common marmosets: what can proximate mechanisms tell us about ultimate causes? Proc. R. Soc. B Biol. Sci. 276, 389–399. https://doi.org/10.1098/rspb.2008.1374

Sharpe, L.L., Rubow, J., Cherry, M.I., 2016. Robbing rivals: interference foraging competition reflects female reproductive competition in a cooperative mammal. Anim. Behav. 112, 229–236. https://doi.org/10.1016/j.anbehav.2015.12.009

Shen, S.-F., Reeve, H.K., 2010. Reproductive skew theory unified: The general bordered tug-of-war model. J. Theor. Biol. 263, 1–12. https://doi.org/10.1016/j.jtbi.2009.11.009

Spong, G.F., Hodge, S.J., Young, A.J., Clutton-Brock, T.H., 2008. Factors affecting the reproductive success of dominant male meerkats. Mol. Ecol. 17, 2287–2299. https://doi.org/10.1111/j.1365-294X.2008.03734.x

van Schaik, C.P., Pradhan, G.R., van Noordwijk, M.A., 2004. Mating conflict in primates: infanticide, sexual harassment and female sexuality, in: Kappeler, P.M., van Schaik, C.P. (Eds.), Sexual Selection in Primates: New and Comparative Perspectives. Cambridge University Press, pp. 141–163.

Vehrencamp, S.L., 1983. A model for the evolution of despotic versus egalitarian societies. Anim. Behav. 31, 667–682.

Wiley, E.M., Ridley, A.R., 2016. The effects of temperature on offspring provisioning in a cooperative breeder. Anim. Behav. 117, 187–195. https://doi.org/10.1016/j.anbehav.2016.05.009

Williams, D.A., 2004. Female control of reproductive skew in cooperatively breeding brown jays (Cyanocorax morio). Behav. Ecol. Sociobiol. 55, 370–380. https://doi.org/10.1007/s00265-003-0728-7

Young, A.J., 2009. The causes of physiological suppression in vertebrate societies: a synthesis, in: Hager, R., Jones, C.B. (Eds.), Reproductive Skew in Vertebrates: Proximate and Ultimate Causes. Cambridge University Press, Cambridge, UK, pp. 397–438.

Zöttl, M., Heg, D., Chervet, N., Taborsky, M., 2013. Kinship reduces alloparental care in cooperative cichlids where helpers pay-to-stay. Nat. Commun. 4, 1341. https://doi.org/10.1038/ncomms2344

Fig. 1: Probability of female competition: a) effect of subordinate age (days); b) effect of rainfall (mm). Dots represent raw data.

Fig. 2: Probability of male competition: a) effect of subordinate age (days); b) effect of rainfall (mm); c) effect of relationship with competitor, the dominant male, d) raw data of the effect of the relationship with the dominant male. Dots on a-c represent raw data.

Fig. 3: Probability of female subordinate reproductive success: a) effect of subordinate age (full dataset) and b) effect of mass (restricted dataset). Dots represent raw data.

Fig. 4: a) effect of the presence of an unrelated subordinate female on the probability of male subordinate reproductive success, b) raw data of the same effect.

	Females	Males
Total breeding attempts directly observed	95	113
Seen engaged in competition, consisting of:	57	65
Nest-building	40	46
Courtship and/ or copulation	5	18
Infanticide	12	N/A
Reproduction	17	12

Table 1: Sample sizes of males and females observed during fertile periods with a breakdown of the relative frequencies of each type of evidence used for competition for each sex. For several breeding attempts, subordinates were observed engaged in more than one type of reproductive behavior.

2A) FEMALES: LIKELIHOOD OF COMPETITION

Model	df	Log lik.	AICc	Δ AICc
Age + rainfall + subordinate partner	**6**	**-44.76**	**102.5**	**0**
Age + rainfall	**5**	**-46.04**	**102.8**	**0.28**
Age + rainfall + group size	**6**	**-45.58**	**104.1**	**1.65**
Full model: age + rainfall + subordinate partner + group size + relationship to competitor + queue position	10	-41.86	106.3	3.80
Null model	3	-54.35	115.0	12.48

Parameter	Estimate	Standard error	Confidence interval	*p*
Intercept	0.414	0.760	-1.095, 1.922	0.591
Age	**3.457**	**1.483**	**0.513, 6.404**	**0.021**
Subordinate partner	1.088	1.726	-2.318, 4.494	0.531
Rainfall	**-2.130**	**1.057**	**-4.229, -0.030**	**0.047**
Group size	0.223	0.716	-1.192, 1.639	0.758

2B) FEMALES: LIKELIHOOD OF COMPETITION – MASS DATASET

Model	df	Log lik.	AICc	Δ AICc
Age	**4**	**-32.04**	**72.8**	**0**
Mass	4	-35.46	79.6	6.83
Null model	3	-40.36	87.1	14.35
Full model: mass + age†	5	-29.99	71.0	--

Parameter	Estimate	Standard error	z	*p*
Intercept	0.712	0.583	1.221	0.222
Age	**4.558**	**1.922**	**2.372**	**0.018**

†Full model is not included in the top model set because terms in the full model are co-linear.

Table 2: Likelihood of competition to breed at observed nests by female subordinates with unrelated potential breeding partners. 2A) full dataset (N = 95 nests attended by 31 subordinate females at 17 groups); 2B) restricted dataset of females that were weighed (N = 64 nests attended by 23 subordinate females at 12 groups). Top part of table shows model comparisons of Δ2 AICc models (in bold) with the full and null models, bottom part shows model outputs with strongly supported variables in bold.

3A) MALES: LIKELIHOOD OF COMPETITION

Model	df	Log lik.	AICc	Δ AICc
Age + rainfall + relationship to competitor	**7**	**-65.34**	**147.5**	**0**
Full model: Age + rainfall + relationship to competitor + subordinate partner + group size + queue position†	10	-63.61	149.4	1.90
Null model	3	-77.04	160.3	14.56

Parameter	Estimate	Standard error	z	*p*
Intercept	-1.799	1.117	-1.610	0.107
Relationship to competitor (father)	2.022	1.153	1.754	0.079
Relationship to competitor (brother)	**2.842**	**1.173**	**2.424**	**0.015**
Age	**1.054**	**0.516**	**2.041**	**0.041**
Rainfall	**-1.391**	**0.484**	**-2.873**	**0.004**

3B) MALES: LIKELIHOOD OF COMPETITION – MASS DATASET

Model	df	Log lik.	AICc	Δ AICc
Null model	**3**	**-57.71**	**121.7**	**0**
Full model: mass + age	5	-56.66	124.1	2.40

Parameter	Estimate	Standard error	z	*p*
Intercept	0.425	0.221	1.927	0.054

†Full model is not included in the top model set because terms in the full model are co-linear.

Table 3: Likelihood of competition to breed at observed nests by male subordinates with unrelated potential breeding partners. 3A) full dataset (N = 113 nests attended by 29 subordinate males at 20 groups); 3B) restricted dataset of males that were weighed (N = 86 nests attended by 21 subordinate males at 16 groups). Top part of table shows model comparisons of Δ2 AICc models (in bold) with the full and null models, bottom part shows model outputs with strongly supported variables in bold.

4A) FEMALES: LIKELIHOOD OF REPRODUCTIVE SUCCESS

Model	df	Log lik.	AICc	Δ AICc
Age + subordinate partner	**5**	**-25.74**	**62.8**	**0**
Age	**4**	**-27.82**	**64.5**	**1.69**
Age + group size	**5**	**-26.72**	**64.8**	**1.97**
Null model	3	-31.76	70.0	7.21
Full model: age + rainfall + relationship to competitor + group size + subordinate partner	9	-24.60	71.7	8.90

Parameter	Estimate	Standard error	Confidence interval	*p*
Intercept	-1.180	0.661	-2.503, 0.143	0.080
Age	**2.271**	**0.985**	**0.290, 4.252**	**0.025**
Subordinate partner (yes)	1.009	1.191	-1.352, 3.370	0.402
Group size	0.222	0.533	-0.832, 1.277	0.679

4B) FEMALES: LIKELIHOOD OF REPRODUCTIVE SUCCESS – MASS DATASET

Model	df	Log lik.	AICc	Δ AICc
Mass	**4**	**-16.69**	**43.0**	**0**
Full model: mass + age†	5	-15.86	44.3	1.30
Age	4	-17.75	45.2	2.13
Null model	3	-19.26	45.5	2.43

Parameter	Estimate	Standard error	z	*p*
Intercept	-0.426	0.424	-1.004	0.316
Mass	**2.112**	**0.973**	**2.172**	**0.030**

†Full model is not included in the top model set because terms in the full model are co-linear.

Table 4: Factors affecting reproductive success by subordinate females with unrelated potential breeding partners as measured by parentage in genotyped clutches. 4A) full dataset (N = 50 parentage determinations for 22 subordinate females in 13 groups); 4B) restricted dataset of females that were weighed (N = 29 parentage determinations for 17 subordinate females in 9 groups). Top part of table shows model comparisons of Δ2 AICc models (in bold) with the full and null models, bottom part shows model outputs with strongly supported variables in bold.

5A) MALES: LIKELIHOOD OF REPRODUCTIVE SUCCESS

Model	df	Log lik.	AICc	Δ AICc
Subordinate partner + relationship to competitor	**5**	**-24.54**	**60.2**	**0**
Subordinate partner + group size + age	**6**	**-24.00**	**61.6**	**1.40**
Subordinate partner + group size	**5**	**-25.48**	**62.0**	**1.89**
Full model: subordinate partner + age + rainfall + relationship to competitor + group size	8	-22.87	64.5	4.30
Null model	3	-31.60	69.6	9.46

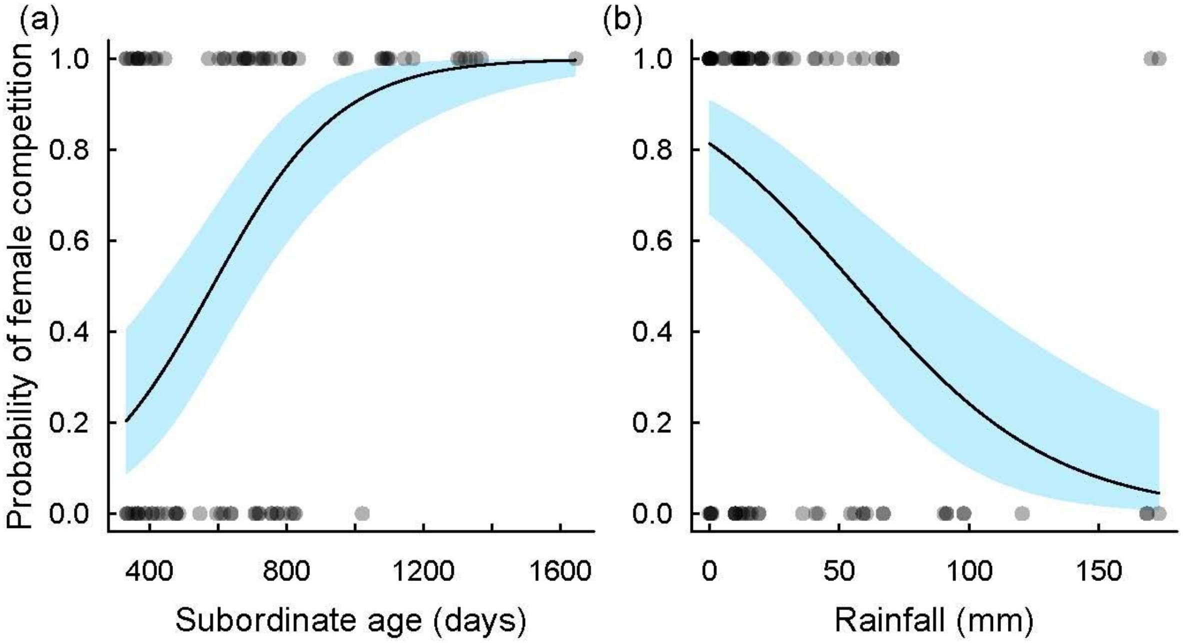
Parameter	Estimate	Standard error	Confidence interval	*p*
Intercept	**-1.812**	**0.530**	**-2.868, -0.755**	**0.001**
Subordinate partner (present)	**2.936**	**1.105**	**0.729, 5.144**	**0.009**
Relationship to competitor (sibling)	-1.235	1.478	-4.156, 1.685	0.407
Age	0.359	0.730	-1.083, 1.801	0.626
Group size	0.588	0.792	-0.977, 20153	0.462

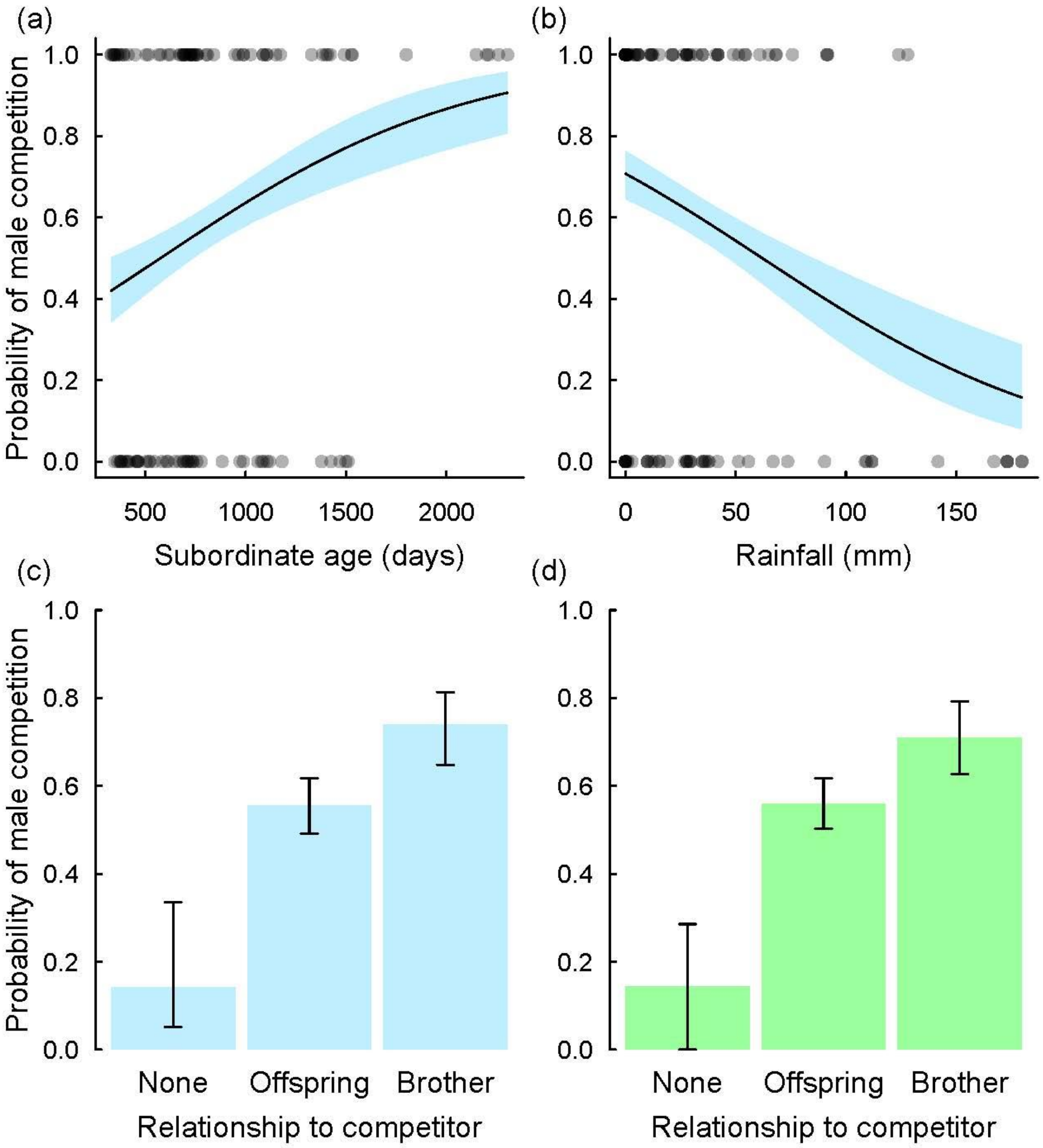
5B) MALES: LIKELIHOOD OF REPRODUCTIVE SUCCESS – MASS DATASET

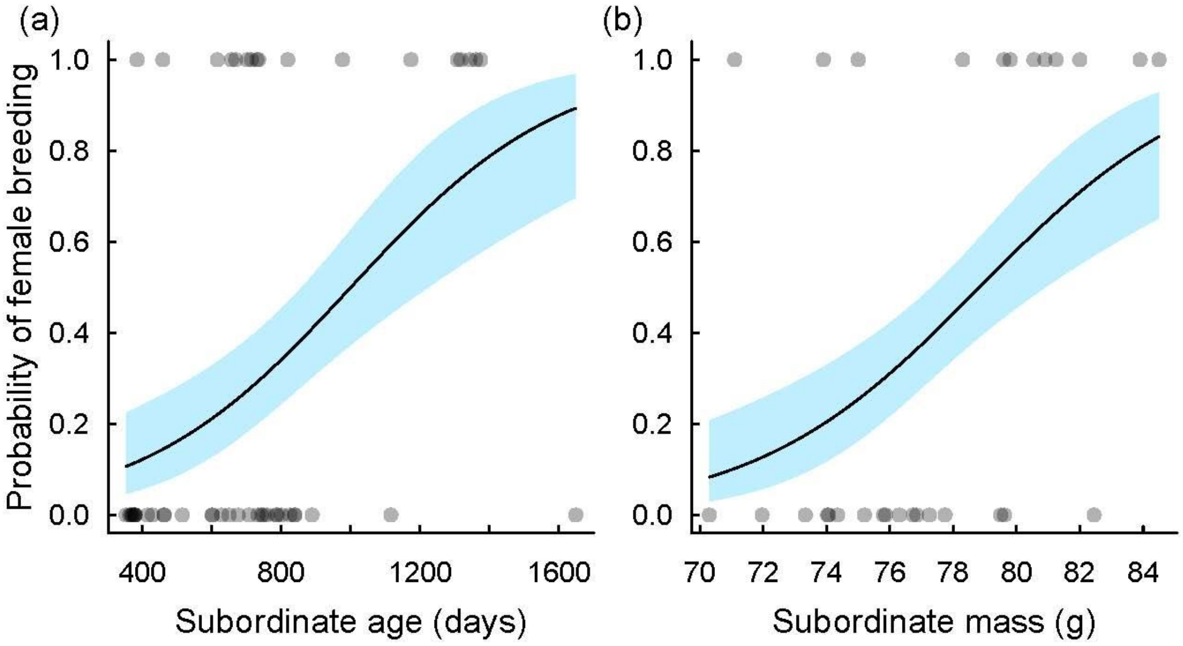
Model	df	Log lik.	AICc	Δ AICc
Null model	3	**-21.89**	50.4	**0**
Full model: mass + age	**5**	-21.55	54.9	4.50

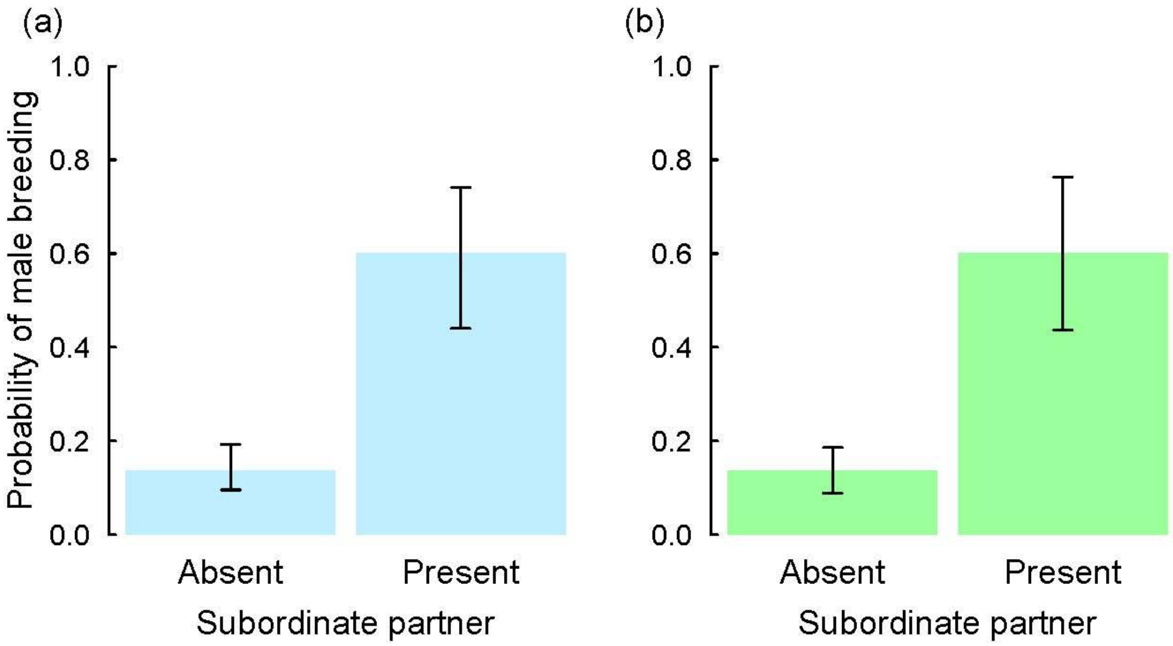
Parameter	Estimate	Standard error	z	*p*
Intercept	-1.819	1.318	-1.379	0.168

Table 5: Factors affecting reproductive success by subordinate males with unrelated potential breeding partners as measured by parentage in genotyped clutches. 5A) full dataset (N = 61 parentage determinations for 22 subordinate males in 15 groups); 5B) restricted dataset of males that were weighed (N = 40 parentage determinations for 17 subordinate males in 12 groups). Top part of table shows model comparisons of Δ2 AICc models (in bold) with the full and null models, bottom part shows model outputs with strongly supported variables in bold.


(a)
Probability of female competition
1.0
0.8
0.6
0.4
0.2
0.0
400
800
1200
1600
Subordinate age (days)
(b)
1.0
0.8
0.6
0.4
0.2
0.0
0
50
100
150
Rainfall (mm)


(a)
(b)
(c)
(d)
Probability of male competition
1.0
0.8
0.6
0.4
0.2
0.0
500
1000
1500
2000
Subordinate age (days)
0
50
100
150
Rainfall (mm)
None
Offspring
Brother
Relationship to competitor


(a)
(b)
Probability of female breeding
1.0
0.8
0.6
0.4
0.2
0.0
400
800
1200
1600
Subordinate age (days)
70
72
74
76
78
80
82
84
Subordinate mass (g)


(a)
Probability of male breeding
1.0
0.8
0.6
0.4
0.2
0.0
Absent
Present
Subordinate partner
(b)
1.0
0.8
0.6
0.4
0.2
0.0
Absent
Present
Subordinate partner