



Research

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Author for correspondence:

Dustin R. Rubenstein
e-mail: dr2497@columbia.edu

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Bateman's principle is reversed in a cooperatively breeding bird

Kathleen Apakupakul and Dustin R. Rubenstein

Department of Ecology, Evolution and Environmental Biology, Columbia University, 1200 Amsterdam Avenue, New York, NY 10027, USA

Bateman's principle is not only used to explain sex differences in mating behaviour, but also to determine which sex has the greater opportunity for sexual selection. It predicts that the relationship between the number of mates and the number of offspring produced should be stronger for males than for females. Yet, it is unclear whether Bateman's principle holds in cooperatively breeding systems where the strength of selection on traits used in intrasexual competition is high in both sexes. We tested Bateman's principle in the cooperatively breeding superb starling (*Lamprolornis superbus*), finding that only females showed a significant, positive Bateman gradient. We also found that the opportunity for selection was on average higher in females, but that its strength and direction oscillated through time. These data are consistent with the hypothesis that sexual selection underlies the female trait elaboration observed in superb starlings and other cooperative breeders. Even though the Bateman gradient was steeper for females than for males, the year-to-year oscillation in the strength and direction of the opportunity for selection likely explains why cooperative breeders do not exhibit sexual role reversal. Thus, Bateman's principle may not hold in cooperative breeders where both sexes appear to be under mutually strong sexual selection.

1. Introduction

Because males typically compete more intensely for mating opportunities and invest less in parental care than females [1], males can often obtain greater fitness benefits from mating multiply [2]. This phenomenon, referred to as 'Bateman's principle', is used not only to explain sex differences in mating behaviour, but also to determine which sex has the greater opportunity for sexual selection [2,3]. Bateman's principle predicts that the relationship between the number of mates and the number of offspring produced ('Bateman gradient' [4]) should be stronger for males than for females [2]. Bateman gradients in some species are similarly shaped in males and females [5], suggesting that selection on traits used to gain access to mates may be strong in both sexes. Although males in most species have more exaggerated secondary sexual characteristics than females, elaborate ornamentation in both sexes may be common in cooperatively breeding species where more than two individuals care for young. In cooperative breeders, the strength of selection on traits used in intrasexual competition is similar in males and females [6,7], and the variance in reproductive success is typically higher in females than males [8]. Moreover, females in cooperatively breeding species may be particularly likely to benefit from multiple mating because they can gain both indirect genetic benefits and direct benefits (e.g. additional parental care from helpers) through extra-pair matings [9].

Here, we use Bateman gradients to examine the strength of sexual selection in both sexes of the plural cooperatively breeding superb starling, *Lamprolornis superbus*. Although the functions of superb starlings' secondary sexual characteristics are not fully understood, both sexes have equally elaborate plumage [6], use similarly complex songs in a social context [10] and benefit from extra-pair matings [9]. Moreover, the opportunity for selection (measured as the standardized

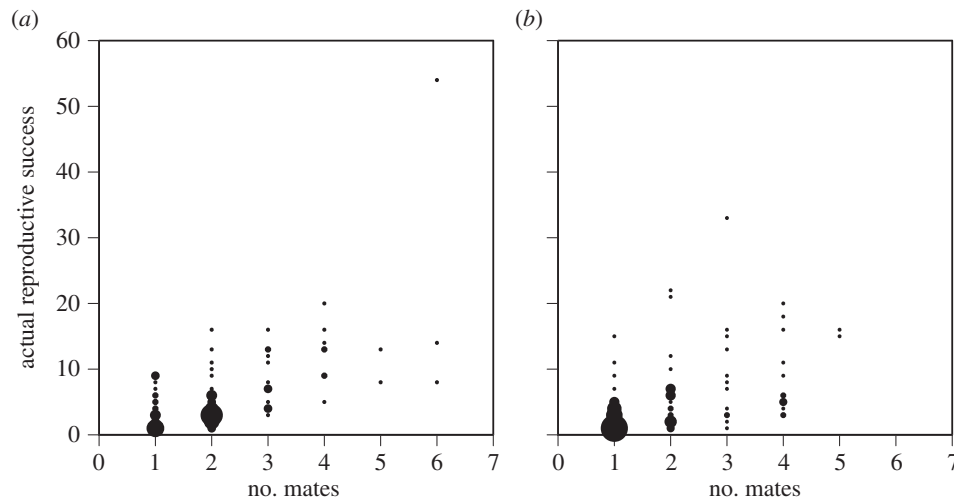


Figure 1. Bateman gradients showing the relationship between the number of mates and the actual reproductive success across years for (a) females and (b) males. The size of the circle represents the frequency of each observation (range = 1–9 and 1–12 for females and males, respectively). Although one female breeder sired 52 offspring over the study period, 32 more than the next highest female breeder, excluding her from the analysis did not qualitatively change the results.

variance in relative fitness [11]) is greater in female than in male starlings [12], as it is in other cooperative breeders [8]. If sexual selection underlies ornament elaboration in female superb starlings, we expect to see not only positive Bateman gradients in both sexes, but also steeper gradients in females because they have a higher variance in reproductive success than males.

2. Material and methods

(a) Study system

Nine social groups were studied from April 2001 to June 2013 at the Mpala Research Centre, Kenya (0°17' N, 37°52' E). Nests were monitored every 1–3 days during the long (March–June) and short rains (October–December) [12]. Over 25 breeding seasons, blood samples were collected from 578 nestlings and 315 adults. Parentage was assigned to nestlings using 15 microsatellite markers as described previously [13] (see the electronic supplementary material).

(b) Statistical analyses

Reproductive success was quantified over the lifetime of each breeding individual as the actual reproductive success (total number of offspring hatched for each individual breeding in the population over the study period; 578 offspring: $n = 292$ females, 284 males and two of unknown sex). We used general linear models with a Poisson error distribution to calculate Bateman gradients [3] for each sex by plotting actual reproductive success against the total number of mates (social and extra-pair), while controlling for the number of seasons that a bird bred. We included only those breeders that fledged at least one offspring during the study (*sensu* [5]). Because there has been debate about whether Bateman gradients should consider all offspring produced (i.e. hatched), or only those at the age of recruitment (i.e. fledged) [14], we repeated the analyses using only those offspring that survived to fledge. Bateman gradient analyses with both metrics were qualitatively similar, though there were differences in the analyses of the opportunity for selection.

Because not all individuals bred in each year of the study, our data likely reflect some individuals at the beginning or end of their breeding tenure. To confirm that this did not bias our results, we repeated the analyses including only those individuals ($n = 51$ females and 36 males) for which lifetime reproductive success data were available (*sensu* [15]). Because the results from using actual and lifetime reproductive success were qualitatively similar

(see the electronic supplementary material), our analyses do not appear to be biased by the inclusion of breeders with lifespans that extended beyond the 13-year study period. Finally, we re-estimated the opportunity for selection (I) separately for each sex as (variance in reproductive success)/(mean reproductive success)² (*sensu* [12,16]), but also determined annual differences in the opportunity for selection between males and females ($\Delta I, I_m - I_f$).

3. Results

(a) Bateman gradients

The actual reproductive success of females increased with the total number of mates ($\chi^2_{119} = 17.51, p < 0.0001$) while accounting for the number of breeding seasons ($\chi^2_{119} = 124.99, p < 0.0001$; figure 1a). When considering only those offspring that fledged, reproductive success still increased with the total number of mates ($\chi^2_{119} = 9.60, p < 0.0019$) while accounting for breeding seasons ($\chi^2_{119} = 102.43, p < 0.0001$). In contrast to the patterns observed in females, the actual reproductive success of males did not increase with the total number of mates ($\chi^2_{114} = 0.24, p = 0.63$) while accounting for breeding seasons ($\chi^2_{114} = 151.35, p < 0.0001$; figure 1b). Similarly, when considering only those offspring that fledged, there was no increase in reproductive success with an increase in the total number of mates ($\chi^2_{114} = 1.24, p = 0.27$) while controlling for breeding seasons ($\chi^2_{114} = 127.18, p < 0.0001$). The results from the analyses on lifetime reproductive success were qualitatively similar to those on actual reproductive success (see the electronic supplementary material).

(b) Opportunity for selection

As has been shown previously for this species [12], the opportunity for selection (I) was higher on average for females than for males when considering total offspring hatched (paired $t_{12} = 3.90, p < 0.0021$; electronic supplementary material, table S1). However, there was no sex difference in the opportunity for selection when considering only those offspring that fledged (paired $t_{12} = 1.74, p = 0.11$; electronic supplementary material, table S2). The annual difference in the opportunity for selection (ΔI) was on average less than zero both when considering total offspring hatched ($\Delta I = -1.15$)

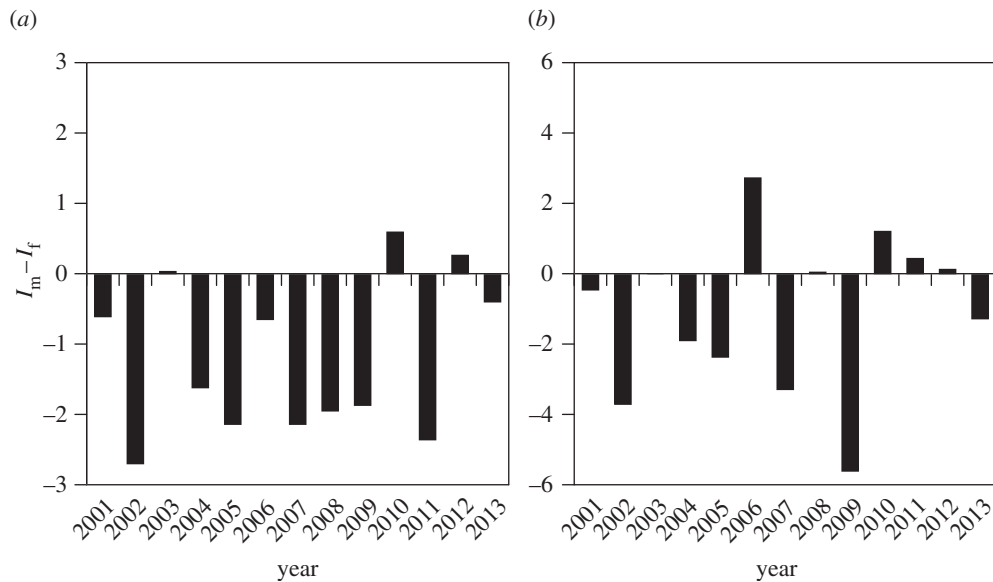


Figure 2. Annual differences in the opportunity for selection, ΔI ($I_m - I_f$), for (a) total offspring hatched and (b) total offspring fledged. ΔI was on average less than zero for both datasets, indicating a greater opportunity for selection in females in most years.

and only those offspring that fledged ($\Delta I = -1.08$), further indicating that females tended to have a greater opportunity for selection than males (figure 2).

4. Discussion

Bateman gradients showed a significant relationship between the number of total mates and reproductive success—whether using offspring produced (i.e. hatched) or recruited (i.e. fledged)—in females, but not in males. These results are consistent with the hypothesis that sexual selection acts more intensely on female than male superb starlings, as has been proposed for cooperative breeders in general [6,8]. Our results are also consistent with the idea that female secondary sexual traits are under strong sexual selection and are used to gain access to mates. While social selection (i.e. selection on traits used to increase social status or gain access to resources related to reproduction [17]) could still be occurring in this and other cooperatively breeding species, mutual sexual selection seems to be important.

Bateman's classic work on *Drosophila* has recently been challenged [18], and the significance of positive Bateman gradients in females has been questioned [5]. Instead of reflecting selection on females to mate multiply, positive female Bateman gradients could result from males targeting fecund females, the increased likelihood of extra-pair mate detection with increases in brood size, or iteroparous mate resampling [5]. Moreover, the phenotypic traits that predict high mating success may be different for males and females even though they can result in similar gradients for both sexes [5], showing that reproductive success in each sex may be subject to different selective pressures and trade-offs [19]. However, many of the issues underlying the interpretation of female Bateman gradients may be less of a concern in cooperatively breeding birds because (i) female fecundity is likely to be constrained by available parental care rather than egg production (clutch sizes are relatively small and invariable) and (ii) patterns of mate resampling in a permanent social group will differ from those in a larger population. Thus, we believe that males and females

face similar reproductive constraints in cooperatively breeding species, and Bateman gradients can be used to accurately assess the opportunity for selection in both sexes.

We also confirmed that the opportunity for selection [11,15] was higher for females when considering offspring hatched (*sensu* [11]), but not when considering offspring fledged. The differences among the datasets (and the greater variation in the fledgling dataset) were likely the result of smaller samples sizes in the latter. Moreover, the sex difference in variance in relative fitness (ΔI , $I_m - I_f$) was less than zero for most of the years of the study, indicating that I was typically greater for females than males. The oscillation that we observed in the opportunity for selection across years may explain why we fail to see sexual role reversal in this or other cooperatively breeding species [7]. Although it is not yet clear what is driving this oscillation, further studies should examine the environmental and demographic correlates.

In summary, Bateman's principle is reversed in the cooperatively breeding superb starling. This is consistent with the hypothesis that sexual selection is acting strongly in female cooperative breeders [6,8], though the strength and direction of the opportunity for selection oscillates annually. Thus, both male and female cooperative breeders appear to be under similar evolutionary pressures to gain access to mates, which likely results in mutually strong sexual selection in both sexes. Ultimately, this work demonstrates that living in altruistic societies has important implications for how selection operates on elaborate secondary sexual traits.

Ethics statement. This work was approved by the Columbia Institutional Animal Care and Use Committee (AC-AAAB1128).

Data accessibility. Data are available in the electronic supplementary material.

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Authors' contributions. D.R. designed the study. K.A. assembled the long-term data. D.R. analysed the data. Both authors wrote the paper.

Conflict of interest. The authors declare no competing interests.

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