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Greater opportunities for sexual selection in male than in female obligate brood parasitic birds

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Abstract

Females are expected to have evolved to be more discriminatory in mate choice than males as a result of greater reproductive investment into larger gametes (eggs vs. sperm). In turn, males are predicted to be more promiscuous than females, showing both a larger variance in the number of mates and a greater increase in reproductive success with more mates, yielding more intense sexual selection on males vs. females (Bateman's Paradigm). However, sex differences in costly parental care strategies can either reinforce or counteract the initial asymmetry in reproductive investment, which may be one cause for some studies failing to conform with predictions of Bateman's Paradigm. For example, in many bird species with small female-biased initial investment but extensive biparental care, both sexes should be subject to similar strengths of sexual selection because males and females are similarly restricted in their ability to pursue additional mates. Unlike 99% of avian species, however, obligate brood parasitic birds lack any parental care in either sex, predicting a conformation to Bateman's Paradigm. Here we use microsatellite genotyping to demonstrate that in brood parasitic brown-headed cowbirds (*Molothrus ater*), per capita annual reproductive success increases with the number of mates in males, but not in females. Furthermore, also as predicted, the variance of the number of mates and offspring is greater in males than in females. Thus, contrary to previous findings in this species, our results conform to predictions of the Bateman's Paradigm for taxa without parental care.

KEYWORDS
anisogamy, Bateman's gradient, brood parasitism, parental investment

1 | INTRODUCTION

In a foundational experimental study, Bateman (1948) proposed and tested a set of predictions to explain why and how the strength of sexual selection is often stronger in males. Known as Bateman's Paradigm (or Bateman's Principle), the relationship between reproductive success and the number of mates (Bateman's Gradient) is expected to be positive for males but not for females, and the number of mates and reproductive success is predicted to be more variable for males than females (Wade, 1979). In turn, Bateman's Paradigm has long been used to explain differences in sex-specific mating behaviours (Dewsbury, 2005), even though a growing number of studies fail to corroborate these predictions (reviewed in Tang-Martínez, 2016).

One potential leading cause for contradictory results with the Bateman Paradigm is the parental care strategy of the focal study organism (Janicke, Häderer, Lajeunesse, & Anthes, 2016). Indeed, costly parental investment (Clutton-Brock, 1991), when it differs between the sexes, can either reinforce or counteract the predictions of Bateman's Principle. For example, sexual selection should be greater for males that invest less in parental care because males may be able to pursue additional mates whereas females provide the care. Alternatively, females can have positive Bateman's Gradients and more variability in reproductive success in species with "sex-role reversal," in which males provide the majority or all of parental investment (Clutton-Brock, 2007; Jones, Rosenqvist, Berglund, Arnold, & Avise, 2000), as well as in cooperative breeding, with a male-biased pattern of helping and greater intrasexual competition in females (Apakupakul & Rubenstein, 2015; Hauber & Lacey, 2005). By contrast, for species with low initial asymmetry in gametes followed by extensive biparental care, both sexes should be subject to similar and low pressures of sexual selection, although the realized amount of parental care performed by each sex is often difficult to measure (Gerlach, McGlothlin, Parker, & Ketterson, 2012).

Unlike 99% of avian species, obligate brood parasitic birds lack any parental care by either sex, thus providing a system to disentangle the effects of parental care from the predictions of reproductive investment according to the Bateman's Paradigm (Hauber & Dearborn, 2003). These bird species still display anisogamy of their gametes (eggs > sperm), and therefore, without parental investment by either sex, male brood parasites are predicted to have a positive Bateman's gradients and more variability in the number of mates and reproductive success than females. In turn, sexual selection is predicted to be stronger for male brood parasites which may provide an explanation for the complex and, occasionally extravagant, male-biased sexual dichromatism and behavioural displays seen across several lineages of brood parasitic species (Barnard, 1990; Hasegawa & Arai, 2018; Payne & Payne, 1977; West, King, & Eastzer, 1981).

Here we investigated the sex-dependent relationship between the number of mates and reproductive success in brown-headed cowbirds (*Molothrus ater*), a widespread and generalist obligate brood parasitic species in North America. In the only previous studies of Bateman's Paradigm in brood parasitic cowbirds, Woolfenden, Gibbs, and Sealy (2002) reported greater variability in the number of mates for males versus females but, surprisingly, positive Bateman's gradients for both sexes. The authors concluded that opportunities for sexual selection are similar and high for the two sexes, potentially as a result of females receiving greater access to hosts' nests within male territories (Alderson, Gibbs, & Sealy, 1999; Woolfenden et al., 2002). Similarly, Bolopo et al. (2017) found positive Bateman's gradients for both males and females of the obligate brood parasitic Great Spotted Cuckoo (*Clamator glandarius*). In this species, males helping females by misdirecting host's mobbing aimed at the parasite near the host nest, which can cause injury from larger and aggressive hosts such as European Magpies *Pica pica* (Soler, Pérez-Contreras, & de Neve, 2014), may be a form of male-biased reproductive investment that

equalizes the greater initial investment into the eggs by females and generates similar slopes of Bateman gradients across the sexes. Furthermore, a likely benefit of polyandry for female Great Spotted Cuckoos may be ensuring egg fertilization (Bolopo et al., 2017). As parasitic females lay eggs for a longer period than nesting species, they may need to mate with several males to maximize fertilization success throughout the breeding season (Sheldon, 1994). Multiple mating may also prevent a fitness loss due to encounters with partially or totally infertile males. Finally, females may keep searching throughout the entire breeding season for better quality and the genetically most compatible mates to copulate with, to enhance the quality and diversity of their offspring. However, both the cowbird and the spotted cuckoo studies also highlighted the variability in the type of mating system detected for these two parasitic species across multiple years and/or populations sampled (Bolopo et al., 2017; Feeney & Riehl, 2019).

Given the secretive nature of reproduction by brood parasitic birds, parentage results can also be dramatically affected by logistical difficulties in locating brood parasitic propagules (eggs and chicks) and technical difficulties in using offspring data to reconstruct the genotypes of unsampled parents in the population (Strausberger & Ashley, 2003). Such limitations in the collection of adequate sample sizes for reproductive success per adult can dramatically affect the resulting analyses and the patterns yielded (Hauber & Dearborn, 2003). Here we used a host–parasite nest box study system, which provides large sample sizes of brood parasitic offspring in predetermined locations, to overcome limitations in collecting representative sample sizes (e.g. Hoover & Hauber, 2007; McKim-Louder, Hoover, Benson, & Schelsky, 2013). We then tested the prediction that, relative to females, male cowbirds exhibit positive Bateman's Gradients and increased variance of reproductive success and number of mates.

2 | METHODS

2.1 | Species and study system

We studied the parentage of brown-headed cowbirds within the Cache River watershed, southern Illinois, U.S.A. During 2007–2013, we placed artificial nest boxes prior to the onset of the breeding season 50–100 m apart within 15 study sites that contain suitable habitat of the prothonotary warbler, *Protonotaria citrea*, a cavity-breeding species commonly parasitized by cowbirds at our site (~70%; Hoover & Hauber, 2007; Louder, Schelsky, Albores, & Hoover, 2015a). The prothonotary warbler is a Neotropical migratory songbird that breeds in bottomland swamps throughout the southeastern United States. Nest boxes were checked every 3–5 days. To find additional cowbird offspring, we also searched for nests of alternative cowbird host species near nest boxes, such as Acadian flycatcher (*Empidonax virescens*), northern cardinal (*Cardinalis cardinalis*) and indigo bunting (*Passerina cyanea*) (Lowther, 1993). To assess parentage of cowbird offspring, we collected cowbird eggs when abandoned by hosts (laid too early) or when too many were laid for nestling survival (>2/
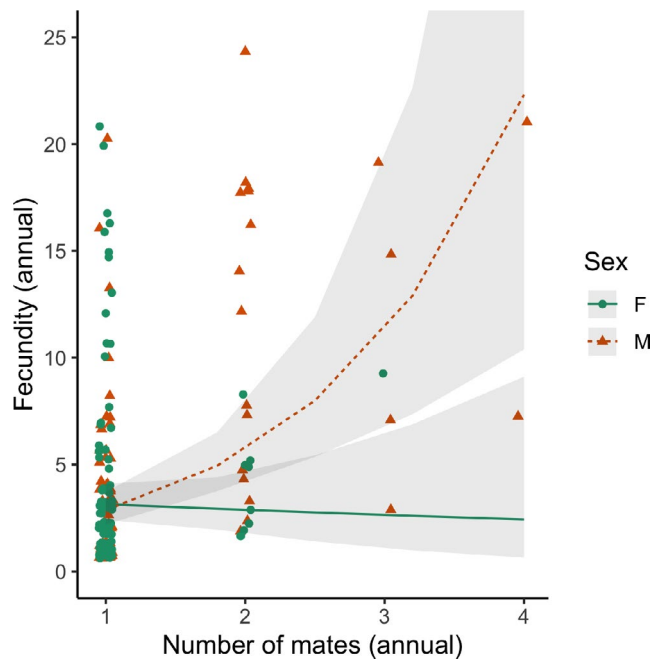
FIGURE 1 The comparison between the number of mates and the number of offspring (fecundity) detected annually via microsatellite DNA analyses for male and female brown-headed cowbirds, with predicted slope results from the negative binomial generalized linear model (95% confidence intervals are shown for each slope)

nest) and incubated them artificially for 5 days to extract tissue from embryos.

Embryonic tissue samples were stored in 95% ethanol and later frozen at -20°C. We also collected blood samples from cowbird nestlings with sterile needles (~50 μl) from the brachial vein of nestling cowbirds from naturally parasitized nests. Blood samples were stored in lysis buffer at ambient temperatures or at 4 °C until DNA extraction. We captured and blood sampled adult cowbirds with playbacks of conspecific songs and calls and mistnets within the forest near nest boxes and at feeder traps near the study sites (as in Louder, Ward, Schelsky, Hauber, & Hoover, 2015b).

2.2 | Parentage assignment

DNA from embryonic tissue or nestling blood was extracted with DNeasy Blood and Tissue kit (Qiagen). Samples were genotyped with nine microsatellite primer pairs (described in Louder et al., 2015b). However, we removed one microsatellite locus (CB 1) that deviated from Hardy–Weinberg equilibrium for parentage assignment (Louder et al., 2015b). On average, we identified 23 alleles (range = 9–32) among the 8 loci, resulting in an estimated nonexclusion p-value <0.001. We used program COLONY (version 2.0.6.5) to infer the parents of each offspring (Jones & Wang, 2010). COLONY uses genotypes of the offspring and candidate adults to assign a full pedigree structure and determine the parentage within a maximum-likelihood framework (Jones & Wang, 2010). Among parentage assignment approaches tested by Harrison, Saenz-Agudelo, Planes,

Jones, and Berumen (2013), the program COLONY is the best in assignment accuracy. Furthermore, because COLONY can reconstruct genotypes of unsampled parents, it is particularly useful in study species that are challenging to sample, such as brood parasitic birds without focal nest sites (e.g. Bolopo et al., 2017; Fossøy et al., 2016). We set parameters as follows: "long" run length, full-likelihood estimation with "high" precision, genotyping error was set for 0.01, a minimum of 4 microsatellite loci and allowing for male and female polygamy. Offspring were assigned to parents with p-values ≥ .95. We assigned offspring to males and females of either known genotype (i.e. adults captured) or from reconstructed genotypes with the sex of the unsampled individual determined from opposite sex matings with a candidate parent of known sex. To test whether our ability to detect adults given that they are alive (detection probability) differs between adult males and adult females, we used mark–recapture modelling (Cormack–Jolly–Seber) in program MARK (White & Burnham, 1999). Here we defined the first time an adult had assigned offspring as "marked" and each subsequent year as either "recaptured" if offspring were detected or "absent" if no offspring were assigned. We compared a model in which detection probability was equal between sexes versus different between adult males and females with the Akaike information criterion (AIC).

2.3 | Statistical analyses

Our annual parentage data include observations of ≥1 assigned offspring detected for a given year for known individuals and reconstructed individuals of known sex. To test for the effect of sex and number of annual mates on fecundity (i.e. Bateman's Gradient), we used a negative binomial generalized linear model in program R version 3.5 (package lme4). For explanatory factors, we included the sex of each parent, its number of mates for a given year and an interaction between those two factors. To account for repeated measures of an individual's reproductive and mating patterns across years, the individual identity of adult cowbirds was included as a random effect. We used a variance ratio test to test for the differences in the variance for fecundity and number of mates between all observations of male and female cowbirds. We also present the standardized variance (SV = variance/mean^2) of the number of mates and offspring for male and female cowbirds (Woolfenden et al., 2002).

3 | RESULTS

We successfully genotyped 1567 brown-headed cowbirds, including 113 candidate adults (46 Females; 67 Males) and 1454 offspring. Most cowbird offspring were collected from nests of prothonotary warblers (n = 1374), and 80 were opportunistically located in the nests of 12 additional songbird species. Program COLONY assigned at least 1 parent of known identity or reconstructed identity with inferred sex to 863 offspring.

A total of 54 (known identity = 16) adult males and 43 (known identity = 30) adult females were detected with at least 1 offspring

for a given year. A model which included equal detection probabilities between sexes (mean probability = 0.65, range = 0.58-0.76 95% C.I.) ranked higher than a model that included sex-specific detection probabilities (ΔAIC = 1.94; male probability = 0.63, range = 0.43–0.79 95% C.I.; female probability = 0.67, range = 0.51–0.80 95% C.I.). Using a negative binomial generalized linear model, annual fecundity was not significantly predicted by the number of mates per year ($Z = -0.38$, $p = 0.71$), but was significant for sex ($Z = -2.38$, $p = 0.02$) and for the interaction between the annual number of mates and sex ($Z = 2.90$, $p = 0.004$). Specifically, annual fecundity (eggs and nestlings combined) was greater in males (mean = 5.20 ± 0.61 SE) than females (4.64 ± 0.48 SE) and was positively correlated with the number of mates for males, but not for females (Figure 1). Furthermore, similar results were found when only including the parents of known identity, whereby the interaction between the annual number of mates and sex was significant ($Z = 3.23$, $p = 0.001$) and positively correlated with the number of mates for males, but not for females.

Overall, 24% of females and 23% of males were observed to have more than 1 genetic mate for a given year. The annual number of mates was not significantly different between sexes (mean females = 1.12 ± 0.02 SE; mean males = 1.32 ± 0.06 SE; negative binomial regression, $Z = 1.185$, $p = 0.21$) or among the years of the study ($Z < 0.67$, $p > 0.50$). However, the standardized variance (SV) for number of mates was 2 times greater for males (SV = 0.25) than females (SV = 0.11); the variance (non-normalized) was significantly greater for males (variance ratio test; $F_{92,89} = 3.50$, $p < 0.001$). In turn, the variance for number of offspring was significantly greater for the males (variance ratio test; $F_{92,89} = 1.54$, $p = 0.02$), and the standardized variance was slightly greater for males (SV = 1.23) than females (SV = 1.20).

4 | DISCUSSION

Using a productive study system of mostly nest box-breeding hosts to generate large sample sizes of brood parasitic progeny detected and sampled, we found consistent support for some of the critical predictions and patterns of Bateman's Paradigm in brown-headed cowbirds, an avian species with anisogamous reproduction and one that fully lacks costly parental care. Specifically, as predicted, we detected positive Bateman's Gradients in male cowbirds but not in females (Figure 1). We also detected, as predicted by Bateman's Paradigm, greater variance in the number of mates and number of offspring in males than in females. Therefore, the opportunity for sexual selection (Shuster & Wade, 2003) is predicted to be greater for males in the obligate brood parasitic brown-headed cowbird, and overall, the species is deemed to conform to Bateman's Paradigm.

Support for the male-biased strength of sexual selection in brown-headed cowbirds is seen in the prominent sexual dimorphism in size (larger males: Lowther, 1993), diverse vocalizations (male-only dialectic flight whistles and acoustically complex songs: West et al., 1981; O'Loghlen & Rothstein, 2003) and plumage dichromatism (costly iridescent black plumage in males only: McGraw, Mackillop,

Dale, & Hauber, 2002). In turn, female preferences for some of these traits are known to be strong and to generate differential mating patterns and reproductive outputs (Kohn, 2018; West et al., 1981). Similarly, other mechanisms of sexual selection, including male–male competition through visual and acoustic displays, are known to be involved in establishing dominance hierarchies with potential fitness differentials in brown-headed cowbirds (Rothstein, Yokel, & Fleischer, 1986; White, King, West, Gros-Louis, & Tuttle, 2010).

Given the lack of costly parental care, mating systems in obligate brood parasites are potentially more plastic than in species that provide parental care and able to adjust to many factors including parasite and/or host densities (Bolopo et al., 2017; Feeney & Riehl, 2019; Hauber & Dearborn, 2003). Indeed, Woolfenden et al. (2002) found the frequency of polygamy to change among years (e.g. relative to Alderson et al., 1999 who studied the same population in a single year), yet on average to be greater in male (58%) than female (31%) cowbirds. Similarly, the frequency of polygamy in great spotted cuckoos increased with population density (Bolopo et al., 2017). We did not find interannual variation in the mating system of cowbirds (see Results) but our study was also limited to a single study system without strong apparent variation in host or parasite density. In fact, the median number of genetic mates detected was both 1 for female and male cowbirds in this and in previous studies (Alderson et al., 1999; Woolfenden, Gibbs, Sealy, & McMaster, 2003), implying an unexpected prevalence of both genetic and social (Yokel, 1986) monogamy in a nonparental species (Feeney & Riehl, 2019; Hauber & Dearborn, 2003; Kohn, 2018; Sorenson & Payne, 2002). Therefore, it remains possible that the potential for male-biased differential sexual selection in brood parasites, as found in our population, is not stationary, but closely depends on annual and/or geographical variation in ecological factors.

Critically, in our study we limited our analysis to adult parental cowbirds with 1 or more progeny detected in a breeding season. Analyses of Bateman's Gradients will necessarily yield a positive slope when including adults with no progeny and, thus, no mates. Inclusion of adults with no observed fecundity in the quantitative analyses may have generated the significantly positive Bateman's slopes in a prior study on the same species, albeit in a different population (Woolfenden et al., 2002). Therefore, we considered that limiting the subject pool to adults with at least 1 assigned progeny would provide a more appropriate test for the slope and shape of Bateman's gradient, independent of statistical artefacts (Gerlach et al., 2012; Krakauer, Webster, Duval, Jones, & Shuster, 2011).

Overall, our research benefited from a logistically feasible, effective and biologically productive study system, which in turn generated large enough samples to confidently report the statistical conclusions derived from our analyses. The comparisons with previous works on monogamous and cooperative species (Gerlach et al., 2012; Hauber & Lacey, 2005; Rubenstein & Lovette, 2009) show that our results are also consistent with both theory and empirical conclusions drawn from within and between avian and other lineages (Brown, Laland, & Mulder, 2009; Jones, Rosenqvist, Berglund, & Avise, 2005). These patterns increasingly imply

critical and broadly applicable roles for the relative extents of sex-biased initial vs. parental investment in modulating differences in Bateman's Gradient and the resulting strength of sexual selection.

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