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BROWN-HEADED COWBIRDS SKEW HOST OFFSPRING SEX RATIOS

LIANA ZANETTE,^{1,4} ELIZABETH MACDOUGALL-SHAKLETON,¹ MICHAEL CLINCHY,^{1,2} AND JAMES N. M. SMITH³

¹*Department of Biology, University of Western Ontario, London, Ontario N6A 5B7, Canada*

²*Centre for the Neurobiology of Stress, University of Toronto at Scarborough, Scarborough, Ontario M1C 1A4, Canada*

³*Department of Zoology, University of British Columbia, Vancouver, British Columbia V6T 1Z4, Canada*

Abstract. Predators (or parasites) can have both direct and indirect effects on prey (or host) demography. Recent theory suggests that the impact of either effect may be greater if predators and parasites skew the sex ratio of survivors. Brown-headed Cowbirds (*Molothrus ater*) are obligate brood parasites. Many studies have shown that adult cowbirds directly cause host offspring mortalities. Cowbird young may indirectly cause additional mortalities by increasing competition in the nest. The sex ratio of surviving host offspring will be skewed if one sex is a poorer competitor and thus more likely to die. We studied whether and how cowbird parasitism affects host offspring sex ratios in Song Sparrow (*Melospiza melodia*) nests. The proportion of female sparrows in parasitized nests (0.28 ± 0.01) was half that in unparasitized nests (0.57 ± 0.05) at six days post-hatch and at fledging (0.27 ± 0.06 vs. 0.52 ± 0.11). Consistent with their being at a competitive disadvantage, female sparrows were smaller and lighter than male sparrows in parasitized mixed-sex (both sexes present) nests. This indirect effect of cowbirds on the sex ratio of surviving host offspring may dramatically affect host demography. We suggest that predator- or parasite-mediated sex ratio biases could be important to the demography of many prey or host species.

Key words: brood parasitism; Brown-headed Cowbird; *Melospiza melodia*; *Molothrus ater*; nestling competition; predator-prey interactions; sex ratios; sexual size dimorphism; sibling competition; Song Sparrow.

INTRODUCTION

Predators affect their prey in many ways other than by simply killing them. The mere presence of a predator almost invariably changes the prey's behavior. Parasites can also have both direct and indirect effects on their hosts. The potential effects on prey or host demography in either case will be greater if female prey or hosts are more adversely affected than males given the assumption common to all models of vertebrate demography that females are the limiting sex. Accordingly, recent demographic modeling (Engen et al. 2003, Lande et al. 2003) has highlighted the dramatic effects on prey or host populations that can result if predators or parasites skew the sex ratio of survivors. It is increasingly untenable, therefore, to assume that predators and parasites affect both sexes equally, as has commonly been done in species in which the sexes are difficult to distinguish (e.g., Pease and Gryzbowski 1995, Gryzbowski and Pease 2000). Fortunately, it is

also increasingly unnecessary, given new genetic sexing techniques.

Many studies have shown that adult Brown-headed Cowbirds (*Molothrus ater*) directly cause host offspring mortalities by destroying eggs, killing nestlings, and inducing nest abandonment (Elliot 1999, Smith et al. 2003), and it is well-known that the presence of cowbirds can drastically reduce the total number of host offspring produced. Smith et al. (2002) showed that Song Sparrows (*Melospiza melodia*) reared almost twice as many offspring in areas where cowbirds were experimentally reduced in number compared to control areas, in a five-year study with spatial replication. Correlative studies have found comparable negative effects of cowbirds on host offspring numbers, and cowbird removal is frequently used as a management technique in the recovery of declining host populations (Hall and Rothstein 1999; also see Morrison et al. 1999, Smith et al. 2000).

Cowbird nestlings may indirectly cause additional mortalities among their heterospecific nest mates, as they are frequently larger and have superior begging behavior, allowing them to outcompete host nestlings for parental food provisioning (Lichenstein and Sealy

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⁴ E-mail: lzanette@uwo.ca



PLATE 1. Song Sparrow nestlings begging. Photo credit: J. A. Pfaff.

1998, Dearborn 1998; reviewed in Lorenzana and Sealy 1999). This in turn may affect host offspring sex ratios, if one sex is a poorer competitor and thus is more likely to die. Differences between the sexes in nestling competitive ability and survival are sometimes related to size (Bortolotti 1986, Cotton et al. 1999, Parker et al. 2002, Brommer et al. 2003, Magrath et al. 2003, Smiseth et al. 2003). Oddie (2000) showed experimentally that under stressful conditions, where competition for food provisioning was extreme, the larger size of male nestling Great Tits (*Parus major*) allows them to out-compete females for food. Under such poor rearing conditions, female Great Tit nestlings exhibit greater mortality, and sex ratios at fledging tend to be male biased (Dhondt 1970, Smith et al. 1989, Lessells et al. 1996).

In this study, we tested whether cowbird parasitism affects the sex ratio of Song Sparrow nestlings and fledglings. Adult and nestling Song Sparrows exhibit some sexual size dimorphism, with males being larger (Hochachka and Smith 1991). We expected cowbird young to increase competition among nest mates for food provisioning. We predicted that parasitized broods would be male biased if their larger body size gives males a competitive advantage over females, resulting in more female mortality. We tested for male competitive advantage by examining body mass and size in nests consisting of both male and female sparrow nestlings (i.e., mixed-sex broods) and all-male or all-female nests (i.e., single-sex broods). We expected females to be lighter and smaller when together with males (i.e., in mixed-sex broods) especially when these mixed-sex broods were parasitized. We discuss the impact on host

demography that may result from this previously un-considered effect of cowbirds on their hosts.

METHODS

Field procedures

We monitored Song Sparrows for the entire 2003 breeding season near Victoria, British Columbia, Canada (see Plate 1). Song Sparrows are multibrooded and can rear up to four broods of 1–4 young per female per year. Three-egg and four-egg clutches predominate. Nests containing cowbird eggs or nestlings were classified as parasitized. Nests were monitored regularly (usually every 3–4 days) and noted as active, failed, or fledged. Fledging generally occurs on day 11 post-hatch (range day 9–13). Nestlings were uniquely color banded, mainly at day 6 post-hatch (range day 5–7). At this time, we measured mass using a spring balance (to 0.1 g) and tarsus length using calipers (to 0.1 mm) and took ~25 μ L of blood from the brachial vein for molecular sexing. Blood was immediately stored in lysis buffer.

Molecular sexing

We used PCR (polymerase chain reaction) amplification of genes located on the sex chromosomes (Griffiths et al. 1998) to determine the sex of nestlings. Genomic DNA was isolated from the blood samples following the guanidine-based method described in Ausubel et al. (1988), and was quantified using a spectrophotometer (Eppendorf BioPhotometer, Eppendorf, Hamburg, Germany). PCR amplifications were carried out in a total volume of 10 μ L and included 50–100

ng DNA, 10 mmol/L Tris-HCl pH 8.3, 50 mmol/L KCl, 10 μ g BSA, 2.5 mmol/L MgCl₂, 0.2 mmol/L of each deoxynucleotide (Fisher Chemicals, Fairlawn, New Jersey, USA), 0.5 units Taq polymerase (Fisher), and 0.2 μ mol/L of each primer (P2 and P8, described in Griffiths et al. [1998]). Thermocycling was done in a Biometra T1 thermocycler (Biometra, Gottingen, Germany); conditions included an initial denaturing step at 94°C for 90 s, followed by 30 cycles of 48°C for 45 s, 72°C for 45 s, and 94°C for 30 s, followed by a final step of 48°C for 60 s and 72°C for 5 min. We then separated PCR products by electrophoresis for 50–90 min at 60–90 V, on 1.5% agarose gels stained with ethidium bromide. Because females are the heterogametic sex in birds, samples taken from females exhibit two distinct bands (CHD-Z, CHD-W) and samples taken from males show only one (CHD-Z). We had 100% correspondence between our molecular sexing technique and control samples taken from 16 adults of known sex (Griffiths et al. 1998). Once sparrow nestlings were sexed, we categorized nests as mixed-sex (broods containing both males and females) or single-sex (all-male or all-female broods).

Statistical analyses

We considered broods for which we had DNA for all nest mates aged day 6 post-hatch (day 0 = hatch day). We randomly selected one nest per breeding female to analyze sex ratios ($n = 67$ nests) using a generalized linear model with a logit link function and binomial errors (Statsoft 2000). All models examining sex ratios were corrected for brood size by adding it as a covariate. The proportions of mixed-sex vs. single-sex broods were analyzed as for sex ratios. Each binomial model was derived using backward elimination of possible explanatory variables and their interaction terms, until no further terms could be removed without reducing the model's explanatory power (following Wilson and Hardy [2002] and Boomsma and Nachman [2002]). All models were checked for overdispersion (Wilson and Hardy 2002) and all proportions presented are means \pm 1 SE.

We evaluated the competitive ability of Song Sparrow nestlings using mass and size (tarsus length) of the largest nestling of each sex in the nest. Body mass and size were not related to brood size (simple linear regressions, $P > 0.35$), but increased with age at banding ($P < 0.001$). We first examined how parasitism status (unparasitized vs. parasitized nests) and sex composition of the brood (mixed-sex vs. single-sex) influenced mass and size of each sex separately using two-way ANCOVAs, with age as the covariate. We then examined single-sex and mixed-sex broods separately and determined whether mass and size varied between the sexes and with parasitism status. For single-sex broods, we conducted two-way ANCOVAs with age at banding as the covariate. For mixed-sex broods, we performed one-between, one-within repeated-measures

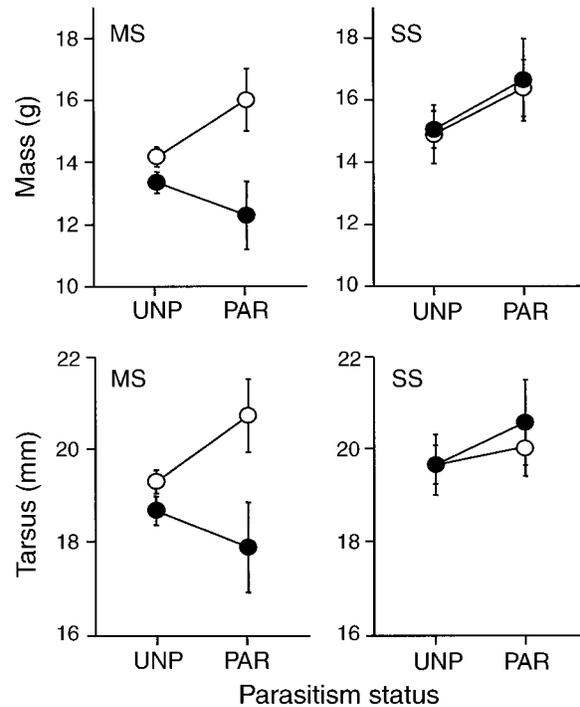


FIG. 1. Mean (\pm 1 SE) mass (g) and tarsus length (mm) of male (open circle) and female (closed circle) nestling Song Sparrows in mixed-sex (MS, males and females together in the nest) and single-sex (SS, males together or females together in the nest) broods that were parasitized (PAR) or unparasitized (UNP) by Brown-headed Cowbirds.

ANCOVAs with parasitism status as the between variable, sex as the repeated-measures term, and age at banding as the covariate.

RESULTS

Song Sparrow nestling and fledgling sex ratios varied significantly with cowbird parasitism (for nestlings, $\chi^2_1 = 6.5$, $P = 0.01$; for fledglings, $\chi^2_1 = 7.8$, $P = 0.001$). The proportion of female sparrows in parasitized nests (0.28 ± 0.01) was half that in unparasitized nests (0.57 ± 0.05) at six days post-hatch, and at fledging (0.27 ± 0.06 vs. 0.52 ± 0.11).

Female Song Sparrow nestlings were at a disadvantage when in the nest with male Song Sparrow nestlings, particularly when these mixed-sex broods were parasitized (Fig. 1). Taking each sex separately, the presence of male nestlings significantly affected female nestlings. Females in mixed-sex broods, i.e., together with males, were lighter and structurally smaller than females in single-sex broods, i.e., in all-female nests (mixed-sex vs. single-sex, respectively: for female mass, 12.8 ± 0.66 g vs. 16.1 ± 0.69 g, $F_{1,46} = 11.8$, $P = 0.001$; for female tarsus, 18.3 ± 0.50 mm vs. 20.3 ± 0.53 mm, $F_{1,46} = 7.2$, $P = 0.01$). The presence of female nestlings did not affect their male nest mates, because males in mixed-sex broods were of comparable mass and size to males in single-sex broods (for male

mass, 15.0 ± 0.53 g vs. 15.5 ± 0.49 g, $F_{1,41} = 0.5$, $P = 0.47$; for male tarsus: 19.9 ± 0.42 mm vs. 19.8 ± 0.39 mm, $F_{1,41} = 0.0$, $P = 0.83$). Between the sexes, the disadvantage that female nestlings faced when in the presence of male nest mates was significantly increased when these mixed-sex nests were parasitized (Fig. 1; repeated-measures ANCOVA). For mass, sex of nestling ($F_{1,30} = 2.6$, $P = 0.12$) and parasitism status, ($F_{1,30} = 0.2$, $P = 0.70$) were not significant; sex \times parasitism ($F_{1,30} = 9.5$, $P = 0.004$) was strongly significant. For body size, sex of nestling ($F_{1,30} = 2.1$, $P = 0.15$) and parasitism status ($F_{1,30} = 0.1$, $P = 0.71$) were not significant; sex \times parasitism ($F_{1,30} = 7.3$, $P = 0.011$) was. Considering females only, parasitism tended to increase their mass and size in single-sex broods, but decreased their mass and size in mixed-sex broods (Fig. 1), with the net result being no overall effect of parasitism per se (unparasitized vs. parasitized nests; for female mass, 14.6 ± 0.89 g vs. 14.3 ± 0.34 g, $F_{1,46} = 0.1$, $P = 0.78$; for female tarsus, 19.3 ± 0.68 mm vs. 19.2 ± 0.26 mm, $F_{1,46} = 0.0$, $P = 0.93$). For males, however, parasitism increased their mass and size in both single-sex and mixed-sex broods (Fig. 1), resulting in a significant positive effect of parasitism on male mass and a trend in the same direction on size (for male mass, 12.8 ± 0.66 g vs. 16.1 ± 0.69 g, $F_{1,41} = 4.5$, $P = 0.04$; for male tarsus, 18.3 ± 0.50 mm vs. 20.3 ± 0.53 mm, $F_{1,41} = 2.4$, $P = 0.43$).

Brood sizes were significantly smaller in parasitized (2.1 ± 0.24 nestlings) than unparasitized nests (2.8 ± 0.12 nestlings; one-way ANOVA, $F_{1,65} = 5.2$, $P = 0.025$) and losses from parasitized mixed-sex broods appeared to be female biased. Although the majority of unparasitized nests contained mixed-sex broods (54% of 54 nests), most parasitized nests contained single-sex broods (i.e., only 23% of 13 nests were mixed sex; $\chi^2_1 = 10.0$, $P = 0.002$). This suggests that many broods that started out as mixed sex (e.g., 2 males : 1 female), lost one sex or the other when parasitism occurred (e.g., 1 female) resulting in more single-sex broods (e.g., 2 males : 0 females). If the higher incidence of single-sex broods in parasitized nests were due to the differential loss of one sex, then the sex ratio in parasitized single-sex broods should differ from that in single-sex unparasitized broods. Indeed, losses from parasitized broods appeared to involve mainly females, because single-sex broods contained a significantly greater proportion of males than females in parasitized nests, but a greater proportion of females than males in unparasitized nests ($\chi^2_1 = 9.4$, $P = 0.002$; proportion of females 0.26 ± 0.10 vs. 0.67 ± 0.06 in parasitized vs. unparasitized nests, respectively). The sex ratios in nests that remained mixed sex were comparable in parasitized and unparasitized nests (proportion of females 0.44 ± 0.18 vs. 0.43 ± 0.05).

We have argued that losses from parasitized nests were female biased. It is possible, however, that any mortality in the nest is generally female biased. To

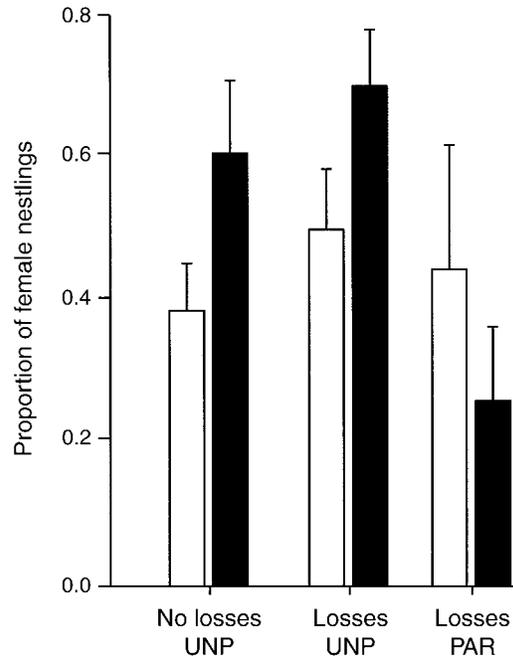


FIG. 2. Proportion of female Song Sparrow nestlings (mean \pm 1 SE) in mixed-sex (open bars) and single-sex (closed bars) broods in (left to right): 22 unparasitized nests in which no losses of nest contents occurred; 32 unparasitized nests with losses; and 13 parasitized nests with losses (all parasitized nests suffered some loss).

check this, we identified (Fig. 2) nests in which there were no losses, nests in which there was mortality unassociated with parasitism, and nests where cowbird parasitism had occurred (all parasitized nests experienced some mortality). Comparing all three types of nests, we found comparable sex ratios in both types of unparasitized nests, whereas parasitized nests differed significantly (Fig. 2; nest type \times sex composition interaction, $\chi^2_2 = 9.3$, $P = 0.01$), suggesting that female-biased mortality was specific to parasitized nests.

DISCUSSION

Cowbird parasitism significantly affected the sex ratio of surviving host offspring. The proportion of female sparrows in parasitized nests was half that in unparasitized nests. Our data suggest that the most likely mechanism is that the presence of cowbird young exacerbates the competitive disadvantage that female Song Sparrow nestlings face when together with male Song Sparrow nestlings (Fig. 1), resulting in female-biased mortality (Fig. 2).

Regardless of the mechanism responsible, parasitized nests have proportionately fewer females. This result is unambiguous. What this means is that the adverse effect of cowbirds on host demography is greater than previously imagined, at least with respect to Song Sparrows. Although many studies have shown that cowbirds reduce the absolute number of host young

produced (Stutchbury 1997, Whitfield et al. 1999, Smith et al. 2000), it has generally been assumed that there are an equal number of males and females among the survivors. Our results show that there are actually fewer females than expected among these survivors. It is because there are proportionately fewer females that the potential demographic significance is so great. Given our results, if no Song Sparrow nests were parasitized, 52% of fledglings in the population should be female. At the other extreme, if all nests suffered some parasitism, this number would be cut in half, reducing the percentage of fledglings that are female to just 27%. In any conventional demographic model, a 50% drop in the number of female offspring produced must alter the projected population growth rate (Engen et al. 2003, Lande et al. 2003). How much of an alteration this entails depends, of course, on the life history of the species in question, but species with a life history sensitive to effects on offspring survival (P_j ; Oli and Dobson 2003) will also be sensitive to this effect on the sex ratio of survivors.

The mechanism most likely responsible for the skewed sex ratio of surviving host offspring is cowbird-mediated exacerbation of intraspecific competition (Figs. 1 and 2). Luttbegg et al. (2003) recently reviewed the many ways in which predators can affect intraspecific competition in their prey. Our results suggest that it may be important to investigate whether predator-mediated intraspecific competition in turn affects the sex ratio of surviving prey. The importance of such indirect predator effects to prey population dynamics could be considerable if, as in our case, there are far fewer females.

Our data (Fig. 1) suggest that intraspecific competition between male and female sparrow nestlings causes females to lose mass and size, whereas interspecific competition with cowbird nestlings causes both male sparrow nestlings and female sparrow nestlings in single-sex broods to gain mass and size. Given the vast literature on begging behavior and parent-offspring conflict, there is no shortage of potential explanations for why the mechanisms, and hence the effects of intraspecific and interspecific competition, might differ. With regard to interspecific competition, the presence of cowbird nestlings often leads to an increase in overall begging intensity in the nest (Bengtsson and Rydén 1983, Kilner 2003), both because cowbirds are better beggars, begging sooner, longer and at a higher intensity (Dearborn 1998, Lichtenstein and Sealy 1998), and because host nestlings themselves beg more in parasitized nests in the face of this increased competition (Dearborn et al. 1998). All this extra begging may stimulate parents into provisioning parasitized nests at a higher rate than unparasitized nests, as is often observed (Dearborn et al. 1998, Kilpatrick 2002, Glassey and Forbes 2003; but see McMaster and Sealy 1999). The greater mass and size of host nestlings in parasitized nests is therefore less surprising if they are getting

at least some of this extra food. With regard to intraspecific competition, male sparrows may be able to outcompete their female nest mates by monopolizing feedings due to their larger size, more intensive begging, or better positioning in the nest (Magrath 1990, Wright and Leonard 2002). The condition of Song Sparrow nestlings is positively correlated with survival to independence for males, but not for females (Hochachka and Smith 1991). Thus, parents may also put more effort into feeding males (Clotfelter 1996, Smith et al. 2003). The overall increase in begging intensity stimulated by cowbirds may then exaggerate this otherwise adaptive bias toward feeding male nestlings, with adverse consequences for female survival.

Mechanisms other than cowbird-mediated intraspecific competition may contribute to the skewed sex ratio in parasitized nests. Although our data support the role of competition during brood-rearing, events during egg-laying may also be important. Adult cowbirds often remove or puncture host eggs as they are being laid, so first-laid eggs are more likely to be removed than final eggs. In some birds, laying order differs by sex (Ankney 1982, Ryder 1983, Weatherhead 1985, Clotfelter 1996, Badyaev et al. 2002). If Song Sparrows lay female eggs first and early eggs are more likely to be damaged by adult cowbirds, then host offspring sex ratio would be biased. Establishing the sex ratio at laying is much more logistically difficult than during brood-rearing, but this alternative mechanism for skew among parasitized offspring needs to be investigated.

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