

Limits to sexual size dimorphism in red-winged blackbirds: the cost of getting big?

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A fundamental assumption of sexual selection theory is that the reproductive advantage of large size is balanced by a survival disadvantage. Previous studies of the sexually size-dimorphic red-winged blackbird (*Agelaius phoeniceus*) have indicated that the largest adult males have a survival advantage, suggesting that the limit to male size may be the cost of getting big rather than the cost of being big. If the cost of getting big limits male size, then starvation rates for male nestlings should exceed those of female nestlings. In addition, given high heritability of body size, larger parents should lose more nestlings, particularly males, to starvation. We tested these predictions for red-winged blackbirds using data on the sex of 1356 fledglings from 465 nests collected over 10 years. We found no disadvantage for male nestlings relative to females – 49% of fledglings were male and previous research had shown that 48% of hatchlings are male. We also found no disadvantage for male nestlings that would become large adults (i.e. those with larger parents) – partial brood loss and fledging sex ratios did not vary with mid-parent size. Given no apparent disadvantage to large size for males either as adults or as nestlings, this leaves only the period between fledging and adulthood during which natural selection might limit sexual size dimorphism, although other mechanisms might explain the failure to find a limit to male size. © 2005 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2005, 85, 353–361.

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INTRODUCTION

Body size is often the trait that most easily allows us to distinguish males from females among animal species (Andersson, 1994). The prevalence of such sexual size dimorphism (SSD) and the ecological (Peters, 1983) and evolutionary (Roff, 1992; Stearns, 1992) importance of variation in body size account for the enduring interest in SSD. It is therefore surprising that there is a fundamental gap in our understanding of the evolutionary processes contributing to SSD. Specifically, although much is known about the factors that promote SSD, information about factors that limit the extent of SSD remains scant (Blanckenhorn, 2000), although recent studies are beginning to change that (e.g. Ferguson & Fairbairn, 2000; Preziosi

& Fairbairn, 2000; Badyaev, Whittingham & Hill, 2001; Quinn, Hendry & Buck, 2001; Schulte-Hostedde, Millar & Gibbs, 2002; Wilson, Hutchings & Ferguson, 2003). Here we address this deficiency with a novel test of one of the mechanisms hypothesized to limit SSD. Specifically, we explore the possibility that SSD is limited by the cost of growing large.

Darwin (1871) established much of the theoretical framework for the contemporary view of SSD. Competition for mates favours increased body size in the more competitive sex because large individuals generally are expected to prevail over small individuals. As individuals of the sexually selected sex increase in size, they become progressively less ecologically adapted (the ecological optimum is assumed to be the size of the sex that is not sexually selected). The resulting viability cost favours smaller individuals, so that the observed size of the larger sex arises from the equilibrium between the reproductive advantages of being bigger and the survival advantages of being smaller. Thus, natural selection limits sexual selection.

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Extensive research has confirmed that sexual selection promotes SSD through the mating advantage realized by larger individuals of the bigger sex. In birds, for example, variation in the number of social mates obtained by males can account for much of the variance in male mating success, even when extra-pair mating is prevalent, and larger males obtain more social mates (e.g. Weatherhead & Boag, 1997). In turn, variation in the social mating system explains much of the variation in SSD across species (Webster, 1992; Dunn, Whittingham & Pitcher, 2001). The same general positive relationship between variance in mating success among males and the degree of SSD has also been documented across other taxa (Andersson, 1994).

If viability costs limit the extent to which sexual selection can increase male size, we should see evidence of these costs once males have achieved adult size (the cost of being big) or while they are growing (the cost of getting big). Most effort to date has been devoted to assessing the former. Comparisons of sex-specific mortality rates relative to SSD among birds and mammals show that adult males survive less well relative to adult females as SSD increases (Searcy & Yasukawa, 1981; Promislow, 1992; Promislow, Montgomerie & Martin, 1992), a pattern that might be attributable to increasing vulnerability to parasites as males get larger (Moore & Wilson, 2002). Higher male mortality associated with SSD indicates that larger size imposes a viability cost on males collectively. It does not follow, however, that viability costs disproportionately affect the largest males (Weatherhead & Clark, 1994). For example, selection on males to migrate early to secure breeding territories could expose males to harsh spring weather. This would cause high male mortality overall, while actually favouring the largest individual males because the energetic advantage conferred by their large size would make them the most likely to survive harsh weather (Weatherhead & Clark, 1994; Kissner, Weatherhead & Francis, 2003). Thus, demonstrating that viability costs for males limit SSD requires evidence that the survival disadvantage is greatest for the largest individuals.

Studies of episodic mortality in birds indicate that body size can affect survival (e.g. Bumpus, 1899; Price, 1984; Brown & Brown, 1998). However, episodic mortality will not necessarily reflect how selection acts on body size across all factors (e.g. predation, disease, starvation) affecting mortality (Weatherhead, Greenwood & Clark, 1984). Thus, longer-term data provide better tests of the viability hypothesis. Long-term survival data for red-winged blackbirds (*Agelaius phoeniceus*), a species with pronounced SSD, revealed stabilizing selection on female body size as predicted by theory, but contrary to theory, larger males survived better than smaller males (Weatherhead, Green-

wood & Clark, 1987; Weatherhead & Clark, 1994). Thus, selective mortality in adult birds promoted rather than reduced SSD. Experimental evidence from other taxa suggests that intense sexual selection may favour increased viability in males (Promislow, Smith & Pearse, 1998; Lindström, 2001), so the pattern in adult male red-winged blackbirds may be not be atypical. Overall, therefore, the limited data that are available provide little support for the hypothesis that viability selection on adult male birds limits SSD.

If viability selection acting on adults does not limit SSD, and perhaps even promotes it, then the cost of large size in sexually dimorphic species may be realized during growth (Clutton-Brock, Albon & Guinness, 1985; Weatherhead & Teather, 1991). In open-nesting passerine birds, males and females hatch from eggs of approximately equal size (e.g. Weatherhead, 1985), grow rapidly and reach a substantial proportion of their adult size in periods of less than 2 weeks that they are in the nest (Faaborg, 1988). Experimental evidence suggests that sex differences in nutritional requirements during the nestling period are likely to be responsible for sex differences in performance (Sheldon *et al.*, 1998). In dimorphic species, SSD is apparent soon after hatching, resulting in significantly higher energetic costs of rearing sons vs. daughters (Fiala & Congdon, 1983; Teather & Weatherhead, 1988). Thus, if there are costs to getting big, they should be apparent by the time nestlings leave the nest.

At the population level, female-biased fledging sex ratios in sexually dimorphic birds (e.g. Howe, 1976; Cronmiller & Thompson, 1981; Røskaft & Slagsvold, 1985; Teather & Weatherhead, 1989) are consistent with large size being costly to male nestlings. Other studies have failed to find the predicted bias in fledging sex ratios (Richter, 1983), however, so the pattern is by no means universal. Because biased fledging sex ratios are associated with periods of food shortage (e.g. Howe, 1976; Teather & Weatherhead, 1989), which may be infrequent, long-term data from the same population may provide the most reliable estimate of fledging sex ratio biases (also see Kruuk, Merilä & Sheldon, 2001; Griffith *et al.*, 2003). Our first objective was to assess annual fledging sex ratios in the same population of red-winged blackbirds over a 10-year period. The prediction that the cost of SSD will produce female-biased fledging sex ratios assumes that the sex ratio at hatching is even. In support of this assumption, Weatherhead (1983, 1985) sexed 898 eggs at hatching over 3 years in the same study population of red-winged blackbirds we use here and found a sex ratio of 48% males.

Even if male nestlings are more likely to die than female nestlings, that mortality need not be selective with regard to male size. The critical test of the hypothesis that survival costs imposed on nestlings

limit male size requires demonstrating that male nestlings that would have become the largest adults are more likely to die. The obvious difficulty in testing this hypothesis, and presumably the reason the test has not been conducted to date, is that one must know how large nestlings that die would have become had they not died. The size or growth rate of nestlings prior to death are not informative, because both are likely to be affected by the fact that the nestling is starving. This is a general problem when testing hypotheses about viability costs in juveniles associated with their body size as adults (Reznick, 1985; Blanckenhorn, Reusch & Mühlhäuser, 1998).

The solution to this problem that we pursue here was proposed by Weatherhead & Clark (1994). Because body size is moderately to highly heritable in birds (typically $h^2 = 0.4\text{--}0.6$; Merilä & Sheldon, 2001), one can predict the size that nestlings will become as adults from the size of their parents. Furthermore, parental effects can be expressed before nestlings fledge (Sheldon *et al.*, 1997). Thus, if male nestlings that would have become the largest adults suffer higher mortality in the nest, two predictions follow. First, partial brood loss should increase with parental size. Disappearance from the nest of only some nestlings (partial brood loss) is indicative of those nestlings having starved, whereas the loss of all nestlings is associated with predation. Second, offspring sex ratios should become increasingly female biased as parental size increases. The central objective of this study was to test these two predictions.

RED-WINGED BLACKBIRDS

Red-winged blackbirds are sexually dimorphic, socially polygynous North American passerine birds. Males are approximately 20% larger structurally and more than 50% heavier than females. After hatching from eggs of the same size (Weatherhead, 1985), male and female nestlings immediately begin to diverge in size (Searcy, 1979; Fiala, 1981; Weatherhead & Clark, 1994). By the time of fledging, mean male weight exceeds that of females by approximately 40% and the cumulative energy invested in a male nestling exceeds that of a female nestling by 27% (Fiala & Congdon, 1983).

In the population used in this study, sexual selection favours larger males, primarily through their success at attracting social mates (Weatherhead & Boag, 1995). Natural selection on adults also favours larger males, while favouring intermediate-sized females (Weatherhead & Clark, 1994).

METHODS

We conducted this study from 1985 to 1993 and in 1995 at the Queen's University Biological Station in

eastern Ontario (45°37'N, 76°13'W) in beaver pond and lakeshore marshes. Nest searches were conducted from May to the end of July, encompassing the entire nesting season. We checked nests daily or every second day until they either failed or the young fledged. Nestlings were individually marked on the first nest visit after they hatched. On each visit we weighed each nestling and measured its tarsus length. More detailed information on the study area and general field methods are available from Weatherhead (1995).

We assigned nestling sex based on the bimodal distribution of body size as nestlings approach fledging (Weatherhead & Dufour, 2000). Sex was initially assigned based on the most conservative guidelines collectively provided by Holcomb & Twiest (1970), Fiala (1981) and Westneat, Clark & Rambo (1995) as follows:

Age 7, < 26 g = female, > 33 g = male,
 Age 8, < 31 g = female, > 33 g = male,
 Age 9 or older, < 33 g = female, > 35 g = male.

When the sex of a given nestling fell between the size thresholds, we visually inspected plots of the mass vs. age relationship for all individuals in the brood. Often, the sex of the nestling in question was obvious when its pattern of weight gain was compared with that of its known-sex nest-mates. If not, the nestling was classified as 'sex unknown'. Using this approach we were able to sex approximately 90% of all nestlings that fledged. Although natal philopatry is < 3% in our study population (Weatherhead & Dufour, 2000), 48 birds sexed as nestlings were later seen as adults and all had been sexed correctly.

We designated a nestling as having fledged using several criteria in addition to observing the nestlings leaving the nest or being outside the nest. If nestlings were gone on or after the date they would have been at least 9 days old (the earliest age at which fledging was observed), and the nest was undisturbed, we assumed they had fledged. When nestlings hatched asynchronously, we assumed all nestlings had fledged if they had all disappeared synchronously, the nest was undisturbed and the oldest nestlings were at least 9 days old. Because we applied these criteria uniformly, any bias in our assumptions should not influence our conclusions with respect to the hypothesis being tested.

Testing the prediction that large parents should fledge fewer sons requires knowing the true parentage of nestlings, because the prediction is based on body size being heritable. Approximately 25% of all nestlings in our study population are sired by extra-pair males, so paternity analyses were required. From 1986 to 1991 and in 1993 we collected blood samples from all nestlings when they were 6 days old, although we only conducted paternity analyses using samples

from three of our study marshes. Details of the methods used are available from previous publications (Gibbs *et al.*, 1990; Weatherhead & Boag, 1997; Dufour & Weatherhead, 1998).

We determined parental size using the first component (PC1) from a correlation-based principal components analysis of wing chord (± 1 mm), tarsus length (± 0.1 mm) and bill length (± 0.1 mm), conducted separately for males and females. Mid-parent size was taken as the average size (PC1 score) of the two parents. We also repeated all analyses using wing chord alone as our index of adult size, but because the results were qualitatively unchanged, we only report results obtained using PCA.

RESULTS

PARTIAL BROOD LOSS

The predictions we test here all require that some nestlings that hatch do not survive to fledging in nests that fledge at least some offspring (i.e. partial brood loss). Furthermore, the cause of partial brood loss is assumed to be starvation, because it is the greater energetic cost of raising sons that is predicted to underlie the disproportionate mortality of male nestlings (Searcy & Yasukawa, 1995). Note that we could not assign sex to nestlings that disappeared because many disappeared well before the size of male and female nestlings diverged enough to make sexing by size reliable (Weatherhead & Teather, 1991). Over the 10 years of the study we collected data from 465 nests that fledged at least one offspring. Excluding 11 nests in which only one egg hatched, and thus in which partial brood loss was not possible, 132 nests (29.1%) suffered partial brood loss.

Consistent with larger broods being more costly to rear, the probability of partial brood loss increased with brood size (logistic regression: $G = 18.70$, d.f. = 1, $P < 0.001$). To determine whether per capita risk of mortality increased with brood size, we used the binomial expansion to predict expected rates of partial brood loss for each brood size, based on an overall nestling mortality rate of 0.11 (175 of 1553 nestlings in the 454 nests). Observed mortality rates were not different from expected ($G = 7.12$, d.f. = 4, $P = 0.13$). Thus, per capita risk of starvation did not increase with brood size. This could mean that factors other than starvation accounted for at least some partial brood loss. Alternatively, if variation in brood size reflects the ability of individual females to feed nestlings, starvation risk would not be expected to increase with brood size. Regardless, with nearly one-third of all successful nests experiencing partial brood loss, the potential for sex- and size- selective mortality was substantial.

OVERALL FLEDGLING SEX RATIOS

Over the 10 years of the study we sexed 1356 fledglings. The proportion of fledglings that was male varied from 0.45 to 0.58 across years, but did not differ significantly from 0.50 in any year (Table 1). Over all years the proportion of nestlings that was male was 0.49, whether annual means were weighted by sample size or not. The overall sex ratio was also not significantly different from 0.50 (Table 1). A heterogeneity G -test (Sokal & Rohlf, 1981) revealed no evidence of significant heterogeneity among years ($G_H = 11.8$, d.f. = 9, $P > 0.10$) and confirmed that the pooled sex ratio estimate did not differ from random expectation ($G_P = 0.9$, d.f. = 1, $P > 0.25$). These data do not support the hypothesis that the collective survival of male nestlings was less than that of female nestlings.

Another approach to determining whether fledgling sex ratios were biased by sex is to assess whether the distribution of males and females among broods conformed to random binomial expectation (Sokal & Rohlf, 1981). Specifically, if male nestlings are more likely to starve than female nestlings, then broods with all males (or a preponderance of males) should be less common than expected by chance. Contrary to this prediction, brood sex ratios did not differ significantly from those expected by chance (brood size 2: $G = 0.72$, d.f. = 1, $P = 0.39$; brood size 3: $G = 1.16$, d.f. = 2, $P = 0.56$; brood size 4: $G = 2.36$, d.f. = 3, $P = 0.50$).

SEX RATIOS AND PARENTAL SIZE

Low return rates of birds banded as nestlings precluded a strong test of the assumption that body size is heritable in our study population. However, we did

Table 1. Annual variation in sex composition (proportion male) of red-winged blackbird broods at fledging

Year	No. of broods	Proportion male*	SE	t^\dagger	P
1985	30	0.48	0.07	-0.27	0.79
1986	41	0.48	0.05	-0.42	0.68
1987	51	0.45	0.05	-0.99	0.32
1988	72	0.54	0.04	1.16	0.25
1989	64	0.50	0.03	0.14	0.88
1990	93	0.45	0.03	-1.47	0.14
1991	22	0.48	0.06	-0.32	0.75
1992	30	0.51	0.05	0.22	0.83
1993	43	0.46	0.05	-0.78	0.44
1995	19	0.58	0.06	1.17	0.26
Pooled	465	0.49	0.01	-0.74	0.46

*Mean within-brood sex composition.

†Two-tailed t -test of $H_0: \mu = 0.5$.

obtain measurements from seven males when they were 2 years old (and thus full-grown), for which we also had measurements from both their parents, where paternity had been determined genetically. Linear regression of offspring size on mid-parent size produced a significant positive relationship ($F = 6.91$, $d.f. = 1.5$, $P = 0.047$) with a slope (heritability estimate; Falconer, 1989) of 0.73 (SE = 0.28). For this analysis we used wing chord as our index of size because PCA values were not available for all individuals.

For the 7 years for which parentage was determined genetically we had sex ratio data from 203 nests that fledged at least one offspring. Treating nests as individual observations, we used logistic analysis to test the prediction that the probability of partial brood loss should increase with increasing mid-parent size. To control for potential confounding effects of extra-pair paternity, we restricted our analysis to those nests in which all young were sired by the social mate ($N = 152$). In the full model that included effects of year, mid-parent size and a year \times mid-parent size interaction, the interaction term was not significant ($G = 7.66$, $d.f. = 6$, $P = 0.26$). A reduced model with only main effects was not significant (model $G = 10.84$, $d.f. = 7$, $P = 0.15$) and neither year nor mid-parent size had a significant effect (year: $G = 10.58$, $d.f. = 6$, $P = 0.10$; mid-parent size: $G = 0.00005$, $d.f. = 1$, $P = 0.99$). Thus, the occurrence of partial brood loss was unrelated to parental size (Fig. 1).

To test the prediction that bigger parents should fledge fewer sons we again restricted our analysis to those nests in which all young were sired by the social mate. Because our analysis involved proportional data (i.e. brood sex ratios at fledging), we used logistic regression-based generalized linear modelling (GLMs; Wilson & Hardy, 2002), specifying brood sex ratio (proportion male) as the binomial response variable and treating year and mid-parent size as categorical and continuous predictors, respectively (PROC LOGISTIC, SAS Institute, 2000). Our initial model indicated that the interaction between year and mid-parent size was not significant ($G = 3.10$, $d.f. = 6$, $P = 0.80$). A reduced (main effects only) model was also not significant (model $G = 7.18$, $d.f. = 7$, $P = 0.41$) and neither year nor mid-parent size had a significant effect on fledgling sex ratio (year: $G = 7.00$, $d.f. = 6$, $P = 0.32$; mid-parent size: $G = 1.16$, $d.f. = 1$, $P = 0.28$; Fig. 2). These results provide no support for the prediction that large parents fledge fewer sons.

UNSEXED FLEDGLINGS

Our analyses could potentially be confounded if the sex of the fledglings we were unable to sex varied non-randomly with regard to the hypotheses being tested.

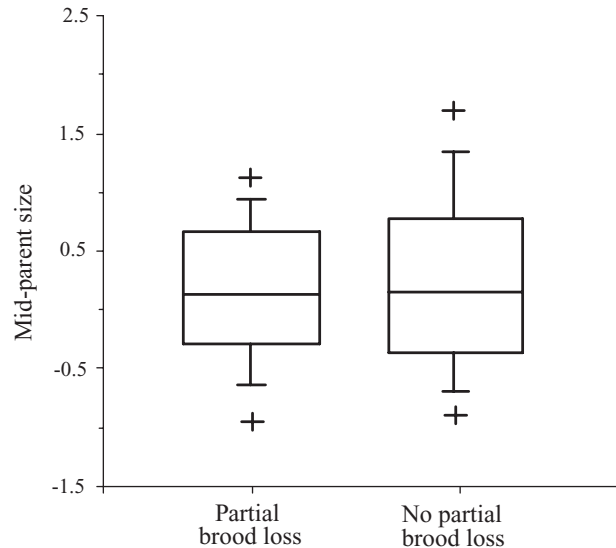


Figure 1. Comparison of red-winged blackbird broods that suffered partial brood loss ($N = 37$) and those that did not ($N = 90$) with respect to parental size. Mid-parent size is computed as the mean size of the two parents, based on scores from principal components analyses involving wing chord, tarsus length and bill length (see text for details). From top to bottom, horizontal lines indicate 90th, 75th, 50th, 25th and 10th percentiles. Upper and lower symbols indicate 95th and 5th percentiles, respectively.

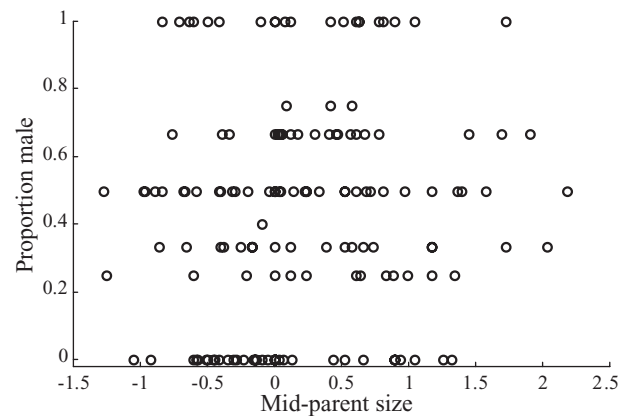


Figure 2. Fledgling sex ratio of red-winged blackbird broods ($N = 120$), relative to parental size. Sex ratio is the proportion of sexed fledglings that were male. Mid-parent size is computed as the mean size of the two parents, based on scores from principal components analyses involving wing chord, tarsus length and bill length (see text for details).

To assess this possibility we determined whether the number of unsexed fledglings varied with any of our dependent variables. Annual fledgling sex ratios did not vary with annual variation in percentage of fledg-

lings sexed ($r = 0.14$, $N = 10$, $P = 0.70$), nor was the percentage of fledglings sexed correlated with annual variation in partial brood loss ($r = 0.49$, $N = 10$, $P = 0.15$). Although the latter analysis suggested a relationship with partial brood loss, removal of the year with the lowest sexing success eliminated the pattern ($r = 0.22$, $N = 9$, $P = 0.57$). Broods containing fledglings of unknown sex were no more likely than completely sexed broods to suffer partial brood loss (7 of 30 vs. 125 of 435, respectively; $G = 0.42$, d.f. = 1, $P = 0.52$). Mid-parent size based on PC1 score did not differ between broods containing fledglings of unknown sex (mean = 0.48 ± 0.22 SE, $N = 13$) and those in which all fledglings were sexed (mean = 0.19 ± 0.06 SE, $N = 126$; $t = 1.37$, d.f. = 137, $P = 0.17$). Finally, sex ratios (mean proportion male) did not differ between broods with and without unsexed fledglings (0.39 vs. 0.51; $t = 0.95$, d.f. = 127, $P = 0.34$).

To test directly whether it is even possible that the failure of our central prediction (i.e. bigger parents should produce fewer sons) could be related to the unsexed nestlings, we arbitrarily assigned those nestlings the sex that would support that prediction and repeated the analysis (i.e. the 'best' case scenario for bias). Unsexed nestlings of parents above and below the median mid-parent size were assigned as males and females, respectively. This only required assigning sexes to seven nestlings from six broods. Our initial GLM indicated that the interaction between year and mid-parent size was not significant ($G = 2.65$, d.f. = 6, $P = 0.85$). A reduced (main effects only) model was not significant (model $G = 5.66$, d.f. = 7, $P = 0.58$) and neither year nor mid-parent size had a significant effect on fledgling sex ratio (year: $G = 5.65$, d.f. = 6, $P = 0.46$; mid-parent size: $G = 0.43$, d.f. = 1, $P = 0.51$). Thus, even with the unsexed nestlings assigned sexes most favourable to the prediction, there was still no evidence that large parents fledged fewer sons.

DISCUSSION

We had predicted that higher rearing costs should cause male nestlings to starve more often than female nestlings, resulting in female-biased fledgling sex ratios. Although partial brood loss occurred in almost one-third of all successful nests, we found no evidence that fledgling sex ratios deviated from 50 : 50. Over 10 years, 49% of fledglings were male, which is almost identical to the proportion of males at hatching (48%; Weatherhead, 1983, 1985). Most importantly, we found no evidence that mortality selected against male nestlings that would have become large adults. Neither the incidence of partial brood loss nor fledgling sex ratios varied with parental size.

Our failure to find an overall female bias in fledging sex ratios seems at odds with previously published data for red-winged blackbirds. A summary of those data by Weatherhead & Teather (1991) indicated an overall percentage of 47.2% male nestlings. In addition to variation among studies in methods used for sexing, however, some of the data used in that summary were for nestlings as young as 2 days old (Fiala, 1981). Our interest here is in sex ratios at fledging and our results are not consistent with the prediction that more male nestlings starve than female nestlings.

There are several possible proximate explanations for males surviving as well as females, and for males destined to be larger as adults surviving as well as males that would be smaller adults. Females may modify the costs of rearing sons by adjusting incubation onset and laying sequence of males and females (Badyaev *et al.*, 2003), or by adjusting the sex and size of their clutches to match their provisioning ability. However, if bigger females and females mated to bigger males adjust offspring sex to compensate for the cost of producing large sons, then the fledging sex ratio should have become increasingly female-biased as parental size increased (and nestling starvation presumably less common). The fact that we did not find that pattern suggests that this explanation cannot account for our results.

Another possible proximate explanation is that heritable variation in size might not be expressed until after fledging. It is also possible that male nestlings compensated for their rearing costs by superior competitive ability (e.g. Teather, 1992). Each of these possibilities postulates either a mechanism to compensate for the rearing costs of bigger male offspring or that those costs do not arise until after fledging. Thus, although these possibilities could explain our results, none alters the conclusion from our results that size-selective mortality among nestlings does not limit adult male size.

By providing empirical evidence that starvation does not select against males that would become the largest adults, we have eliminated the nestling period as the stage during which natural selection counteracts sexual selection, at least for red-winged blackbirds. Because this test has not been conducted for any other species, the generality of our result is unknown. In eliminating the nestling period as the point at which selection operates, we are left with the problem with which we started: what limits male size in red-winged blackbirds? We consider three possible answers.

There remains one life-history stage in which sexual selection for larger males might be balanced by their higher mortality. We have eliminated the period between hatching and fledging in this study, and Weatherhead & Clark (1994) ruled out adulthood.

This leaves the period between fledging and adulthood. Studies of other species suggest that selection on body size during this period might be pronounced (Owens & Bennett, 1994; Merilä, Sheldon & Ellegren, 1997; Badyaev *et al.*, 2001). Most juvenile male red-winged blackbirds do not hold territories or reproduce until they are 2 years old (Selander & Giller, 1960; Payne, 1969; Meanley & Bond, 1970). During this period males continue to grow (Weatherhead & Clark, 1994) and differ from older males in timing of migration (Greenwood & Weatherhead, 1982), competitive ability (Weatherhead & Hoysak, 1984) and foraging ability (Weatherhead & Greenwood, 1981), so body size might affect viability differently in juveniles and adults. Based on relatively small samples, Weatherhead & Clark (1994) found that smaller 1-year-old male red-winged blackbirds were more likely to return the following year than larger males, although the trend was not significant, and mortality could not be distinguished from dispersal.

A second possibility is that male size is limited by selection acting on females. Genetic correlation between males and females restricts the rate at which male size can diverge from female size in the face of sexual selection (Lande, 1980; Reeve & Fairbairn, 1996; Merilä, Sheldon & Ellegren, 1998) and may also explain the expression of traits in one sex that are selected for in the other sex (Muma & Weatherhead, 1989). Thus, selection acting on female body size could affect male body size. The consequences of size variation in female red-winged blackbirds are unclear. Social competition appears to favour larger females in some circumstances (Langston *et al.*, 1990) but not in others (Roberts & Searcy, 1988; Muma & Weatherhead, 1991). In the only direct analysis, Weatherhead & Clark (1994) found that adult female size was under stabilizing selection for survival. Whether that selection pressure on females is sufficient to limit male size is unknown.

A third possibility is that reproductive and viability advantages are currently increasing the size of male red-winged blackbirds. Red-winged blackbirds are agricultural pests (e.g. Weatherhead, Tinker & Greenwood, 1982) whose numbers are closely tied to agricultural production (Blackwell & Dolbeer, 2001). Increased food availability from agricultural production may have allowed males to survive at a larger size. Clark (1985) analysed museum specimens of red-winged blackbirds collected in Quebec, Canada, before and after major increases in corn production in the 1960s, and found some evidence that males had increased in size, although sample sizes were small and results not significant. It is also possible that male size is not currently changing, despite viability and sexual selection favouring large size. A number of studies of wild animals have demonstrated positive

selection on body size with no corresponding response (Kruuk *et al.*, 2001). Among the explanations proposed to explain this phenomenon, environmental change that conceals the underlying evolution has received recent support (Merilä, Kruuk & Sheldon, 2001).

Of the possibilities we have proposed to explain the lack of evidence for limits to male size, some are specific to red-winged blackbirds and others more general. All of these can and should be explored. As Blanckenhorn (2000) indicated, however, to identify the factors that limit SSD arising from sexual selection, we first need evidence that selection is limiting SSD.

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