

Jennifer L. Grindstaff · C. Alex Buerkle
Joseph M. Casto · Val Nolan Jr · Ellen D. Ketterson

Offspring sex ratio is unrelated to male attractiveness in dark-eyed juncos (*Junco hyemalis*)

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Abstract Sex allocation theory predicts that parents should bias investment toward the offspring sex that confers higher relative fitness on the parents. When variance in reproductive success is higher in males than females, and some males are more attractive to females than others, thereby achieving higher reproductive success, female parents mated to attractive males are expected to bias reproductive allocation toward sons. Modification of the primary sex ratio is one mechanism by which avian parents may bias allocation. In mate choice trials, captive female dark-eyed juncos (*Junco hyemalis*) prefer to associate with males whose circulating testosterone level has been elevated experimentally. We asked whether females socially mated to testosterone-treated males in nature might bias the sex ratio of progeny in favor of sons. We determined the primary sex ratio of broods using a sex-linked molecular marker, the CHD gene on the W chromosome. We found no relationship between the hormonal treatment of males and the primary or secondary sex ratios of offspring produced by their social mates. Sex ratio was also unrelated to breeding-season date, study year, male viability, or female age. While unlikely, it is possible that female juncos are not able to manipulate the primary sex ratio of their broods. More likely, possible benefits to female juncos of producing attractive sons may be small because (1) attractive males do not necessarily have higher fitness, depending on the trade-offs involved for males, and (2) when such benefits exist, they may be outweighed for

females by the costs of compensating for the reduced paternal care of attractive males.

Keywords Sexual selection · Testosterone · Bird · Mate choice · Differential allocation

Introduction

Recent evidence from diverse vertebrate taxa reveals that females of some species are able to bias the sex ratio of the young they produce. Among a variety of reported mechanisms that affect offspring sex ratio are nest-site temperature in reptiles (Bull 1980; Korpelainen 1990; Crews et al. 1988) and differential implantation in mammals (Krackow 1995b). Deviation from equality in the primary sex ratio occurs in some species of birds and may be a consequence of non-random ovulation of Z and W ova within the ovulation sequence (Krackow 1993). Because not all ova mature into eggs (Wood-Gush and Gilbert 1979), any predilection of Z or W ova toward developmental failure could be the basis for facultative bias in the sex ratio at ovulation or hatching (Krackow 1995a).

Deviation from an equal sex ratio is predicted when parents can enhance their fitness by preferentially producing, or allocating resources to, one sex (Fisher 1958; Charnov 1982). Adults capable of producing attractive sons should experience selective pressure to bias their reproductive resources toward male offspring when the variance in reproductive success is greater in males than in females, more attractive males achieve greater reproductive success than less attractive males, and there is a genetic basis to attractiveness (Burley 1986). Sex ratio bias in avian broods on the basis of parental attractiveness was first detected as modification of the secondary sex ratio by female zebra finches (*Taeniopygia guttata*) mated to males with color-bands that experimentally enhanced attractiveness (Burley 1982, 1986). Recent applications of molecular techniques have revealed that females mated in nature to attractive males sometimes bias

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J.L. Grindstaff (✉) · C.A. Buerkle · J.M. Casto · V. Nolan Jr
E.D. Ketterson
Department of Biology and Center for the Integrative Study
of Animal Behavior, Indiana University, Bloomington, IN 47405,
USA
e-mail: jgrindst@indiana.edu
Tel.: +1-812-8551096, Fax: +1-812-8556705

Present address:

C.A. Buerkle, Department of Biology,
University of Wisconsin-Eau Claire, Eau Claire, WI 54702-4004,
USA

allocation at the level of the primary sex ratio (Ellegren et al. 1996; Sheldon et al. 1999). For example, when the size of the sexually selected forehead patch of male collared flycatchers (*Ficedula albicollis*) was reduced through experimental elevation of parental investment in the previous breeding season, females mated to males with smaller patches produced relatively more daughters than did controls (Ellegren et al. 1996). Conversely, when the size of the mate's forehead patch was increased, females produced relatively more sons (Ellegren et al. 1996). Similarly, in blue tits (*Parus caeruleus*), in which ultraviolet reflectance of the crown is a potential viability indicator, experimental masking of male ultraviolet reflectance reversed the positive correlation between reflectance and sex ratio that had been observed in control pairs (Sheldon et al. 1999). However, not all studies have documented a relationship between primary sex ratio and parental attractiveness. Experimental manipulation of the sexually selected tail length of male barn swallows (*Hirundo rustica*) did not influence the primary sex ratio (Saino et al. 1999). Further, the sex ratio of extra-pair offspring was not correlated with tail length of the genetic sire (Saino et al. 1999). One primary determinant of whether sex ratio bias may be predicted in a population is the mechanism of sexual selection that is currently operating. A recent model suggests that sex ratio bias may not be predicted under Fisherian runaway selection, and only occasionally under 'good-genes' processes (Pen and Weissing 2000).

Across various avian species, experimental elevation of testosterone increases male attractiveness to females (Wingfield 1984; Beletsky et al. 1995; Alatalo et al. 1996). Previous research on dark-eyed juncos (*Junco hyemalis*) has demonstrated that testosterone-implanted males (T-males) are more attractive to females than are controls given empty implants (C-males) (Enstrom et al. 1997; Hill et al. 1999; D.A. Enstrom, M. Soenksen, C. Ziegenfus, V. Nolan Jr., E.D. Ketterson, unpublished data). Not only do female juncos in aviary mate choice trials prefer to associate with T-males, they also are more likely to solicit copulations from them (Enstrom et al. 1997). Further, when T- and C-implanted males are released on their territories and permitted to breed freely for entire seasons, T-males are more successful at siring young by extra-pair fertilizations (EPFs) (Raouf et al. 1997), which may reflect female choice in the field.

To assess the consequences of male treatment with testosterone for the females that socially mate with them, and to determine whether females alter the sex ratio of their brood in relation to attractiveness, we asked whether broods of more attractive males, i.e., of male juncos treated with testosterone, would have a primary sex ratio in which males were more frequent than in broods of males that received empty implants. We also assessed the consequences of male treatment with testosterone on secondary sex ratios, and the effects of male viability, female age, study year, and laying date on primary and secondary sex ratios.

Methods

Study site and species

The study population of dark-eyed juncos was located at the University of Virginia's Mountain Lake Biological Station in western Virginia (37°22' N, 80°31' W) at 1,180 m elevation. The breeding biology of this population has been the focus of study by E.D.K, V.N Jr. and colleagues since 1983. The data reported here were collected over 4 years (1995–1998).

Testosterone treatment

Adult males were captured each year between 15 April and 15 May, before or shortly after pair formation, and implanted with either empty implants or implants filled with crystalline testosterone (see Wingfield and Farner 1983; Ketterson et al. 1992). Unbanded males, both yearlings and older individuals, were assigned randomly to treatment groups. Previously banded and treated males were assigned the same treatment as the year before. T-males and C-males were equally represented in both yearling and older age classes and were randomized across the study site. Earlier studies have demonstrated that the natural level of testosterone peaks at the beginning of the breeding season and then falls, and that testosterone implants prolong the peak testosterone level throughout the breeding season (Ketterson et al. 1992; Chandler et al. 1994). T-males were included in our analyses only if they were implanted with testosterone at least 5 days prior to egg laying by their social mate, and we knew that the implants remained in place throughout the breeding season.

Field methods

We collected blood samples from 185 young in 48 broods: 28 broods produced by the social mates of C-males and 20 broods produced by the social mates of T-males. Blood samples were collected (10–50 µl by brachial venipuncture) on or prior to day 6 (halfway through the nestling period) from broods in nests that were found before egg laying, and in which no eggs or young were lost prior to blood collection.

Offspring were weighed 6 days after hatching (day 0=hatching day) and again at fledging (day 12). In statistical analyses of offspring sex and body mass, data points represent nest means for each sex. Some broods were naturally reduced between day 6 and fledging and we noted the sex of young that disappeared. Intensive mist-netting at the end of the breeding season permitted us to compare the likelihood of recapturing male and female juvenile offspring from broods of T- and C-males. Sex ratios measured at fledging and at the end of the breeding season estimate the sex ratio of surviving members of the brood.

Adult females were classified into one of two age classes (yearling or older) on the basis of body size (E.D. Ketterson and V. Nolan Jr., unpublished data), eye color, and plumage traits (Yunick 1981; Mulvihill and Chandler 1990; E.D. Ketterson and V. Nolan Jr., unpublished data), or exact ages based on previous banding records.

Sex determination

Adults were sexed using a combination of morphological traits (e.g., body size, plumage coloration, presence/absence of brood patch or cloacal protuberance); these methods result in 100% accuracy. Blood samples from eight adult males and nine adult females were used to determine whether a sex-specific molecular marker could be amplified by the polymerase chain reaction (PCR) in dark-eyed juncos. PCR primers (CHD-1237L and CHD-1272H) for the chromohelicase-DNA-binding protein (CHD; Kahn et al. 1998) amplified two products [approximately 275 and 235 base pairs (bp) in length] in female juncos, within the ex-

pected range of molecular weights, and a single product in males (235 bp). In all cases, molecular sexing generated the same results as morphological sexing techniques. These products were separated on 1.5 or 2% agarose gels. The banding pattern for males and females is consistent with two copies of CHD, one on the female-specific W chromosome, and one on the Z chromosome (or an autosome), and a difference between loci in the length of the PCR product (Kahn et al. 1998). Hence nestlings with two bands were scored as female; those with the single, shorter marker were scored as male.

Statistical analysis

Sex ratios were expressed as the proportion of male offspring. Four adult males had more than one nest included in the analyses. Because there was no consistency in their brood sex ratio (e.g., each had broods of sex ratio <0.5 and >0.5) and one male was assigned a different treatment for his two broods, we treated each brood as an independent event.

Because sex ratios are expected to be binomially distributed, they are most appropriately analyzed using generalized linear models fitted with binomial errors and logit links using a statistical package such as GLIM [Crawley 1993; Hartley et al. 1999; see Krackow and Tkadlec (in press) for a recent refinement of statistical methods]. To determine whether sex ratio varied significantly among broods and departed from the binomial distribution, we examined the deviance of the null model, which assumes a binomial distribution. If a variable such as sex ratio is distributed binomially, the model's deviance is distributed asymptotically as χ^2 . When brood sizes are small, however, deviances from the null model may overestimate departure from the binomial distribution (Hartley et al. 1999; C.M. Lessells, personal communication). The robustness of any significant departures was, therefore, further tested by performing randomization tests, which compare the observed deviance of the null model with deviances obtained from a series of randomly generated data sets (C.M. Lessells, personal communication). Nestlings were randomized between broods while maintaining the original distribution of brood sizes and total number of male and female nestlings. The randomization process was repeated 1,000 times, and the significance of departure from the binomial distribution taken as the proportion of the deviances in the randomized data that exceeded the observed deviances.

We next calculated deviances of models that did or did not include male treatment, female age, male viability (whether or not the male associated with the brood returned in a subsequent year), study year, and laying date (Julian date on which the first egg of each brood was laid). The statistical significance of explanatory independent variables was assessed by calculating the deviance between models that did and did not include such variables. To calculate degrees of freedom (df), we determined the difference in df between models with and without specific independent variables. The change in deviance from the null model was computed for each explanatory variable independently and with all explanatory variables added stepwise, regardless of whether or not they were significant, with male hormone treatment always added last. Small brood sizes do not inflate the change in deviance from the null model when explanatory variables are added to the model; therefore, randomization tests are not necessary to verify the robustness of significant departures (C.M. Lessells, personal communication).

Results

Primary sex ratios

Without regard to whether broods were testosterone or control, we found no evidence that the primary sex ratio was other than binomially distributed (mean brood

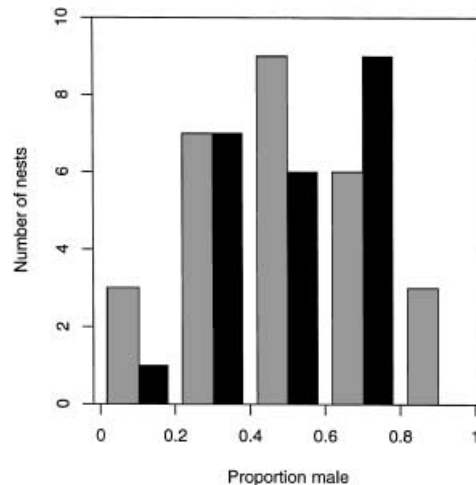


Fig. 1 Proportion of males in dark-eyed junco broods of control (left) and testosterone-treated (right) males

sex ratio = $49.4 \pm 3.6\%$ male offspring, $\chi^2 = 57.6$, $df = 45$, $0.05 < P < 0.1$). When male hormonal treatment was added to the model, we found no effect of treatment on sex ratio (change in deviance = 0.035, $df = 1$, $0.5 < P < 0.9$). Of the offspring in 20 T-broods, $49.6 \pm 5.0\%$ (mean \pm SE) were male, and of offspring in 28 C-broods, $49.4 \pm 5.0\%$ SE were male (Fig. 1).

Again without regard to treatment, brood sex ratio did not change with laying date (change in deviance = 0.34, $df = 1$, $0.5 < P < 0.9$) or study year [proportion (\pm SE) of male offspring by year: 1995, $51.6 \pm 7.5\%$, $n = 12$; 1996, $36.0 \pm 10.3\%$, $n = 6$; 1997, $51.7 \pm 5.0\%$, $n = 15$; 1998, $50.4 \pm 7.1\%$, $n = 18$; change in deviance = 2.48, $df = 3$, $0.1 < P < 0.5$]. Other variables that did not affect brood sex ratio were female age (change in deviance = 0.45, $df = 1$, $0.5 < P < 0.9$) and male viability (change in deviance = 0.42, $df = 1$, $0.5 < P < 0.9$). For older females, the mean brood sex ratio was $48.9 \pm 6.0\%$ male ($n = 24$); for yearling females, it was $49.8 \pm 4.4\%$ male ($n = 26$). For returning males, mean brood sex ratio was $51.9 \pm 5.2\%$ male ($n = 27$); for non-returning males, it was $46.5 \pm 4.9\%$ male ($n = 24$). The model incorporating effects of male hormone treatment, female age, study year, laying date, and male viability (with each variable added stepwise and male hormone treatment added last) also did not reveal any collective influence of these variables on the primary sex ratio (change in deviance = 0.005, $df = 1$, $0.9 < P < 0.975$).

Secondary sex ratios

After we collected blood samples to determine sex ratios, seven broods were reduced in size, most likely as a result of starvation or predation. In five of these, all remaining young were male (three broods with two remaining offspring and one brood each of three or four remaining offspring). In the other two broods, all remaining young were female (one with two offspring, the other with three). Another 21 broods were lost in their

entirety to predators. Based on a comparison of the null deviance with χ^2 , the sex ratio of surviving offspring at fledging and at the juvenile stage appeared to deviate significantly from a binomial distribution (fledging: mean brood sex ratio=54.3±6.3% male, $\chi^2=40.6$, $df=26$, $0.025 < P < 0.05$; juvenile stage: mean brood sex ratio=47.8±10.9%, $\chi^2=30.0$, $df=18$, $0.025 < P < 0.05$). However, after analysis with the more conservative randomization tests, the deviance of the randomized data was no longer significant (fledging: $P=0.18$; juvenile: $P=0.09$), indicating that brood sex ratio sampled at fledging and at the juvenile stage fit a binomial distribution. As with primary sex ratio, male treatment, female age, male viability, study year, and laying date had no influence on the sex ratio at fledging (43.1±8.6% of offspring in 12 T-broods were male, 63.3±8.6% of offspring in 15 C-broods were male; change in deviance when treatment was added to the model=3.0, $df=1$, $0.05 < P < 0.1$) or at the juvenile stage (39.8±15.6% of offspring in 9 T-broods were male, 55.0±15.7% of offspring in 10 C-broods were male; change in deviance=0.401, $df=1$, $0.5 < P < 0.9$).

Offspring sex and body mass

Mid-way through the nestling interval (6 days post-hatch) the mean mass of female and male nest-mates did not differ ($t=1.47$, $df=56$, $P=0.15$; mean mass of females=13.2±0.27, mean mass of males=13.8±0.27). At fledging, surviving males weighed significantly more than females ($t=2.37$, $df=24$, $P=0.026$; mean mass of females=16.5±0.28, mean mass of males=17.5±0.30).

Discussion

Our results differ from studies of several avian species that were based on similar sample sizes, yet documented modification of the primary sex ratio in relation to paternal attractiveness (Ellegren et al. 1996; Sheldon et al. 1999; but see Saino et al. 1999; Radford and Blakey 2000). Female juncos may not bias brood sex ratios for one of three alternative reasons: (1) they lack the genetic or physiological ability to modify sex ratios, (2) they are able to modify sex ratios, but do not because more attractive males do not have higher overall fitness, or (3) they are able to modify sex ratios, but do not because the future reproductive success that more attractive sons might represent is offset by the costs entailed in rearing them.

In studies unrelated to male attractiveness, sex ratio modification has been documented in a variety of other avian species (e.g. Seychelles warbler, *Acrocephalus sechellensis*, Komdeur et al. 1997; great tit, *Parus major*: Lessells et al. 1996; but see: Radford and Blakey 2000, lesser black-backed gull, *Larus fuscus*, Nager et al. 1999). While it is unlikely, therefore, that junco females lack the ability to bias sex ratio, the extreme sex ratio modification observed in the Seychelles warbler may be

exceptional and primarily related to their small clutch sizes (one or two eggs) (Emlen 1997).

Females should produce male-biased broods in response to greater attractiveness of their mates only if attractiveness predicts greater fitness for sons (Burley 1986). In juncos T-males are more attractive (Enstrom et al. 1997), yet data indicate that the net reproductive success of T- and C-males on a season-long basis does not differ (Raouf et al. 1997). While T-males gain greater numbers of EPFs than C-males and suffer fewer EPF losses than C-males in the home nest (Raouf et al. 1997), these advantages are counterbalanced by the lower survivorship to fledging of nestlings in broods of females socially mated to T-males (Ketterson et al. 1996; Raouf et al. 1997). Thus, there may be little basis for expecting an overall selective advantage for T-females to produce male-biased broods. If we extrapolate from experimentally enhanced variation in attractiveness to natural variation in attractiveness, and if attractiveness in general enhances some components of fitness but reduces others (Brooks 2000), then the conditions favoring excess production of sons by mates of attractive males may rarely be met. This would be particularly true, of course, if the heritability of male attractiveness characters is low (but see Price and Burley 1993).

The net reproductive success of T- and C-males does not differ, despite the increase in the number of EPF-young sired by T-males, because T-males reduce parental investment in the brood (Ketterson et al. 1992; Schoech et al. 1998). Our hormone manipulation mimics the testosterone profile observed in polygynous species such that peak levels of testosterone are maintained throughout the breeding season (Ketterson et al. 1996). As in polygynous species, this extension of elevated testosterone levels is associated both with increased attractiveness and reduced paternal care (Ketterson et al. 1996). T-females compensate for the reduction in paternal care by increasing maternal effort (Ketterson et al. 1992) but, nevertheless, they successfully fledge fewer offspring than females mated to C-males (Ketterson et al. 1996; Raouf et al. 1997). Therefore, even if hormonally mediated male attractiveness were heritable and provided potential fitness benefits to sons, mothers might have to trade the delayed benefits of producing more, attractive sons against the immediate expense of compensating for reduced paternal investment, especially if sons are more expensive to rear (male junco body mass at fledging is higher than female body mass; present study). If male attractiveness in general is associated with reduced male parental effort (Burley 1988; see also Saino and Møller 1995), then the conditions favoring excess production of sons by females mated to attractive males may be uncommon.

Sex ratio manipulation has previously been documented in response to experimental phenotypic manipulations of male attractiveness in collared flycatchers (male forehead patch size reduced by elevating parental investment in the previous breeding season: Ellegren et al. 1996), blue tits (UV reflectance of the male's crown:

Sheldon et al. 1999), and zebra finches (band color: Burley 1986). Interestingly, manipulation of male tail length in barn swallows does not induce primary sex ratio bias by females (Saino et al. 1999). The length of the sexually selected outermost tail feathers in this species is positively correlated with endogenous circulating levels of testosterone (Saino and Møller 1994) and, as in juncos, elevated testosterone levels in barn swallows are associated both with enhanced attractiveness and decreased paternal care (Saino and Møller 1995). The congruence of results in juncos and barn swallows further suggests that sex ratio bias may be uncommon when attractiveness and paternal care are inversely related.

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