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FIFTY:FIFTY OFFSPRING SEX RATIOS IN SAVANNAH SPARROWS (*PASSERCULUS SANDWICHENSIS*)

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ABSTRACT.—Over a 14 year period, we determined offspring sex ratios in a population of Savannah Sparrows (*Passerculus sandwichensis*) breeding on Kent Island, an isolated 80 ha island in the Bay of Fundy, New Brunswick, Canada, based on morphological measurements of 318 independent juveniles and 361 returning adults of known parentage. The mean annual offspring sex ratio was exactly 1.00 (±0.23, range= 0.61–1.41, *n* = 14). In no year did offspring sex ratio deviate significantly from 50:50, regardless of the sex ratio of breeding adults. Offspring sex ratio did not vary as a function of the timing of breeding, maternal or paternal age, or parental mating status (monogamy vs. polygamy). Overall, our data provide strong support for 50:50 offspring sex ratios at the population level (Fisher 1930), but no support for the notion of adaptive modification of offspring sex ratios by individuals (Trivers and Willard 1973).
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RESUMEN.—Durante 14 años se determinaron las proporciones de los dos sexos en las crías en una población de Gorriones de Savannah (*Passerculus sandwichensis*) que se reproduce en Kent Island, una isla aislada de 80 hectáreas en la Bahía de Fundy, New Brunswick, Canadá. Las calculaciones se basaron en medidas morfológicas de 318 juveniles independientes y de 361 adultos que habían regresado y cuyos padres eran conocidos. La proporción media anual de los sexos en las crías fue exactamente 1,00 (±0,23, variación = 0,61–1,41, *n* = 14). En ningún año se desvió significativamente de 50:50 la proporción de los sexos en las crías, independientemente de la proporción de los sexos de los adultos reproductivos. La proporción de los sexos en las crías no varió como función de la fecha de reproducción, ni de la edad maternal o paternal, ni de la situación reproductiva de los padres (monógama o polígama). En total, nuestros datos apoyan sólidamente las proporciones de los sexos en las crías de 50:50 al nivel de población (Fisher 1930) pero no ofrecen ningún apoyo para la noción de modificaciones adaptativas de proporciones de los sexos de las crías por individuos (Trivers y Willard 1973).

TRIVERS AND WILLARD (1973) hypothesized that natural selection should favor the ability of animals to modify the sex ratio of their offspring whenever the net fitness benefits of producing sons or daughters vary as a function of parental condition. For example, when males compete strongly for females and have greater variance in reproductive success than females, parents in good condition should invest more in sons. Parents in poor condition, on the other hand, should invest more in daughters because they are unlikely to produce sons that would be successful in male–male competition. By focusing on offspring sex-ratio manipulation by individuals of different quality, Trivers and Willard (1973) extended work by Fisher (1930) who sought to explain overall 50:50 sex ratios in natural populations, which he hypothesized was driven by the advantage of investing in offspring of the rarer sex. Inspired by Fisher (1930) and Trivers and Willard (1973), numerous researchers have investigated offspring sex ratios in a variety of bird species, with mixed results (reviews in Clutton-Brock 1986, Gowaty 1991, Sheldon 1998).

Many of the best examples of adaptively skewed offspring sex ratios involve birds maintained in captivity (Clotfelter 1996, Kilner 1998) or provisioned with artificial nest boxes (Ellegren et al. 1996, Svensson and Nilsson 1996, Bradbury et al. 1997, Kolliker et al. 1999, Albrecht 2000, Oddie 2000, Whittingham and Dunn 2000). Other studies supporting the Trivers-Willard model focus on birds with particular ecological characteristics: species that occupy habitats that are highly variable in quality (Cooch et al. 1997, Komdeur et al. 1997, Korpimaki et al. 2000), species that are highly polygynous or strongly sexually dimorphic in size (Dijkstra et al. 1998, Westerdahl et al. 2000), or species that breed cooperatively (Gowaty and Lennartz 1985, Komdeur et al. 1997).

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Offspring sex ratios are poorly known for the vast majority of species, particulary those that lack marked sexual dimorphism. Although the recent application of molecular techniques has resulted in numerous new studies, rarely have investigators determined offspring sex ratios at independence, despite the explicit dependence of Fisher's (1930) predictions—and the implicit dependence of Trivers and Willard's (1973) predictions—on measuring offspring sex ratios at the termination of parental care.

Recently, several authors have warned that support for models of adaptive modification of sex-ratio variation in birds may be partly due to selective reporting of significant results (Palmer 2000, Radford and Blakey 2000). Those authors have called for longer term studies—only a handful of studies have examined offspring sex ratios over more than a few years (Edwards et al. 1988, Koenig and Dickinson 1996, Rosenfield et al. 1996). In fact, in the last few years, a growing number of studies of passerine species have failed to find evidence that birds modify the sex ratio of their offspring as a function of parental quality, habitat features, or other variables (Pagliani et al. 1999, Saino et al. 1999, Questiau et al. 2000). In this study, we report 50:50 offspring sex ratios at the cessation of parental care in an island population of Savannah Sparrows (*Passerculus sandwichensis*) over a 14 year period, as predicted by Fisher (1930). In contrast to the predictions of Trivers and Willard (1973), however, the timing of breeding, parental age, and mating status do not appear to affect offspring sex ratio in this population.

METHODS

Since 1987, we have studied a migratory population of Savannah Sparrows at the Bowdoin Scientific Station on Kent Island, an 80 ha island in the Bay of Fundy, New Brunswick, Canada (44°35′N, 66°46′W) (Wheelwright and Mauck 1998). Each year, all adults and offspring within the 10 ha study area are uniquely marked with aluminum federal bands and randomly assigned combinations of plastic color bands. Savannah Sparrows return to Kent Island in early May and build cryptic nests on the ground in open habitats. Birds frequently forage in undefended common areas such as the forest edge or the marine intertidal zone, and territories are small and do not differ markedly in food quality or abundance (although nest predation risks vary among territories; see Wheelwright et al. 1997). If females successfully fledge young from their first clutch, they generally attempt to raise a second brood. Depending upon the year, 15–40% of males are socially mated with more than one female within a given breeding season (Wheelwright et al. 1994). Extrapair paternity is higher among nestlings cared for by monogamously mated males (Freeman-Gallant 1997). Lifetime reproductive success (measured by number of fledglings produced and by number of offspring recruited into the breeding population) is more variable for males than for females in this polygynous population (N. T. Wheelwright unpubl. data). Both parents typically care for fledglings, dividing the brood roughly equally (secondary and tertiary females mated to polygynous males generally receive less male help than primary females) (Wheelwright et al. 1992, 2003; Freeman-Gallant 1996, 1997; N. T. Wheelwright unpubl. data). Cooperative breeding has never been observed in Savannah Sparrows (Wheelwright and Rising 1993).

Compared to yearling females, older female Savannah Sparrows (two to six years old) lay earlier and larger clutches, replace destroyed clutches more quickly, and lose less weight in the process, which translates into higher reproductive success (Wheelwright and Schultz 1994). Compared to yearling males, older male Savannah Sparrows return to Kent Island earlier in the season, but otherwise their reproductive success is similar, and territory size does not increase with male age (N. T. Wheelwright and K. Oh, unpubl. data).

In this population, young birds are strongly philopatric and return rates are high (11.6% of birds banded as 7 day old nestlings return to breed the following year; $n = 3178$). The median distance of natal dispersal (~220 m) does not differ between males and females (Wheelwright and Mauck 1998). Because of the high degree of both natal and breeding philopatry, the ages of 72% of adults in the study population are known precisely, and the ages of new recruits can be estimated based on wing length and feather shape (Wheelwright and Mauck 1998).

When we began this study, molecular techniques for determining the sex of young birds were not readily available (e.g. Rabenold et al. 1991, Griffiths et al. 1996). Like other long-term (>12 years) studies of offspring sex ratio (Edwards et al. 1988, Koenig and Dickinson 1996, Rosenfield et al. 1996), our study used standard morphological features to assign sex. The sex of adults (≥ 1 year old) can be determined unambiguously during the breeding season by the presence of a cloacal protuberance in males or a brood patch in females (Wheelwright and Rising 1993). Nestlings cannot be sexed with confidence using morphological measurements, but after juveniles reach independence at ~27 days of age, sex can be determined with 94% certainty using body mass and wing length (Wheelwright et al. 1994). We confirmed accuracy of our sex assignments of juveniles by repeating the analyses of Wheelwright et al. (1994) with much larger sample sizes (N. T. Wheelwright unpubl. data, 1994–2001). Of 237 individuals that were measured as juveniles and whose sex was determined as adults, only 3 females (2.6%) and 13 males (10.8%) were incorrectly sexed. As in the earlier study, >94% of juveniles were correctly sexed.

In this study, we determined the sex of 679 Savannah Sparrows whose parents were of known age. Of those, 361 were sexed unambiguously when they returned to breed on Kent Island as adults; the other 318 (which were not recaptured as adults) were sexed as juveniles 27 days old or older, as described above. Offspring sex ratios were not significantly different for birds whose sex was confirmed as adults versus those sexed only at the juvenile stage in any year of the study or across all years combined (chi-square tests: $P > 0.20$). Moreover, the mean age of the mothers of offspring sexed as adults versus those sexed as juveniles did not differ significantly (1.92 vs. 2.01 years; $n = 679$; t-test: $P = 0.23$), indicating no bias in our methods of sexing offspring. Consequently, we combined both groups of offspring for further analyses.

Adult Savannah Sparrows on Kent Island are sexually dimorphic in size, with males averaging 12% heavier and 6% longer-winged than females. Sexual dimorphism in size is apparent by the time nestlings are ready to fledge, with 7 day old males averaging 9% heavier and 4% longer-winged than females. By the time juveniles reach independence, males average 12% heavier and 6% longer-winged than females (Table 1; Wheelwright et al. 1994). Although we have no data on whether parental feeding rates differ for male versus female fledglings, the duration of post-fledging parental care (15 days on average) is the same for male and female offspring (Wheelwright et al. 2003).

In analyzing offspring sex ratios, we included only birds whose (putative) parents were known as a result of direct observations of adults attending nests and feeding banded fledglings. Intraspecific brood parasitism is rare in this population (Freeman-Gallant 1997), so our assignment of genetic mothers was probably accurate. Our assignment of genetic fathers was much less certain, given that extrapair paternity is common (34% of nestlings in 63% of nests; Freeman-Gallant 1997). Because we could not determine sex of all nestlings within broods (using our methods, offspring had to survive and be recaptured after independence to determine their sex), we could not conduct brood-level analyses of offspring sex ratio. Instead, to test Trivers and Willard's (1973) predictions about adaptive modification of offspring sex ratio, we considered each juvenile as an independent observation and combined samples among parents as a function of age, mating status, and other variables. For example, for all offspring that survived to the age at which they could be sexed, we counted the number that were males versus females, and then (knowing the age of each bird's parents) determined whether offspring sex ratios differed between yearling and older females. Individual females often were the parents of more than one juvenile in our sample (mean number of offspring per adult female = 2.45, $n = 261$ females), creating the potential problem of pseudoreplication for tests of the Trivers-Willard predictions. Therefore, we repeated our analyses using only females that had a single offspring in the sample ($n = 104$ females). Our results comparing offspring sex ratios for females that were yearlings versus older birds, monogamously versus polygynously paired, primary versus secondary mates, and early versus late breeders were similar to those of the entire sample and no different from 50:50 in any case. Statistical tests were performed using STATVIEW (SAS Institute 1999). Where appropriate, significance tests were one-tailed (see below) and

TABLE 1. Mean size of male versus female Savannah Sparrows at different ages (±1 SD, n). Males are significantly larger than females in wing length, tarsus length, and mass as 7 day old nestlings (two to three days before fledging), as independent juveniles (27–40 days old), and as adults (t-tests: $P < 0.01$). The sample of juveniles includes only birds later definitively sexed as adults. Adult mass includes only measurements taken outside the period of egg-laying. Percent difference = ([male size/female size] – 1.0) × 100.

Age class	Trait	Males		Females		% Difference
Nestlings	Wing (mm)	30.8	(3.5, 153)	29.7	(3.7, 152)	3.7
	Tarsus (mm)	20.1	(1.4, 157)	19.8	(1.2, 155)	1.5
	Mass (g)	16.2	(1.6, 160)	14.8	(1.5, 158)	9.5
Juveniles	Wing (mm)	68.9	(1.8, 59)	65.0	(1.4, 41)	6.0
	Tarsus (mm)	21.1	(0.9, 38)	20.7	(0.5, 21)	1.9
	Mass (g)	18.5	(1.0, 54)	16.5	(1.0, 40)	12.1
Adults	Wing (mm)	68.8	(1.8, 856)	64.8	(1.7, 892)	6.2
	Tarsus (mm)	21.5	(0.7, 702)	20.9	(0.6, 755)	2.9
	Mass (g)	20.1	(1.2, 311)	17.9	(1.4, 230)	12.3

were corrected by the sequential Bonferroni method to control the Type I error rate (Rice 1989). Data are presented as means ±1 SD.

Predictions

If Savannah Sparrows adaptively modify sex of their offspring, offspring sex ratio should vary as a function of six variables: adult population sex ratio, female age, male age, season, clutch size, and mating status. Our first prediction was that, in years when the sex ratio of breeding adults is more heavily female biased, parents that produced sons would have an advantage. Likewise, when the breeding population was male-biased, producing daughters would be favored (Fisher 1930). As a consequence, adult and offspring sex ratios should be negatively correlated, assuming current adult sex ratios are a reasonable predictor of the sex ratio an offspring might be expected to encounter when it returned to breed a year later. In the study population, the ratio of breeding adult males and females has varied from 0.65 to 1.00 in different years (*n* = 14 years; N. T. Wheelwright unpubl. data).

The fact that male Savannah Sparrows are larger on average than females at fledging and that sexual dimorphism is even greater by the end of the period of parental care (Table 1) suggests that male offspring may be more costly than female offspring for parents to produce (Howe 1977, Teather and Weatherhead 1989, Riedstra et al. 1998, Torres and Drummond 1999, Cordero et al. 2000). Any excess costs of raising sons may be more easily borne by older, more experienced birds, which tend to be in better condition and have higher reproductive success than younger males (Blank and Nolan 1983, Wheelwright and Schultz 1994; see Nager et al. 1999). Thus, our second prediction was that older females would be more likely to raise sons, whereas yearling females would be more likely to raise daughters (Trivers and Willard 1973, Blank and Nolan 1983, Heg et al. 2000, Whittingham and Dunn 2000). (If reproductive success declines late in life, one might expect the very oldest females also to raise daughters.)

Our third prediction was that females mated to older males would be more likely to raise sons than females mated to yearling males, assuming that older males make higher quality mates (see Ellegren et al. 1996, Svensson and Nilsson 1996, Kolliker et al. 1999). Fourth, we predicted that offspring from clutches laid early in the season would be disproportionately male because resources would be more abundant then and parents would be in better condition to invest in offspring. As the breeding season progresses, food becomes scarcer (as evidenced by insect samples and observations of reduced adult foraging success), the expenses of reproduction accumulate (as evidenced by declining adult body mass and increasing feather wear), and birds must begin to prepare for their prebasic molt and migration (N. T. Wheelwright unpubl. data; see Dijkstra et al. 1990). In addition, there could be an advantage to producing sons early in the season because juvenile males would then have more time to investigate and lay claim to territories for the following season (Smith and Arcese 1989).

Fifth, we predicted that female offspring would be more likely to have hatched from large versus small clutches (Weatherhead 1985, Dijkstra et al. 1998). As a female completes her clutch, she has fewer resources available to allocate to later eggs. If males are more costly to produce, one might expect more females as the clutch progresses (Svensson and Nilsson 1996, Nager et al. 1999, Albrecht 2000). Our data did not include knowledge of egg order so we used clutch size as a surrogate, given that large clutches included a higher percentage of eggs laid later. Moreover, if the amount of resources available for reproduction is fixed, females have less to invest per offspring in large clutches, which would favor the production of the less expensive sex (Dijkstra et al. 1998). We also looked for evidence that sex-specific mortality occurred at different stages of reproduction.

Our last prediction was that monogamously mated females would be more likely to produce sons than polygynously mated females because the former could anticipate greater parental care by their mates (Patterson et al. 1980, Wheelwright et al. 1992, Nishiumi 1998; although see Freeman-Gallant 1998). For the same reason, the primary females of polygynously mated females should be more likely to produce sons than secondary females.

Results and Discussion

Forty-nine percent of all offspring sampled over a 14 year period were males, a proportion that does not differ from that expected under the null hypothesis of a 50:50 sex ratio (binomial

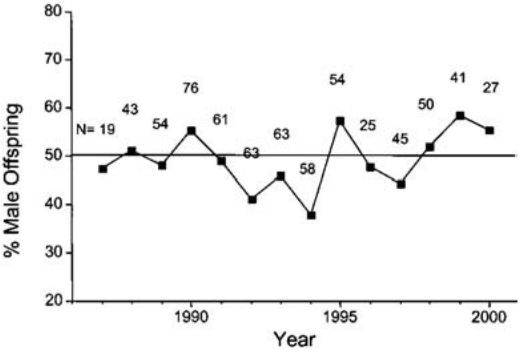

Fig. 1. Percentage of Savannah Sparrow offspring that were male over a 14 year period on Kent Island, New Brunswick. Line indicates 50:50 offspring sex ratio. Sample sizes are given above annual percentages. In no year did offspring sex ratio deviate significantly from 50:50 (binomial tests: $P > 0.09$). Total $n = 679$ offspring.

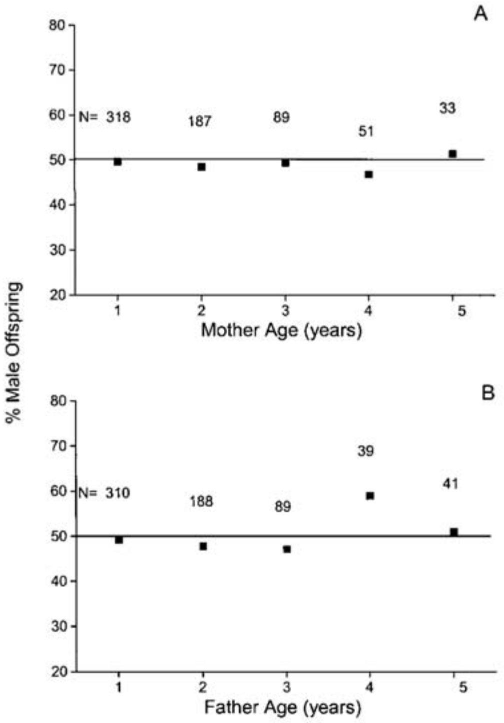

FIG. 2. Percentage of Savannah Sparrow offspring that were male as a function of (A) their mother's age and (B) their father's age (see Fig. 1). There was no relationship between an offspring's sex and the age of either its mother or father (chi-square tests: $P > 0.77$).

test: $P = 0.73$; $n = 334$ males and 345 females). The mean annual offspring sex ratio (number of males / number of females) in our sample was exactly 1.00 (±0.23, range= 0.61–1.41, $n = 14$). In no year did offspring sex ratio deviate significantly from 50:50, either before or after Bonferroni correction, despite annual variability in physical conditions (binomial tests: $P > 0.09$; Fig. 1). Males slightly outnumbered females among offspring in six years; females outnumbered males in eight years (Fig. 1).

At the population level, offspring sex ratio did not appear to be adjusted in response to the relative frequency of adult males or females in the breeding population. The sex ratio of breeding adults (mean = 0.79 ± 0.11, $n = 14$) was not correlated with offspring sex ratio in the same year or in the following year (linear regressions: $P > 0.47$).

There was no relationship between an offspring's sex and the age of its mother (maternal ages: 1–6 years old); male offspring were no more likely to have had older mothers than were female offspring (chi-square test: $P = 0.99$; Fig. 2A). Similarly, we found no relationship between an offspring's sex and the age of its (putative) father (paternal ages: 1–8 years old) (chi-square test: $P = 0.77$; Fig. 2B). No age group of adult males or females had a significantly biased offspring sex ratio (binomial tests with Bonferroni correction: $P > 0.10$). When we summed the ages of both members of a breeding pair as an index of their collective parental experience, we found no significant effect on offspring sex (chi-square test: $P = 0.72$).

To test for a seasonal effect on offspring sex ratio, we divided the breeding season into four, two-week periods. The sex ratio of offspring that fledged during different periods did not vary seasonally (chi-square test: $P = 0.42$). In fact, in no two week period did offspring sex ratio deviate from 50:50 (binomial tests: $P > 0.12$). With respect to our fifth prediction, the probability of being male or female was independent of the clutch size of its natal nest. Offspring sex ratio was also independent of number of eggs that hatched and number of young that fledged from the nest (chi-square tests: clutch size: $P = 0.25$; eggs hatched: $P = 0.21$; fledglings: $P = 0.28$).

The fact that offspring sex ratio did not seem to be affected by egg or nestling mortality may indicate that differential mortality of male versus female offspring does not occur during development. In another attempt to assess whether offspring mortality was sex-specific (and a potential mechanism of adaptively skewing offspring sex ratio; Krackow 1995, Albrecht 2000), we tested for a relationship between offspring sex and the frequency of egg or nestling mortality within clutches. We found that males were equally likely to have come from clutches with 100% hatching success (male offspring = 48.9%, $n = 583$) as from clutches with <100% success (male offspring = 51.0%, $n = 96$; chi-square test: $P = 0.70$). Likewise, there was no relationship between offspring sex ratio and nestling mortality (male offspring from broods with 100% fledging success of nestlings = 49.2%, $n = 545$; male offspring from broods with <100% fledging success = 49.3%, $n = 134$; chi-square test: $P = 0.99$).

Finally, we compared the offspring sex ratio of polygynously versus monogamously mated females, and (among polygynously mated females) that of primary females versus secondary or tertiary females. Examined alone, polygynously mated females produced significantly more daughters than sons (50 vs. 34; binomial test: $P = 0.05$), but differences disappeared in a comparison of offspring sex ratios of polygynously versus monogamously mated females (chi-square test: $P = 0.15$). Offspring sex ratios did not differ between primary versus secondary or tertiary females ($P = 0.20$).

Overall, our data on Savannah Sparrows nesting on Kent Island provide strong support for 50:50 offspring sex ratios at the population level, although not necessarily for equal investment overall in male versus female offspring, assuming the slight size differences between male and female offspring impose a sex-specific cost on parents (Fisher 1930). We found no support for the notion of adaptive modification of offspring sex ratios as a function of individual condition (Trivers and Willard 1973). Despite variation in the sex ratio of breeding adults over a 14 year period, and variation in the ages of female and male parents, in the timing of breeding, in clutch size, and in mating status, the sex ratio of Savannah Sparrows at independence (and at the cessation of parental investment) was consistently indistinguishable from 50:50.

Conceivably, biases in offspring sex ratio occur among Kent Island Savannah Sparrows but we failed to detect them. Although we had large sample sizes each year over more than a decade, we did not determine the sex of all members of each brood. Albrecht (2000) argues that examining sex ratios across broods (as in this study) can obscure adaptive sex-ratio adjustments expressed through sex-specific laying sequences and brood reduction. It is also conceivable that different selective pressures on offspring sex ratio cancel each other, making adaptive modifications difficult to isolate (Koenig and Dickinson 1996). For example, we predicted that large clutches would more likely be female-biased, but large clutches also tend to be produced by older females, which were predicted to have male-biased broods (see also Oddie 2000). Because we only determined the sex of birds that survived until independence, our focus was on sex ratios at independence. Biased sex ratios may occur at fertilization or hatching (Ellegren et al. 1996, Whittingham and Dunn 2000), although our failure to find evidence of sex-specific hatching failure or nestling mortality argues against biased sex ratios in that population. In any event, for testing models of offspring sex ratio at the level of populations (Fisher 1930), estimating sex ratios at the end of parental investment may be more appropriate.

The weight of the evidence in this study suggests that skewed offspring sex ratios are uncommon in Savannah Sparrows. Fifty:fifty offspring sex ratios may in fact be typical of the majority of bird species, which do not breed in nest boxes (a habitat alteration that tends to produce abnormally dense, large, and uniformly spaced breeding populations), are not strongly sexually dimorphic, and do not show cooperative breeding (and opportunities for local resource enhancement) or sex-specific natal dispersal (and the possibility of local resource competition) (Clark 1978, Gowaty 1993). In addition, because Savannah Sparrows hatch relatively synchronously compared to some species (e.g. Blank and Nolan 1983, Albrecht 2000), there may be fewer opportunities for parents to adjust offspring sex ratios through sex-specific mortality (Slagsvold 1990, Krackow 1995).

Although male Savannah Sparrows are bigger than females by the end of parental investment, differences in the costs to parents of raising sons versus daughters may be trivial. Offspring size may be an imperfect indicator of parental investments in sons versus daughters, especially if male and female offspring allocate resources differently during development (Droge and Gowaty 1991; see also Richter 1983). Furthermore, the lack of sex-related differences in the duration of postfledging care in Savannah Sparrows (Wheelwright et al. 2003) implies that overall parental investment in male and female offspring may be similar in that population.

Several assumptions of the Trivers-Willard (1973) model need to be tested, namely that marginal increases in parental investment translate into enhanced reproductive success of offspring, or that the fitness gains of producing high-quality sons are disproportionate compared to the gains of producing high-quality daughters. Although Williams (1979) and Charnov (1982) may have been unduly pessimistic in concluding that adaptive modification of offspring sex ratio in vertebrates is unlikely, our study adds another example of a natural bird population with 50:50 offspring sex ratios that are more consistent with the predictions of Fisher (1930) than those of Trivers and Willard (1973).

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