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Offspring sex ratios are poorly known for the vast majority of species, particularly 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 ( ) 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; 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 ( $\geq 1$  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



were corrected by the sequential Bonferroni method to control the Type I error rate (Rice 1989). Data are presented as means  $\pm$  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 (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 pre-basic 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

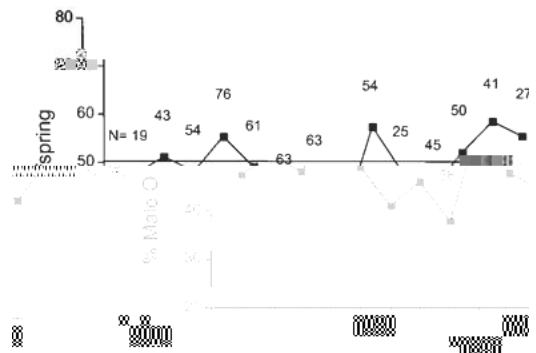


FIG. 1. Percentage of Savannah Sparrow offspring that were male over a 14 year period on Kent Island, New Brunswick. Line indicates 50:50 offspring sex ratio. Sample sizes are given above annual percentages. In no year did offspring sex ratio deviate significantly from 50:50 (binomial tests:  $p > 0.09$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

test: 0.73; 334 males and 345 females). The mean annual offspring sex ratio (number of males / number of females) in our sample was exactly 1.00 ( $\pm 0.23$ , range= 0.61–1.41, 14). In no year did offspring sex ratio deviate significantly from 50:50, either before or after

ary 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 test:



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