



# Postfledging parental care in Savannah sparrows: sex, size and survival

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We investigated postfledging parental care in a philopatric population of Savannah sparrows, *Passerculus sandwichensis*, breeding on Kent Island, New Brunswick, Canada in an effort to understand the factors influencing adult birds' decisions about parental investment in offspring. Brood division was not based on offspring sex: male and female parents were equally likely to care for sons or daughters. The total duration of parental care, from hatching to independence, was similar for sons and daughters (median=23 days), regardless of the sex of the care-giving parent. The duration of parental care also corresponded closely to the time required for juveniles to acquire basic foraging skills. Despite high levels of extrapair paternity, male Savannah sparrows invested as much in postfledging care and were as effective as females in caring for fledglings, based on recruitment of fledglings into the breeding population the following year. Male parents were more likely to care for smaller fledglings and for offspring from early broods (presumably to enable females to dedicate their efforts towards second clutches). Caring for fledglings was costly for parents: survivorship decreased as a function of the duration of postfledging parental care and the number of fledglings cared for. Parental survivorship, however, was not affected by the sex of the fledglings cared for. This study suggests that sex-biased provisioning may be unlikely except in species with strongly sexually dimorphic offspring, biased offspring sex ratios and sex-biased natal dispersal.

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Determining how much parents invest in their offspring is essential for understanding offspring sex ratios, reproductive strategies and life-history evolution (Fisher 1930; Charnov 1982; Slagsvold et al. 1986; Clutton-Brock 1988; Frank 1996; Sheldon 1998). A critical component of avian parental investment remains poorly known, namely parental care of young from fledging to independence (Smith 1978; Weatherhead & McRae 1990; Ogden & Stutchbury 1997). Once nestling birds fledge, it becomes increasingly difficult to follow them and observe interactions with their parents. Given the paucity of data on postfledging parental care, researchers have had to estimate total parental investment in sons versus daughters, using proxies such as the relative size of male and female offspring (Dijkstra et al. 1998; Torres & Drummond 1999).

The postfledging period is important to understand in its own right because it is when young birds learn crucial

life skills and face the highest mortality risks of their lives (Marchetti & Price 1989; Sullivan 1989; Weathers & Sullivan 1991; Wheelwright & Templeton, 2003). In addition, how much parents invest in fledglings from the first brood may determine if and when females lay a second clutch (McGillivray 1983; Verhulst & Hut 1996; Vega Rivera et al. 2000).

One aspect of postfledging parental care in passerines (brood division) has been well established. Typically, within a few days of leaving the nest, each fledgling becomes associated with and has the opportunity to learn from one parent; that parent then assumes sole or at least primary responsibility for feeding and protecting one or more fledglings (Nolan 1978; Smith 1978; Edwards 1985; Price & Gibbs 1987; Byle 1990; Kopachena & Falls 1991; Anthonisen et al. 1997; Ogden & Stutchbury 1997; however, see Wilson & Kikkawa 1988; With & Balda 1990). For many bird species the approximate duration of postfledging parental care is also known (1–3 weeks in most passerines: Davies 1976; Edwards 1985). Less is understood about how parental care is allocated to fledglings of different size or sex (Harper 1985; Price & Gibbs 1987;

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Byle 1990). Very few studies have quantified investments by parents of different age or determined how postfledging parental care affects the survival of adults, or which parent, male or female, is more successful at recruiting offspring into the breeding population.

In this paper, we briefly review major hypotheses about brood division and postfledging parental care, evaluating them with data from a 13-year study of a marked, strongly philopatric island population of Savannah sparrows, *Passerculus sandwichensis*. We examine how care is divided among fledglings of different sex, size and hatching date; differentiate between the contributions of male versus female parents of different ages; and describe how different patterns of postfledging care affect the survivorship of fledglings and their parents. Our results are interpreted in the context of Savannah sparrow offspring sex ratios, sexual size dimorphism and the ontogeny of foraging skills.

### Hypotheses: Brood Division

Various hypotheses have been advanced to explain brood division and make predictions about the allocation of postfledging parental care in birds. Two of these hypotheses predict that broods should be divided without regard to fledgling size or sex, and consider that the main function of brood division is either to minimize the risk of total brood loss due to predation (predation reduction hypothesis: Moreno 1984; McLaughlin & Montgomerie 1985) or to improve the efficiency of feeding offspring (parental efficiency hypothesis: Smith 1978; Moreno 1984; Harper 1985; McLaughlin 1989; Anthonisen et al. 1997). In contrast, three other hypotheses predict advantages to dividing broods and allocating parental care on the basis of the sex of fledglings. Because males tend to settle closer to their natal nests than females (Greenwood 1980) and because sons (but not daughters) compete with their fathers for both mates and territories, the cost of raising sons may be greater for male parents than female parents. Consequently, males have been predicted to prefer to care for daughters (differential dispersal/local resource competition hypothesis: Clark 1978; Gowaty & Droge 1991). Associating with opposite-sex relatives early in life may allow fledglings to learn to distinguish kin and avoid inbreeding in the future (kin recognition hypothesis: McLaughlin & Montgomerie 1985; Wheelwright & Mauck 1998). If sex-specific behaviours (e.g. foraging, habitat use, song, courtship) are learned from parents, parents should preferentially care for fledglings of their own sex in order to teach them such behaviours (cultural transmission of sex roles hypothesis: McLaughlin & Montgomerie 1985; Freeman-Gallant & Rothstein 1999). Thus, the differential dispersal/local resource competition hypothesis and the kin recognition hypothesis predict that parents should mainly care for fledglings of the opposite sex, whereas the cultural transmission of sex roles hypothesis predicts that parents should care for fledglings of the same sex.

Several hypotheses predict brood division and parental care on the basis of fledgling size. Because of the commonness of extrapair paternity, males may be less likely

than females to invest in offspring of whichever sex requires more energy to raise to independence, which in sexually dimorphic species is believed to be males (paternity uncertainty hypothesis; Westneat & Sherman 1993; although see Gottlander 1987; Stamps 1990). Females of many bird species have shorter life expectancies than males, which leads to the prediction that females should invest more heavily in current reproduction than do males (life-history trade-off hypothesis: Slagsvold 1997). Thus, both the paternity uncertainty hypothesis and the life-history trade-off hypothesis predict that females should care for more costly young.

Finally, brood division and postfledging parental care may also differ between early and late broods within a season (Vega Rivera et al. 2000; although see Kopachena & Falls 1993). For females, a trade-off may exist between prolonging care for fledglings from early broods and beginning a second clutch (Weatherhead & McRae 1990; Verhulst & Hut 1996). Accordingly, in double-brooded species, females would be expected to invest less in postfledging parental care of fledglings from early broods. Males, on the other hand, should invest more in fledglings from early broods, especially if offspring raised earlier in the season have higher survival rates (Kuitunen et al. 1996). Males may also direct more care to first-brood young if females use paternal care of the first brood to assess male quality before allocating paternity in second broods (Freeman-Gallant 1996). On the other hand, if caring for fledglings from the first brood constrains a male's ability to guard against extrapair fertilizations in the second brood or to seek extrapair fertilizations on his own (Magrath & Elgar 1997), males would be expected to invest less in postfledging parental care of fledglings from early broods (Weatherhead & McRae 1990; although see MacDougall-Shackleton & Robertson 1998).

### Hypotheses: Parental Care and Survival

In some passerine species, unaided females can raise young, at least to independence (Gowaty 1983; Wolf et al. 1988; Freeman-Gallant 1998), although males rarely do (Magrath & Elgar 1997). If female parents are more effective at caring for fledglings (e.g. by virtue of the superior quality or longer duration of their parental care compared with male parents), fledglings cared for by females would be expected to have higher survivorship than those cared for by males. The age of the parent caring for a fledgling may also influence the fledgling's survival. Compared with older individuals, birds breeding for the first time tend to be less successful in various aspects of reproduction (Clutton-Brock 1988; Wheelwright & Schultz 1994). Therefore, we predicted that fledglings cared for by yearling parents would have lower survival than those cared for by older, more experienced parents.

For parents, caring for young may be costly in terms of energy, time and the increased exposure to predators, competitors, or physical hardships. Investing heavily in postfledging care may tax parents and reduce future fertility or life expectancy (Ricklefs 1974; Nur 1984; Wheelwright & Schultz 1994; Deerenberg & Overcamp

1999). In some species double-brooded females survive less well than single-brooded females (Bryant 1979). If male offspring are more costly to raise because of their larger size (Howe 1977; Slagsvold et al. 1986; Clutton-Brock 1991; Wheelwright et al. 1994), parents caring for male fledglings should have lower survivorship than parents caring for female fledglings.

## METHODS

### Study Site and Species

Since 1987, we have been studying a marked population of Savannah sparrows on Kent Island, an isolated 80-ha island in the Bay of Fundy, New Brunswick, Canada (44°35'N, 66°46'W) (see Wheelwright & Mauck 1998 for a description of the study area). The population is well suited for investigating postfledging parental care and its effects on the survival of fledglings and parents. Savannah sparrows nest at high densities on the island. The study sites are open fields bordering the shore, which makes it easy to observe parent–fledgling interactions. In contrast to the mainland, Savannah sparrows on Kent Island are confined and cannot disperse widely after fledging. The population is strongly philopatric, and almost all surviving fledglings and adults return to Kent Island to breed in subsequent years (Wheelwright & Mauck 1998).

Female Savannah sparrows lay three to five eggs in cryptic nests built on the ground. Depending upon the year, 15–40% of males in the population are simultaneously polygynous (Wheelwright et al. 1992, unpublished data). About 34% of nestlings are the product of extrapair fertilizations; 63% of nests have at least one extrapair young (Freeman-Gallant 1997). Although only females incubate the eggs, both males and females feed nestlings. Males do not feed females on the nest and provide less care to nestlings than do females, making approximately 30% of all feeding trips (Freeman-Gallant 1998). The young leave the nest 9–11 days after hatching and remain on or near their natal territories over the next 10–20 days.

Parents generally divide the brood once the young leave the nest. Freeman-Gallant (unpublished data) found that within 2 days after fledging, brood division was significant in 34 of 92 broods (37%; Fisher's exact test testing for skews in the number of feeding trips by individual parents to different offspring:  $P < 0.05$ ). In the remaining broods, either the brood was not divided because one parent cared for all the fledglings (39 broods, 42%), or some division was apparent but not statistically significant due to the small number of feeding observations (17 broods, 18%). In two cases (2%), both parents cared for all fledglings. Within 7 days of fledging, brood division became increasingly clear (see below).

Beginning when Savannah sparrow fledglings are only 27 days old, their sex can be determined with 94% accuracy based on morphological measurements (juvenile males weigh 12% more and have 6% longer wings than females: Wheelwright et al. 1994;

Wheelwright & Seabury, 2003). At that age, fledglings start to join loose juvenile flocks that remain on the island until their southward migration begins 4–8 weeks later (Wheelwright & Rising 1993).

If offspring from the first brood successfully fledge, most females lay a second clutch 2–3 weeks later; in some cases females simultaneously feed nestlings or fledglings from the first brood while incubating their second clutch (N. Wheelwright, unpublished data). Birds whose first nests are preyed upon produce replacement clutches within a week or so, after which there is not enough time to produce a true second clutch (Wheelwright & Schultz 1994). See Wheelwright & Rising (1993) for additional information on the biology of Savannah sparrows.

### Field Methods

Each year, all breeding adults in the study areas were captured in mist nets and marked with an aluminium U.S. Fish and Wildlife Service band and a unique, randomly assigned combination of plastic colour leg bands. Adults were sexed by the presence of a brood patch (females) or a cloacal protuberance (males). From the end of May through to July, censuses were conducted in the 1.6-ha North Field study site every 2 days to determine the reproductive status of all individuals ( $N=81$  parent–fledgling observations). In the 6-ha South Field study site, which was separated from the North Field by 150 m of forest, censuses were conducted daily on portions of the site by one to two people ( $N=154$ ). There were no differences between the two sites in our estimates of sex-specific brood division (chi-square tests: North Field:  $\chi^2_1=1.85$ ,  $N=27$  parent–fledgling pairs,  $P=0.17$ ; South Field:  $\chi^2_1=0.001$ ,  $N=62$  parent–fledgling pairs,  $P=0.98$ ) or the duration of postfledging parental care (ANOVA:  $F_{1,219}=3.23$ ,  $P=0.07$ ). Individual birds were identified by their colour bands using  $10 \times 40$  binoculars from distances of 5–40 m. We located nests by following females during the incubation stage. Their mates (and the putative fathers of their offspring) were identified by observations of copulations, conspicuous mate guarding, nest defence and nestling feeding (Wheelwright et al. 1992; Wheelwright & Schultz 1994; Freeman-Gallant 1997). To reduce disturbance, nests were checked for hatching only every other day. When nestlings were 7 days of age, we banded them with a U.S. Fish and Wildlife Service band and one plastic colour band to distinguish each nestling from its siblings, and measured mass (to 0.1 g), wing length (to 1 mm) and tarsus length (to 0.1 mm). After the young left the nest, we determined which parents took care of which fledglings by observing feeding behaviour by parents and begging behaviour and close following of parents by fledglings. Male and female parents tended to feed fledglings on different parts of their territory, so there was rarely confusion about which parent cared for each fledgling. Parent–fledgling associations were typically verified by noting repeated feedings during 1–2-h population censuses (parents feed fledglings about once every 5 min: C. Freeman-Gallant, unpublished data).

## Data Analyses

Over a 13-year period, we opportunistically observed interactions between 221 fledglings and 164 adults. Typically, numerous interactions between an adult and a fledgling were observed over several days or weeks; from these observations, we estimated the minimum length of postfledging parental care and characterized brood division in the 221 unique parent–fledgling combinations. Our sample included 18 adults associated with two different offspring, two adults with three different offspring, and one adult with four different offspring. Of these parent–fledgling interactions, 16 were sampled in more than one year of the study. Because more than three-quarters of them had different mates in the different years, we considered each observation as statistically independent. The elimination of parent–fledgling interactions involving this subset of adults did not change any of our results. Evidence for brood division included the fact that no fledglings older than 13 days were observed being fed by both parents on the same day. In two cases, a fledgling was cared for by a male that was not socially mated to the fledgling's mother and that had not fed it in the nest. Both of these adult males subsequently mated with the fledgling's mother during her next nesting attempt, even though her original mate was still alive. Nine fledglings cared for by both parents (on different days) or by males who had not fed them as nestlings were excluded from our analyses.

We classified each fledgling into one of three size categories relative to its siblings when they were 7 days old: smallest, intermediate (1–3 of the 3–5 nestlings from a given nest could fall into this category), or largest. We were able to determine the sex of 91 of the 221 offspring that had been observed with their parents after fledging. Forty-two fledglings returned the next year as adults, at which point they could be sexed definitively; the other 49 fledglings were recaptured at an age when sexual dimorphism in mass and wing length was obvious and sex could be assigned with 94% accuracy (Wheelwright et al. 1994; Wheelwright & Seabury, 2003). Fifty-two of the 91 fledglings of known sex were female (57%).

We estimated the total duration of parental care for a particular fledgling as the length of time between hatching and the last day we observed it being cared for by its parent; the duration of postfledging parental care was considered to be this amount minus 10 days. Although parent–fledgling interactions were generally obvious, this was a minimum estimate of the total duration of parental care because in some cases fledglings may have been fed on a later date but not observed. We also noted the sex and age of the attending parent (ages of adults were known from banding as nestlings, juveniles or yearlings: Wheelwright & Mauck 1998), the brood number of the nest in which the fledgling had hatched (first, replacement, or second), and the occurrence of subsequent nesting attempts by its mother. We defined 'early broods' as those where the female laid a subsequent clutch, and 'final broods' as the female's last nesting attempt of the season. Parental age was categorized as 1-year-old, 2-year-old, or 3–6 years old. Because 25% of parents were

**Table 1.** Postfledging parental care in Savannah sparrows as a function of parent and offspring sex

Fledgling sex	Parent sex	
	Female	Male
Female	20	32
Male	19	20

Parents did not divide broods on the basis of fledgling sex (chi-square test:  $\chi^2_1=0.59$ ,  $N=91$ ,  $P=0.44$ ).

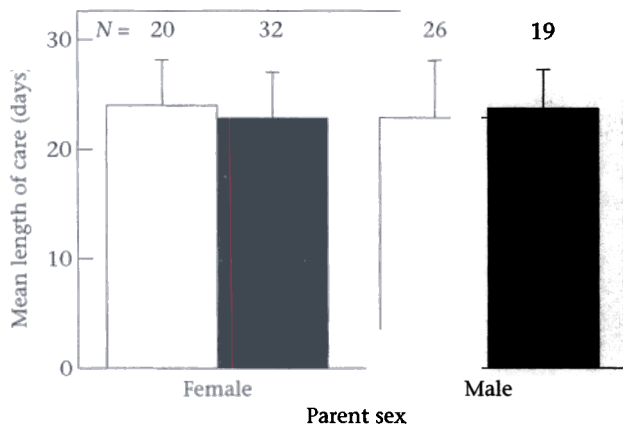
observed feeding more than one fledgling, we divided parents into those where only one fledgling was identified as being cared for, and those where the parent cared for two or more fledglings. Finally, we determined survivorship to the next breeding season for both fledglings and parents (as indicated by return rates the following year: Wheelwright & Mauck 1998). For chi-square tests and ANOVAs, we used Statview (SAS 1999). For multiple logistic regressions, we used JMP (SAS 1997). Data are presented as means  $\pm$  1 SD.

## RESULTS

### Brood Division and Parental Care: Offspring Perspective

Parents divided broods after fledging, but not on the basis of offspring sex. Fledglings were distributed among male and female parents randomly with regard to their sex (chi-square test:  $\chi^2_1=0.59$ ,  $N=91$  parent–fledgling pairs of known sex,  $P=0.44$ ; Table 1). Parents cared for offspring until they reached the age of about 23 days, about 13 days after fledging. There was substantial variation in our estimates of the age at which parental care ceased, however (range 11–35 days). Estimates less than 15 or 16 days almost certainly overlooked additional parental care or involved fledglings that died before independence. The duration of parental care was independent of offspring sex: sons received no more extended parental care than daughters (parent–son pairs:  $\bar{X} \pm \text{SD}=23.5 \pm 4.8$  days,  $N=39$ ; parent–daughter pairs:  $\bar{X} \pm \text{SD}=23.2 \pm 4.0$  days,  $N=52$ ). Moreover, fathers provided as much care as mothers to male and female offspring (two-way ANOVA: offspring sex:  $F_{1,87}=0.18$ ,  $P=0.67$ ; parental sex:  $F_{1,87}=0.02$ ,  $P=0.89$ ; offspring sex–parental sex interaction:  $F_{1,87}=0.98$ ,  $P=0.33$ ; Fig. 1).

Parents appeared to divide broods on the basis of fledgling size. Males cared for disproportionate numbers of the smallest fledglings, whereas care of the intermediate-sized and largest fledglings was divided equally between males and females (chi-square test:  $\chi^2_2=6.09$ ,  $N=221$  parent–fledgling pairs,  $P=0.047$ ; Table 2). (Note that the sample size in this analysis was larger than that for offspring sex distribution above because we measured the relative size of all fledglings in the present analysis, whereas we determined sex for only 91 of the offspring; see Methods). The duration of parental care received by fledglings, however, did not depend upon



**Figure 1.** Mean (+SE number of days of care (from hatching to independence) provided by female and male Savannah sparrow parents to female offspring (□) and male offspring (■). Both male and female parents provided about 23 days of care, irrespective of the sex of their offspring (two-way ANOVA: offspring sex:  $F_{1,87}=0.18$ ,  $P=0.67$ ; parental sex:  $F_{1,87}=0.02$ ,  $P=0.89$ ; offspring sex–parental sex interaction:  $F_{1,87}=0.98$ ,  $P=0.33$ ).

**Table 2.** Postfledging parental care in Savannah sparrows as a function of parent sex and offspring size

Fledgling size	Parent sex	
	Female	Male
Smallest	16	37
Intermediate	54	57
Largest	29	28

Males cared for significantly more of the smallest fledglings, whereas care of the intermediate-sized and largest fledglings was divided equally between males and females (chi-square test:  $\chi^2_2=6.09$ ,  $N=221$ ,  $P=0.047$ ).

fledgling size or parental sex (parent–smallest fledgling pairs:  $\bar{X}+SD=23.0+4.4$  days,  $N=53$ ; parent–intermediate-sized fledgling pairs:  $\bar{X}+SD=22.2+4.6$  days,  $N=111$ ; parent–largest fledgling pairs:  $\bar{X}+SD=23.2+3.8$  days,  $N=57$ ; two-way ANOVA: fledgling size:  $F_{2,215}=1.50$ ,  $P=0.23$ ; parental sex:  $F_{1,215}=0.02$ ,  $P=0.89$ ; fledgling size–parental sex interaction:  $F_{2,215}=0.72$ ,  $P=0.49$ ).

Which parent provided postfledging parental care depended upon brood number and whether or not females produced subsequent broods. Males were more likely to care for fledglings from first broods (87 of 139 broods, 63%), whereas they were less likely than females to care for fledglings from replacement (29 of 66, 44%) and second clutches (6 of 16, 38%) (chi-square test:  $\chi^2_2=8.48$ ,  $N=221$  parent–fledgling pairs,  $P<0.01$ ). Analysing the data in a slightly different way, we found a similar result: males cared for more young from early broods (broods followed by a subsequent nesting attempt), whereas females cared for more young from final broods (broods not followed by a subsequent nesting attempt; chi-square test:  $\chi^2_1=21.95$ ,  $N=221$  parent–fledgling pairs,  $P<0.001$ ).

When we restricted our analysis to first broods alone, the duration of postfledging parental care depended upon whether or not females went on to lay a second clutch. When females produced a successful first brood but did not renest, their fledglings received significantly more care than fledglings from first broods whose parents produced a second clutch (duration of total parental care of first brood when not followed by a subsequent clutch:  $\bar{X}+SD=24.6+3.8$  days;  $N=59$  parent–fledgling pairs; duration of total parental care of first brood when followed by a subsequent clutch:  $\bar{X}+SD=22.6+3.6$  days;  $N=80$  parent–fledgling pairs; two-way ANOVA:  $F_{1,219}=11.2$ ,  $P=0.002$ ).

### Brood Division and Parental Care: Parent Perspective

Male and female parents appeared to invest similarly in postfledging parental care. Forty-five per cent of all parent–fledgling observations involved female parents; 55% involved male parents (chi-square test:  $\chi^2_1=2.39$ ,  $N=221$ ,  $P=0.12$ ; Table 2). Males and females cared for similar numbers of fledglings from each brood (chi-square test:  $\chi^2_1=0.00$ ,  $N=164$  individual parents,  $P=1.00$ ). Moreover, the duration of parental care was equivalent for male and female parents (male parents:  $\bar{X}+SD=22.7+4.2$  days,  $N=122$ ; female parents:  $\bar{X}+SD=22.6+4.62$  days,  $N=99$ ; one-tailed  $t$  test:  $t_{220}=0.60$ ,  $P=0.42$ ). (Note that these means are slightly less than reported above for the subset of 91 fledglings of known sex; in that sample the duration of parental care was also indistinguishable between male and female parents:  $t_{90}=0.68$ ,  $P=0.20$ .)

Parents of different ages did not differ in the sex of the fledglings they cared for (chi-square test:  $\chi^2_2=2.76$ ,  $N=91$  parent–known-sex fledgling pairs,  $P=0.25$ ). Likewise, parents of different ages did not differ in the relative size of fledglings they cared for (chi-square test:  $\chi^2_4=1.51$ ,  $N=221$  parent–fledgling pairs,  $P=0.82$ ). Two-year-old birds showed a nonsignificant tendency to be more likely than yearlings or older birds to care for two or more fledglings per brood (chi-square test:  $\chi^2_2=5.21$ ,  $N=164$  parents,  $P=0.07$ ). However, the duration of postfledging parental care was not affected by parent age (ANOVA:  $F_{2,216}=0.73$ ,  $N=221$  parent–fledgling pairs,  $P=0.48$ ).

### Offspring and Parent Survivorship

Neither the duration of postfledging parental care nor the sex of the care-giving parent appeared to influence fledgling survivorship. In an analysis simultaneously examining the effect of six variables (year, fledgling sex, sex of the care-giving parent, duration of postfledging parental care, mass at fledging and hatching date) on fledgling survival, only mass at fledging ( $P=0.02$ ) and hatching date ( $P=0.01$ ) had a significant influence on survival. Heavier fledglings and fledglings from earlier nests were more likely to return as yearlings (multiple logistic regression: overall model  $\chi^2_{14}=24.09$ ,  $N=79$  parent–fledgling pairs for which all variables had been measured,  $P=0.04$ ). The survivorship of fledglings cared

**Table 3.** Survivorship of young Savannah sparrows as a function of the sex of the parent from which they received postfledging parental care

Fledgling status	Parent sex	
	Female	Male
Did not return	79	105
Returned	20	17

Survivorship was determined by whether fledglings returned the subsequent year (see Wheelwright & Mauck 1998). The survivorship of fledglings cared for by mothers was no different than that of fledglings cared for by fathers (chi-square test:  $\chi^2_1=1.54$ ,  $N=221$ ,  $P=0.29$ ).

for by female parents was not significantly different from the survivorship of fledglings cared for by male parents (chi-square test:  $\chi^2_1=1.54$ ,  $N=221$  parent-fledgling pairs,  $P=0.29$ ; Table 3). Fledgling survivorship was independent of the age of the parent from which it received care (chi-square test:  $\chi^2_2=1.89$ ,  $N=221$  parent-fledgling pairs,  $P=0.39$ ).

We also examined the effect of year, fledgling sex, sex of the care-giving parent, duration of postfledging parental care and number of fledglings cared for on parent survival. The number of fledglings cared for and the duration of parental care significantly affected parental survivorship ( $P=0.05$  and  $0.03$ , respectively; interaction of number of fledglings and duration of care:  $P=0.03$ ; multiple logistic regression: overall model  $\chi^2_{14}=56.40$ ,  $N=66$  parent-fledgling pairs,  $P=0.001$ ). For parents that cared for two or more fledglings, parental survival decreased significantly as parental care increased ( $P=0.03$ , controlling for year and parent sex; multiple logistic regression: overall  $\chi^2_{12}=42.50$ ,  $N=41$  parents,  $P=0.02$ ). An adult's survival was unaffected by the sex of the fledgling for which it had provided care. Of the parents that returned the following year, 19 had cared for female fledglings and eight had cared for male fledglings; of those parents that failed to return the following year, 19 had cared for female fledglings and 20 had cared for male fledglings (chi-square test:  $\chi^2_1=2.24$ ,  $N=66$ ,  $P=0.13$ ).

## DISCUSSION

As in most bird species, Savannah sparrows care for their offspring for several weeks after the young leave the nest, dividing the brood between the male and female parents. The timing of the cessation of parental care, about 23 days after hatching, corresponds closely with the timing of the acquisition of foraging abilities in fledglings. Juvenile Savannah sparrows of various ages captured in the field and tested under aviary conditions were incapable of solving simple foraging tasks until 22–24 days of age, after which their performance was indistinguishable from older juveniles (Wheelwright & Templeton, 2003). Parents apparently must protect their young and subsidize their feeding until they can forage independently.

There may be costs associated with prolonging post-fledging parental care, however. Extending the period of offspring dependence may interfere with moult, migration, or (in double-brooded species such as Savannah sparrows) successive breeding attempts (Kuitunen et al. 1996). The conflict females face between caring for fledglings from their first brood and producing a second clutch is resolved to some degree by the fact that females can overlap care of fledglings from the first brood with incubation of the second clutch. An indication that it is difficult for females to attend to young from two broods comes from the fact that when females do not produce a second clutch, they apparently are able to invest more care in fledglings from their first brood (see also Verhulst & Hut 1996). Males may help liberate females and allow them to concentrate on a second brood by disproportionately caring for fledglings from the first brood. Males have another incentive for investing in fledglings from their first broods: evidence suggests that females evaluate male parental care during the first brood before allocating paternity to the next clutch (Freeman-Gallant 1996).

In spite of males' uncertainty of paternity and lower overall investment in reproduction compared to females (Trivers 1972; Westneat & Sherman 1993; Freeman-Gallant 1997), male Savannah sparrows contributed as much as females in terms of number of fledglings cared for and the duration of postfledging parental care. Males also proved as successful as females in caring for fledglings, based on the survival of fledglings to the following year, another unexpected indication of the equivalence of postfledging care by males and females. This study supports others that have failed to find a positive relationship between parentage and paternal care (Ketterson & Nolan 1994; Freeman-Gallant 1997; MacDougall-Shackleton & Robertson 1998; Schwagmeyer et al. 1999; see also Whittingham et al. 1992). In fact, Freeman-Gallant (1997) found that male Savannah sparrows were actually more likely to care for young from the first brood when there was extrapair paternity, presumably to reduce the risk of extrapair paternity in subsequent broods.

We found that brood division occurred randomly with respect to fledgling sex, in contrast to the predictions of various hypotheses (differential dispersal/local resource competition, cultural transmission of sex roles, kin recognition). Our results were more consistent with hypotheses that make no directional predictions about sex-biased brood division (predation reduction, parental efficiency). Moreover, parental investment during the fledgling period (as reflected by the duration of postfledging parental care) in male and female offspring was equivalent, regardless of the sex of the care-giving parent. Using Gowaty & Droge's (1991) terms, we found no differential investment by sex of parent or by sex of offspring, and no interaction between sex of parent and sex of offspring in Savannah sparrows. This finding is similar to the results of Price & Gibbs (1987), Anthonisen et al. (1997) and Lessells et al. (1998), but in contrast to studies showing more male care to male-biased broods (Byle 1990; Clotfelter 1996; Nishiumi et al. 1996; Hartley

et al. 1999) or to female-biased broods (Harper 1985; Stamps et al. 1987; Gowaty & Droge 1991).

The absence of sex-biased provisioning in Savannah sparrows may be explained by particular aspects of their biology. Natal dispersal does not differ between males and females, at least in this population (Wheelwright & Mauck 1998), so the assumptions of differential dispersal/local resource competition hypothesis (e.g. conflict between parents over sex allocation due to unequal competitive impact of sons versus daughters) are not met (Greenwood 1980; Gowaty & Droge 1991). Mate competition with philopatric offspring of the same sex might still favour caring for opposite-sexed fledglings, but that could be counteracted by the risk of inbreeding, as predicted by the kin recognition hypothesis (McLaughlin & Montgomerie 1985). However, Savannah sparrows apparently use other mechanisms to avoid mating with relatives (Wheelwright & Mauck 1998; C. Freeman-Gallant, unpublished data). It may be that kin recognition develops mainly during the nestling period and is subsequently reinforced after fledging (even in the absence of sex-biased brood division) because siblings cared for by different parents generally remain within 50–100 m of each other on or near their territories. It is also worth considering the possibility that postfledging parental care on islands may not necessarily be the same as on the mainland, where dispersal is less restricted (Higuchi & Momos 1981).

There is some evidence that differences in the costs of raising sons or daughters in this population are not of a magnitude sufficient to select for sex-biased provisioning. Juvenile males appear to acquire foraging skills slightly earlier than juvenile females, which may offset their larger size (Wheelwright & Templeton, 2003; see also Clotfelter 1996). Although juvenile males are 12% heavier on average than females in the Kent Island population, offspring sex ratios are uniformly 50:50 and mortality appears not to be sex specific (Wheelwright & Seabury, in press), which provides further evidence of similar costs of male and female offspring (Fisher 1930; Maynard Smith 1980). In this study, parents who cared for male and female fledglings survived equally well until the following year, another indication of the similar costs of raising sons and daughters.

According to the cultural transmission of sex roles hypothesis, the postfledging period is a period during which sex-specific behaviours are learned from parents (McLaughlin & Montgomerie 1985). In Savannah sparrows, intersexual differences in foraging are minimal (females tend to forage more rapidly and feed lower in trees than males: N. Wheelwright, unpublished data). Male Savannah sparrows feed their nestlings at rates similar to those at which they had been fed; such a behaviour could conceivably be learned during the post-fledging period, although it may be learned in the nest or may have a genetic component (Freeman-Gallant & Rothstein 1999). Parental inability to recognize the sex of fledglings can probably be ruled out as an explanation for the absence of sex-biased provisioning given that, by the time they are 7 days old, nestlings begin to show sexual dimorphism in mass and wing length (and probably

numerous more subtle traits) (Wheelwright et al. 1994; Wheelwright & Seabury, 2003).

Although brood division and postfledging parental care were random with respect to fledgling sex, male Savannah sparrows disproportionately cared for the smallest fledglings. Both the paternity uncertainty and the life-history trade-off hypotheses predict that males should prefer to raise the less costly fledglings (Slagsvold 1997). Smaller fledglings may not necessarily represent less costly investments because their chance of survival may be lower and the time until independence may be longer (Gottlander 1987; see also Maynard Smith 1980). However, we found no difference in the duration of care provided to fledglings of different size (see also Smiseth et al. 1998). Moreover, nestling mass at 7 days of age is a good predictor of mass after 27 days of age (independence) in Savannah sparrows: young are apparently not fed more during the postfledging period to compensate for poor growth during the nestling period (C. Freeman-Gallant & N. Wheelwright, unpublished data). In a recent review, Slagsvold (1997) found only one study in which males preferentially cared for the smallest fledglings (Harper 1985). None the less, his model predicts that the less care-giving parent (which, during the nestling stage in Savannah sparrows, is the male: Wheelwright et al. 1992; Freeman-Gallant 1996) may provision the smallest nestling because large nestlings outcompete their smaller siblings for access to higher food delivery rates by females (Slagsvold 1997). Whether the model can be extended to the fledgling period is an open question, particularly in Savannah sparrows where males turn out to be as effective in caring for fledglings as females.

It could be that males preferentially care for small fledglings for reasons unrelated to their confidence of paternity or to the quality of or cost of raising offspring of different sizes. Male Savannah sparrows are strongly territorial and are more likely than females to remain on territory after their young have fledged. Small fledglings generally fledge a few hours or more later than their larger siblings and probably disperse more slowly during the period of brood division. Females, less concerned than males with territorial defence, may care for the larger fledglings, which move more quickly and farther from the centre of the territory (see McLaughlin & Montgomerie 1985).

Parental age had no effect on any aspect of postfledging parental care, as shown in the house martin, *Delichon urbica* (Bryant 1979). Caring for fledglings apparently exacted a cost, however. Parents that prolonged post-fledging care were less likely to return the following year, especially if they cared for more than one fledgling. Female Savannah sparrows can raise young unaided by males (Freeman-Gallant 1998; see also Wolf et al. 1988). None the less, the disproportionate role of males in caring for first-brood fledglings, the effectiveness of male post-fledging parental care and the long-term survival costs of caring for more than one fledgling, or extending the duration of parental care shown in this study suggest that males play a substantial role in reproduction and highlight the importance of female mate choice (Freeman-Gallant 1996).

Although research on brood division and postfledging parental care has produced a rich array of hypotheses (Harper 1985; Gowaty & Droge 1991; Slagsvold 1997), we are still far from being able to make broad generalizations. Stamps (1990) predicted that sex-biased provisioning would be more likely among species with strongly sexually dimorphic offspring, biased offspring sex ratios and sex-biased natal dispersal, traits that do not apply to Savannah sparrows. Our demonstration that sex-biased provisioning, at least of fledglings, does not occur in Savannah sparrows is consistent with Stamps' (1990) model and suggests that sex-biased provisioning may be the exception, not the rule, among birds.

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