

The Auk 116(4):1132–1136, 1999

## Apparent Heritability of Parental Care in Savannah Sparrows

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Parental effort measures the total amount of time and energy allocated toward care of offspring, and it is often an obvious and variable component of an animal's life history (Winkler and Wilkinson 1988, Clutton-Brock 1991). Among birds, intraspecific variation in parental effort is more quantitative than qualitative. Individual adults differ in feeding rate (Yasukawa et al. 1990, Wright and Cuthill 1992), intensity of offspring defense (Winkler 1992), and tendency to engage in prolonged associations with young (Weatherhead and McRae 1990).

Like all quantitative traits, intraspecific variation in parental effort can be attributed to genetic and environmental causes. However, recent work has focused mostly on environmental sources of variation (Ketterson and Nolan 1994, Gowaty 1996a), and individual birds often are viewed as decision-making machines that respond adaptively to changes in their physical or social environments (Winkler and Wilkinson 1988). Indeed, birds modify parental effort in response to numerous proximate factors, including genetic parentage (Lifjeld et al. 1998), brood size (Ruusila and Pöysä 1998), and offspring age and condition (Whittingham and Robertson 1993). In no case have environmental factors accounted completely for differences among individuals in the intensity of parental care, however, and some role for genetic or cultural determination seems likely.

For quantitative traits, genetic and environmental effects can be distinguished by examining the phenotypic resemblance of relatives. In cases of high narrow-sense heritability ( $h^2$ ), additive genetic effects contribute substantially to overall phenotypic variation, and relatives strongly covary (Falconer and Mackay 1996). Among vertebrates, estimates of heritability are lacking for measures of parental effort and for most quantitative behaviors in the field (Hailman 1986, Boag and van Noordwijk 1987, Mousseau and Roff 1987; but see Waser and Jones 1989). In general, heritabilities for behavioral traits are low (Lemon 1993, Berthold and Pulido 1994), suggesting that quantitative differences among individuals are largely driven by the environment.

Here, we examine the degree to which male and female feeding rates are heritable in an insular population of Savannah Sparrows (*Passerculus sandwichensis*). We show that quantitative differences in feeding rates among males can be attributed to the be-

havioral phenotypes of their fathers, suggesting that parenting strategies are substantially less flexible than commonly presumed.

*Methods.*—We studied the Savannah Sparrows breeding at the Bowdoin Scientific Station on Kent Island, New Brunswick, Canada (44°35'N, 66°46'W) from 1992 to 1995. Every adult in the population bore a unique combination of three colored leg bands. Daily censuses of the 7.5-ha study site allowed us to identify social pairings, the hatching date of all successful clutches, and the reproductive performance of adults. We quantified parental feeding rates during 1.5-h (1992) or 2-h (1993 to 1995) observation periods six days after the young hatched. To maximize the number of nests included in the study, we made no attempt to standardize observation periods for time of day or weather. Feeding rates were highly repeatable within years, suggesting that these short sampling periods were of sufficient duration to detect real behavioral differences among individuals (Wheelwright et al. 1992, Freeman-Gallant 1996). Additional details on field methodology are provided in Freeman-Gallant (1998).

Kent Island Savannah Sparrows are highly philopatric (Wheelwright and Mauck 1998), and the return of yearlings to the study site allowed us to compare the behavioral phenotypes of 24 adult offspring with their parents. Each of these offspring came from a different brood, so 24 families were available for analysis. In an independent data set, we also examined the repeatability of feeding rates across years for 19 females. In all cases, offspring and parents were observed by field technicians who had no knowledge of the genealogy or prior behavior of the sparrows.

Because 15 to 33% of male Savannah Sparrows on Kent Island are polygynous each year, and because males only rarely provision the nests of secondary females, we used feeding effort directed toward the oldest (first-hatched) nest only. Similarly, most female feeding rates were from social situations in which the female was the only mate of a monogamous male or the primary mate of a polygynous male (as determined by hatching date; Freeman-Gallant 1997). In four cases, limited data forced us to use feeding rates from secondary females. No results reported here are changed qualitatively by excluding these four cases.

Narrow-sense heritabilities were derived from simple linear regressions of offspring on male or female parents (slope =  $0.5h^2$ ; Falconer and Mackay

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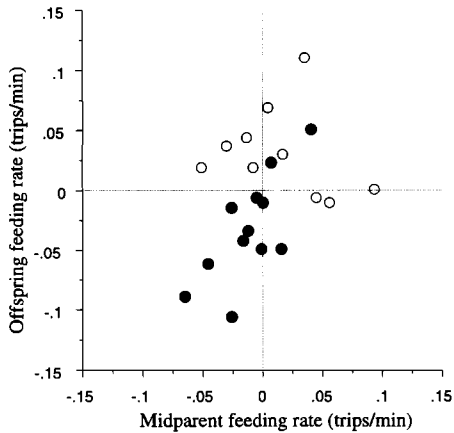


FIG. 1. Offspring-midparent regression of feeding rates in Savannah Sparrows. Feeding rates were derived from two-hour focal observations of color-banded individuals without controlling for brood size, timing of breeding, male mating status (monogamous or polygynous), time of day, year, or weather. Midparent values average the absolute feeding rates of adults. Horizontal and vertical lines occur at average levels of care for offspring ( $0.106 \pm \text{SE of } 0.010$ ) and parents ( $0.071 \pm 0.008$ ) standardized to 0 trips/min. Filled and open circles identify male and female offspring, respectively.

1996). Because sparrows did not mate assortatively (likelihood-ratio test of correlation between male and female feeding rates;  $r = 0.21$ ,  $P > 0.20$ ,  $n = 22$ ), heritability estimates were uncorrected for the behavioral resemblance of mates. For two offspring, we had information on paternal feeding rates only. In all cases, residuals were approximately normal and homoscedastic, which justified the use of standard parametric tests.

**Results.**—Like most birds, Savannah Sparrows vary in the amount of care they provide to their young, but this variation is highly consistent across generations. Based on offspring-midparent regression, a close correspondence appeared to exist between the behavioral phenotypes of parents and their young. Offspring that provided high levels of care as adults had been recipients of substantial parental effort as six-day-old nestlings (ANCOVA controlling for offspring sex,  $F = 4.77$ ,  $df = 1$  and  $18$ ,  $P = 0.04$ ,  $n = 22$ ; Fig. 1).

This phenotypic similarity depended on the sex of the offspring, however (ANCOVA,  $F = 8.65$ ,  $df = 1$  and  $18$ ,  $P = 0.009$ ,  $n = 22$ ; Fig. 1). A one-to-one correspondence existed between the feeding rates of fathers and sons ( $\beta = 0.99 \pm \text{SE of } 0.28$ ,  $P = 0.006$ ,  $n = 12$ ; Fig. 2A), and a strong but nonsignificant relationship occurred between the feeding rates of mothers and sons ( $\beta = 0.70 \pm 0.38$ ,  $P = 0.09$ ,  $n = 12$ ; Fig.

2B). In a bivariate regression of sons on the feeding effort of both parents, only the paternal contribution was significant (offspring-father,  $\beta = 0.86$ ,  $P = 0.02$ ,  $n = 22$ ; offspring-mother,  $\beta = 0.31$ ,  $P = 0.36$ ,  $n = 22$ ). In contrast, the feeding effort of daughters was unrelated to either paternal ( $\beta = -0.07 \pm 0.24$ ,  $P = 0.77$ ; Fig. 2C) or maternal ( $\beta = -0.14 \pm 0.19$ ,  $P = 0.48$ ; Fig. 2D) feeding rates. Although small sample sizes suggest a cautious interpretation of negative results (Alatalo et al. 1997), the daughter-parent regressions appear unambiguously "flat" (Figs. 2C and D).

The dissimilarity between daughters and parents cannot be attributed to the brood size, timing of breeding (hatching date of first nest), body mass, or wing length of daughters (bivariate regressions of maternal or paternal feeding rates and each of the four predictors on female feeding rates; parental effect,  $\beta < 0$ ,  $P > 0.10$ ). The only predictor approaching significance in these bivariate regressions was timing of breeding, which appeared to affect female feeding rates weakly and positively ( $\beta = 0.002$ ,  $P > 0.08$ ).

The sex-specific heritability of parental care in Savannah Sparrows is supported by an independent data set in which the feeding effort of individual adults was compared across years. The repeatability of a trait measures the proportion of phenotypic variation that can be attributed to permanent environmental and genetic effects and is an upper-bound estimate of heritability (Falconer and Mackay 1996, Aragaki and Meffert 1998). The repeatability is given by the intraclass correlation coefficient derived from a one-way ANOVA comparing the average phenotypes of adults (Lessells and Boag 1987). The repeatability of parental care across years was 0.60 for 14 monogamous males ( $F = 3.57$ ,  $df = 13$  and  $14$ ,  $P = 0.012$ ; see Freeman-Gallant 1998) but only 0.20 for 19 females ( $F = 1.93$ ,  $df = 18$  and  $19$ ,  $P = 0.083$ ). The estimate of repeatability for female feeding rates did not depend on whether females changed mating situations between years (i.e. whether females mated to monogamous males in one year became the primary mates of polygynous males in another), because the estimate of repeatability for feeding rates remained 0.20 ( $P > 0.05$ ) regardless of which subset of females we examined.

Estimates of heritability based on the offspring-parent regressions are not precise, and all 95% confidence intervals (CI) exceeded the theoretical limits of  $h^2$ . The 95% CIs of heritability based on daughter-mother ( $-1.02$  to  $0.46$ ), daughter-father ( $-1.08$  to  $0.80$ ), and son-mother ( $-0.09$  to  $0.89$ ) regressions included zero; the 95% CI of heritability derived from the father-son regression was  $0.88$  to  $3.1$ .

**Discussion.**—Parental effort is a key component of avian life-history strategies and commonly is linked to sexual selection and the evolution of social and genetic mating systems (e.g. Maynard Smith 1977). Despite the influence of parental effort on fecundity

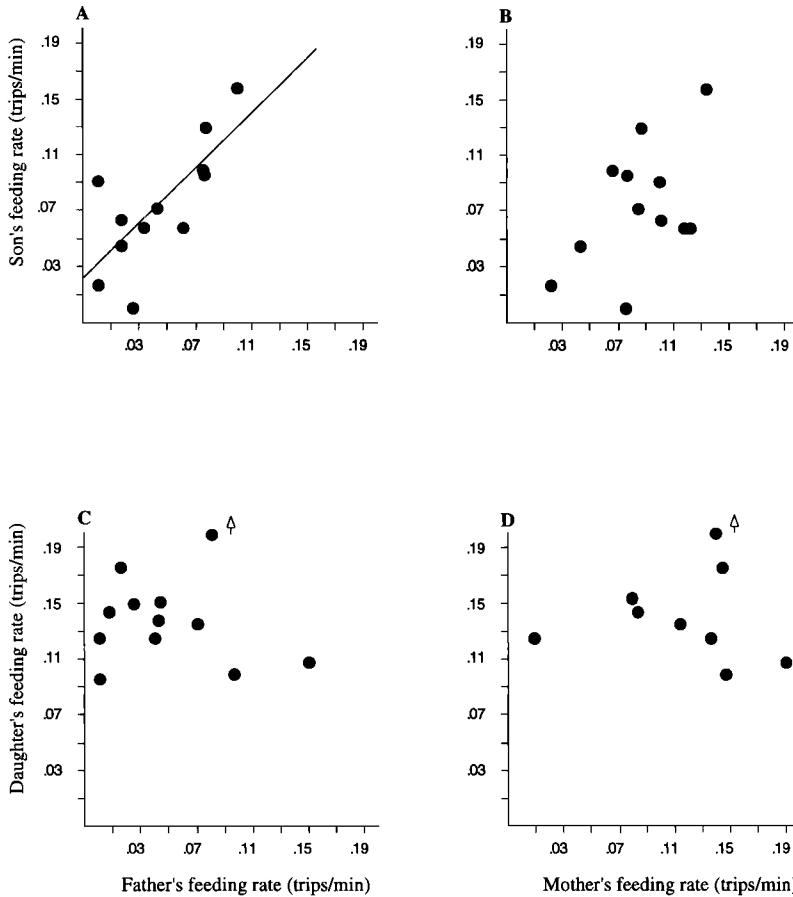


FIG. 2. Offspring-parent regressions of feeding rates in Savannah Sparrows for (A) sons and fathers, (B) sons and mothers, (C) daughters and fathers, and (D) daughters and mothers. Arrows in (C) and (D) indicate points that lie outside plot bounds; regression coefficients do not change substantially when these outliers are omitted, and slopes remain negative and nonsignificant.

(e.g. Gowaty 1996b), adults vary in the magnitude of care that they direct toward their young. Current thinking ascribes this intraspecific variation in parenting effort to additive genetic effects, adaptive behavioral plasticity, and "noise." However, the relative contribution of environmental and genetic effects has not been assessed for any bird. In Savannah Sparrows, quantitative differences among individuals in feeding rate are predicted by the behavioral phenotype of parents. Adult males on Kent Island provide consistent levels of care from year to year and feed at the same rate as their social fathers.

Nonetheless, male feeding rates may lack genetic determination if the phenotypic similarity can be attributed to the quality of care and its effect on offspring condition. This paternal-effects hypothesis predicts that high-quality care yields robust young and that robust young ultimately provide substantial care themselves as a consequence of their good con-

dition. Little support exists for either prediction in Savannah Sparrows. During the 1992 to 1994 breeding seasons (the natal years for all 12 sons considered in the present study), the number and quality of young were unrelated to male feeding effort, in part because of female compensation for poor paternal performance. This result was confirmed by an experiment in which the removal of males had no effect on fledging success and little influence on offspring mass (Freeman-Gallant 1998). In no year did adult size or mass predict male feeding rates (Freeman-Gallant 1998). Similarly, the phenotypic similarity of fathers and sons is unlikely to be explained by the social inheritance of territories and the effect of territory quality on male feeding rates. Savannah Sparrows on Kent Island typically feed in undefended areas of the intertidal zone, and no male in the present study inherited his father's territory.

Lack of support for the paternal-effects hypothe-

sis, combined with the close correspondence between feeding rates of fathers and sons, suggest strong genetic determination. However, this determination need not be direct; parental care may be largely contextual if males base parenting decisions on proximate factors that are genetically determined. In Savannah Sparrows, brood size, timing of breeding, and the parental contribution of social partners influence absolute feeding rates (Wheelwright et al. 1992, Freeman-Gallant 1998), but these elements of a bird's physical and/or social environment do not appear to contribute to the behavioral resemblance of fathers and sons (bivariate regressions of paternal feeding rates and each of the three predictors on male feeding effort; paternal effect,  $0.97 < \beta < 1.2$ ,  $P < 0.04$ ; all other predictors,  $\beta < 0.06$ ,  $P > 0.40$ ).

Although non-zero heritability implies (by definition) the presence of additive genetic effects, genetic transmission may be minimal, and learning may underlie the behavioral similarity of relatives. Extra-pair fertilizations (EPF) are common in Savannah Sparrows, and as many as 30% of the offspring considered in the present study may have resulted from EPFs (Freeman-Gallant 1997). Unfortunately, small sample sizes did not allow us to examine the phenotypic resemblance of relatives within included and excluded parent-offspring groups, and the possibility of cultural transmission cannot be discounted. Certainly, young sparrows have the opportunity to observe feeding rates while in the nest and to learn foraging skills or strategies after they leave the nest.

Regardless of whether transmission is mediated by learning, additive genetic effects, or both (e.g. Mundinger 1995), the striking correspondence between the feeding rates of fathers and sons has important implications for studies of parental care. Quantitatively, if more than 80% of the variation in feeding rates among males can be attributed to the previous generation (lower 95% confidence limit for heritability based on offspring-parent regression = 88%), the scope for adaptive behavioral plasticity and residual error (noise) is substantially reduced. Although males are known to respond to numerous proximate factors when "deciding" on parenting strategies, this behavioral plasticity is likely to occur around absolute levels of care largely determined by an individual's genotype and/or natal environment.

For females, low heritability suggests that their parenting strategies are substantially more flexible than those of males. Whether this flexibility reflects the influence of additional environmental factors, the absence of genetic/cultural constraints, or both is not known. Regardless, differences between the sexes in the proximate causes of variation suggest a distinct evolutionary history and future for maternal and paternal care.

*Acknowledgments.*—We thank S. Wierick, D. Rudnick, D. Chatterjea, M. Palmer, and N. Wheelwright for assistance in the field; and A. Freeman-Gallant,

A. Bohonak, K. Lessells, and two anonymous reviewers for helpful comments on the manuscript. This work was supported by Sigma Xi, the Frank M. Chapman Memorial Fund, the American Ornithologists' Union, and NSF. This is contribution number 141 from the Bowdoin Scientific Station.

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Received 13 July 1998, accepted 10 February 1999.  
Associate Editor: J. Ekman

*The Auk* 116(4):1136–1141, 1999

### Relationships Among Dominance, Foraging Proficiency, and Condition in Juvenile Dark-eyed Juncos

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Social dominance among flocking birds is well documented, and status within a group often varies with age, body size, sex, and prior residence (Piper 1997). The evolutionary significance of dominance relationships has been demonstrated in studies where dominant birds are either more likely to survive or less likely to disperse (Piper 1997). Although numerous studies of dominance in birds have been conducted with adults or with mixed flocks of adults and juveniles, few studies have focused on juveniles

(Arcese and Smith 1985, DeLaet 1985, Piper 1995). Dominance status during the juvenile stage may have important ramifications. For example, the ability of adult White-throated Sparrows (*Zonotrichia albicollis*) to dominate other adults may be determined during a crucial period in the juvenile stage (Piper 1995). Arcese and Smith (1985) found that dominant juvenile Song Sparrows (*Melospiza melodia*) had higher overwinter survivorship and an increased likelihood of becoming breeders the following spring, suggesting a potentially critical role for dominance interactions during the juvenile period.

High dominance status could mediate first-year survivorship in several ways. Dominant individuals may experience enhanced foraging success if they have greater access to preferred foraging areas and prey items or can exploit food resources located by subordinate flock members (Piper 1997). These in-

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