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Male Savannah Sparrows Provide Less Parental Care with Increasing Paternity Loss

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Abstract - Male parental care can significantly affect fledging success and, therefore, is a strong target of both natural and sexual selection. However, for songbird species that exhibit extra-pair paternity, males may reduce parental care based on how much paternity they have lost in a brood. We studied *Passerculus sandwichensis* (Savannah Sparrow) male parental care relative to the proportion of extra-pair young in the nest, to see if males adjusted care in response to increasing loss of paternity. Males brought less food (mass) with increasing rates of extra-pair paternity, although male provisioning did not influence fledging success. These results contrast with a previously published study of an island population of this species, where males provided more parental care with increased loss of paternity. We hypothesize that high rates of annual survival in this mainland population, where males have a greater potential for reproduction in future years, may explain this difference in behavior.

Introduction

Male parental care can significantly affect fledging success and may include activities such as nest construction, incubation, nest and territory defense, and offspring care. However, there is a conflict between the sexes with respect to the extent of parental care and overall fitness; each sex would like the other to do most of the work (Houston et al. 2005) because parental care can be costly in terms of survival (Williams 1966). Male parental care may be especially costly if it is provided for unrelated young (Trivers 1972). As a result of this conflict, male parental care is a target of sexual and natural selection (Trivers 1972). Both direct and indirect benefits of male parental care influence the strength of sexual selection, particularly in species with high levels of extra-pair paternity (EPP) (Møller and Thornhill 1998).

The responses of males to paternity loss may vary with social or environmental contexts (Westneat and Sherman 1993, Whittingham and Lifjeld 1995, Whittingham et al. 1992). Studies to date have provided mixed results concerning the effect of lost paternity on male parental care, with increasing EPP rates resulting in a reduction in male parental care in some species (Briskie et al. 1998, Hoi-Leitner et al. 1999, Møller 2000, Mulder et al. 1994, Seki et al. 2007, Wagner et al. 1996), no effect on parental care in other species (Garcia-Vigón et al. 2009, Peterson et al. 2001, Westneat et al. 1995, Whittingham and Lifjeld 1995), and both increased and decreased provisioning rates depending

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on mating status in still other species (Whittingham and Dunn 1998). Males may also provision nestlings at higher rates when they lose paternity in an attempt to increase their paternity in subsequent broods (Burke et al. 1989, Dixon et al. 1994, Freeman-Gallant 1997). Further, males may provision more if their care influences overall fledging success, thereby increasing their overall fitness (assuming some level of paternity in the brood). Increased male care can give females the ability to increase fitness through investing more energy into the nest and re-nesting sooner (Eliassen and Kokko 2008). Alternatively, although providing parental care can increase their fitness, males may also increase fitness by investing greater energy in mating with additional females and focusing on self-maintenance (Arnold and Owens 2002, Cezilly and Nager 1995, Mauck et al. 1999).

To date, there appears to be no consistent pattern explaining how male birds respond to cuckoldry. This lack of consistency suggests that ecological conditions (e.g., breeding synchrony, nest density, and survival rate) may influence male parental effort (reviewed in Griffith et al. 2002). However, to our knowledge, *Emberiza schoeniclus* L. (Reed Bunting) is the only species that has been studied (with respect to male parental care response to cuckoldry) in multiple habitats across its geographical range. In response to paternity loss, male Reed Buntings can adjust parental care (incubation and nestling provisioning) in subsequent broods (Dixon et al. 1994), but are also known to not adjust parental care (Bouwman et al. 2005).

Passerculus sandwichensis Gmelin (Savannah Sparrow) is an obligate grassland songbird that breeds in diverse grassland habitats across northern North America and show strong behavioral plasticity across their range (Wheelwright and Rising 2008). This multi-brooded species exhibits biparental care, with variable male feeding rates (Freeman-Gallant 1997, Wheelwright et al. 1992, Zalik and Strong 2008), and has a mixed mating strategy (monogamy and polygyny) that includes high rates of EPP (Freeman-Gallant 1998, Perlut et al. 2008a). On Kent Island, NB, Canada, male Savannah Sparrows provided more parental care with increased loss of paternity (Freeman-Gallant 1997). However, the ecology and evolutionary processes of this island population likely differ from mainland populations (e.g., vegetation composition, land-use history, weather, and breeding density), particularly with populations breeding in agricultural habitats (Perlut et al. 2008a).

Given the potential for regional differences in behavior and the paucity of studies exploring EPP and male provisioning behavior across ecological boundaries, we examined how provisioning rates of male Savannah Sparrows varied in response to paternity loss. We explored this behavior in a mainland population breeding in agricultural fields. Due to hay-harvest, this Savannah Sparrow population is under strong ecological and evolutionary pressures. Because this population shows high annual survival rates (Perlut et al. 2008b), we hypothesized that males would lower parental care with increasing rates of EPP, thus providing more time to invest in self-maintenance for future breeding opportunities. Survival rates may influence how males respond to paternity loss; when male annual survival is greater than 70%, as in our study population, they should be less tolerant of paternity loss (Mauck et al. 1999).

Methods

Savannah Sparrows are ground-nesting, grassland obligate songbirds with a breeding distribution extending from the Atlantic to the Pacific oceans (Wheelwright and Rising 2008). In 2004 and 2005, we studied Savannah Sparrows breeding in two hayfields (17.6–18.5 ha) in Vermont's Champlain Valley, which includes 146,000 ha of managed grassland (NASS 2009). One hayfield was mowed in late May or early June and again in mid-July, and the second field was mowed in early August. The two fields were 1.5 km apart, and no breeding adults moved between fields within or between years. To minimize any potential influence of mowing, we focused our study on first broods (before fields were mowed).

Beginning in mid-May of each year, we located nests through behavioral observations. If not already banded, sparrows were captured with mist nets and uniquely banded with 3 color bands and one US Geological Survey band. We also took a small (20–60 μL) sample of blood; for birds that were banded previous to this study, we used stored blood from the original capture. Because only females incubate, female association was identified by flushing incubating birds off nests. Male association was identified by provisioning and territory defense behavior (Wheelwright and Rising 2008) as well as analysis of video recordings (see below). We visited nests every one to two days to assess their status until either fledging or nest failure. We used multiple criteria to determine if young fledged: if they were present in the nest between day 8–10 and not present at the subsequent nest check, if feces were found in the empty nest, and/or if adults were seen nearby carrying food. Blood samples were taken from all nestlings in each brood on day 6–7. Blood was put in a solution following Seutin et al. (1991), and stored in a freezer or placed on a Watman disc filter paper, allowed to dry, stored in plastic zip-loc bags with silica desiccation beads, and kept in a freezer until extraction.

We only videotaped nests where males were observed to actively defend their territory and mate guard (to be assured that the male had not deserted the nest). We videotaped nests when nestlings were 4 to 7 days old (the peak of food demand for this species; Bedard and Meunier 1983, Freeman-Gallant 1998) using either an 8-mm camcorder (Sony TRV-460 Digital8) mounted on a tripod (2004) or a small, wide-angle lens (www.helmetcamera.com) placed 20 to 30 cm from the nest (2005). The lens was connected by cable to the Sony camcorder placed 2 m from the nest and concealed by vegetation. Nests were recorded once for 1.5 hr in the morning, beginning between 0710 and 0936. We excluded the first 15 min of each tape to allow the birds to become acclimated to the camera's presence. One observer (N.J. Zalik) quantified the number of feeding trips during each recording session and converted this data to an hourly rate. We identified males and females by the combination of their colored leg bands. Prey size was estimated by one person (N.J. Zalik) comparing the size of the prey with the exposed portion of the adult's bill (11.2 mm) as a reference and pooling prey into categories in multiples of 11.2 mm. The mass of each prey item was estimated using length-mass regression equations developed from invertebrates collected at our field sites based on mid-points of each length category (i.e., 5.6 mm, 16.8 mm, 28 mm; Zalik and Strong 2008).

All molecular and paternity analysis followed Perlut et al. (2008a). We used four hypervariable microsatellite loci (Table 1) to assess parentage: *Psa*12, *Passerculus sandwichensis* (Freeman-Gallant et al. 2005); *Escu*6, *Emberiza schoeniclus* (Hanotte et al. 1994); *Mme*1 and *Mme*8, *Melospiza melodia* Wilson (Song Sparrow; Jeffery et al. 2001). We assigned paternity by hand. All offspring matched their mothers and fathers at all four loci. Extra-pair males were identified only if they matched all non-maternal alleles at all four loci. Our population showed high allele diversity (Table 1), providing confidence in paternity assignment, with a 0.91547 probability of exclusion.

With SAS 9.2 (SAS Institute, Cary, NC), we used analysis of variance to test the relationship between feeding behavior and the percentage of extra-pair young in broods. Three variables described parental care by males: mass of food (mg) delivered per nestling per hour, average load size (average mass of prey delivered per visit), and number of feeding trips per hour. We controlled for the number of nestlings in a brood by dividing the food mass, load size, or number of trips by the number of nestlings. These models included day (age of nestling) and year as a fixed effect to control for differences in parental care relative to nestling age. We used analysis of variance to test the relationship between male parental care and fledging success (defined as the number of successfully fledged offspring). All analyses are from first broods only (except one analysis comparing EPP in a males' first and second brood with the same female). We controlled for multiple comparisons of individual females because two females were sampled in both years. Values are presented as means ± 1 SD. We used Cook's distance to test if outliers had an unusually strong effect on our sample.

Results

We obtained video and paternity data for 13 nests; nine nests (69%) had at least one extra-pair young, and 47% of all offspring were extra-pair. The average

Table 1. Number of alleles (N_a), observed heterozygosity (H_o), expected heterozygosity (H_e) for 148 breeding adults (53 female, 95 male) Savannah Sparrows in the Champlain Valley, VT. *Escu*6 = *Emberiza schoeniclus* (Hanotte et al. 1994); *Mme*1 and *Mme*8 = *Melospiza melodia* (Jeffery et al. 2001); *Psa*12 = *Passerculus sandwichensis* (Freeman-Gallant et al. 2005).

Locus	N_a	H_o	H_e
*Escu*6	19	0.865	0.923
*Mme*1	38	0.748	0.943
*Mme*8	22	0.859	0.909
*Psa*12	10	0.709	0.754

number of extra-pair young per nest was 1.5 ± 1.3. Brood size (3.2 ± 0.73; range = 2–5) and nestling age at time of videotaping (5.8 ± 0.9 days; range = 4–7 days) were generally consistent across the sample.

Males brought less food (mass) per hour with increasing numbers of extra-pair young in their nests ($F_{2,12} = 6.1$, $P = 0.02$; Fig. 1, see Table 2 for mass rate). Females also brought less food (mass) with increasing rates of EPP ($F_{2,12} = 3.86$, $P = 0.05$). Additionally, male average load size was lower with increasing rates of EPP ($F_{2,12} = 6.6$, $P = 0.01$; Fig. 1). Female load size was also lower with increasing rates of EPP ($F_{2,12} = 5.29$, $P = 0.02$). However, male feeding rates did not change with EPP (range = 0–6 trips per hr; $F_{2,12} = 1.8$, $P = 0.10$). EPP did not affect how often females visited nests ($F_{2,12} = 3.1$, $P = 0.08$).

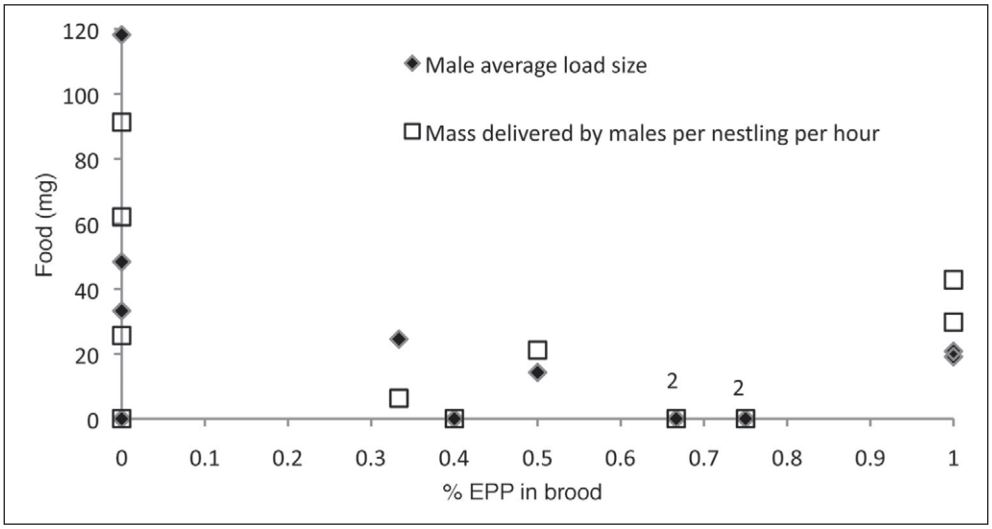

Figure 1. Male Savannah Sparrows in the Champlain Valley, VT, brought less food, both in terms of the overall load and food mass per nestling, to broods where they lost more paternity ($n = 13$ nests). Only 11 data points are shown here because two nests had equivalent values. Cook's distance analysis showed that no single nest caused unusual skew to the data.

Table 2. Load size (mg), feeding rate (trips per hour), and prey mass delivery rate (mg) for 13 Savannah Sparrow nests in the Champlain Valley of Vermont (mean ± SD). EPP represents nests that had at least one extra-pair young. No EPP represents nests that had no extra-pair young.

	Overall	EPP	No EPP
Load size			
Male	21.43 ± 32.99	8.75 ± 10.70	49.94 ± 49.81
Female	27.93 ± 23.01	21.40 ± 13.05	42.62 ± 35.33
Feeding rate			
Male	0.63 ± 0.74	0.60 ± 0.85	0.71 ± 0.53
Female	1.41 ± 1.02	1.39 ± 0.99	1.48 ± 1.23
Mass rate			
Male	21.48 ± 28.96	11.13 ± 16.19	44.77 ± 40.13
Female	54.54 ± 73.73	36.58 ± 27.61	94.97 ± 128.70

Broods with more extra-pair young tended to fledge more young than broods with fewer extra-pair young ($F_{2,12} = 6.7$, $P = 0.03$). Male provisioning (mass) did not affect fledging rates ($F_{2,12} = 0.02$, $P = 0.89$). Cook's distance analysis showed that no single nest caused unusual skew to the data.

Discussion

We found that male Savannah Sparrows delivered less prey mass with increasing rates of paternity loss. Although males that lost more paternity fed less, this lower parental care apparently had little effect on fledging success; nests with more EPP fledged more young. These results contrast to those of an island population of this species, where males provided more parental care with increasing rates of extra-pair paternity (Freeman-Gallant 1997). In both populations, male care may have had little influence on fledging success. While we did find a significant effect of mass and load size, as has been observed with other studies, male feeding rates were not affected by EPP.

Our results suggest that pressures affecting parental care may vary regionally. Although mainland vs. island is the most obvious difference between our study site and Kent Island, abiotic factors, ecological conditions (synchrony, density, food, land use), and the sampling period and study design may also influence differences in results. However, differences between the populations' demographic rates may influence the observed difference in behavior and should be underscored. On Kent Island, male return rates are highly variable (37–73%; Wheelwright et al. 1992), and poor-quality males (low reproductive success) have low survival rates (C.R. Freeman-Gallant, Skidmore College, Saratoga Springs, NY, pers. comm.); a male may therefore make the best of a bad situation by caring for his low paternity brood rather than investing in further mating efforts. There is support for survival rates as being strongly influential on how males respond to paternity loss; when male annual survival is greater than 70%, they should be less tolerant of paternity loss (Mauck et al. 1999). In the Vermont population, male apparent survival is extremely high in hayfields (73–85%; Perlut et al. 2008b). In deciding to lessen their nestling-provisioning efforts, males may choose to either a) prospect for EPP opportunities with secondary females, or b) invest in self-maintenance to increase survival for future mating opportunities. If males indeed decided to invest in their own survival rather than nestling care, then this case is a rare example for migratory passerines that do not establish lasting pair bonds. Moreover, high survival rates can explain EPP behavior for seabirds (Baiao and Parker 2009, Lifjeld et al. 2005) and some passerines (Taylor et al. 2008), but these species typically have low EPP rates and long-term pair bonds. Therefore, comparisons with species that have high EPP rates and seasonal pair bonds may not be informative.

Others have found that reducing parental care did not affect male survival (Bouwman et al. 2005). Therefore, it is important to consider other factors that may have also influenced our results. For example, because males showed differences in load and not feeding rates, our results may also be affected by prey availability or foraging efficiency. Although there is little resource variation within a given field (Zalik and Strong 2008), territory quality could have also affected our findings. Additionally, both within this (Perlut et al. 2008a) and the Kent Island population (Wheelwright and Rising 2008), the social mating status of a male (monogamous, polygynous) affects the amount of paternity loss (however, Dixon et al. [1994] found no effect of mating status). Finally, males who are cuckolded more frequently may simply be lower quality birds with lower survival and less parental care. Future study, including a larger sample, should explore these factors.

That higher male parental care (via mass) did not lead to increased fledging rates may have implications for the evolution of mate choice by females. This finding is important because Lotem et al. (1999) found that female choice may drive male behavior by rewarding males with increased paternity for preferred behaviors like parental care. Thus in our system, females are unlikely to evaluate and reward males (by increasing paternity in subsequent broods) who bring more food mass because this aspect of male parental care does not increase female fitness. On Kent Island, males base their feeding behavior on the potential to increase or gain paternity in subsequent broods (Freeman-Gallant 1997). Our sample was insufficient to test this hypothesis robustly; however, we found no correlation between a male's paternity in his first brood and his paternity in his second brood. Due to the effects of hay harvest on one of our study sites, we could not evaluate whether male parental care provides advantages to females for renesting or second broods. Overall, our findings suggest that in this population male feeding rates are not targets of selection for Savannah Sparrows, and that the ways in which males may respond to lost paternity may vary across a species' range due to variation in life-history traits and ecological conditions. Because our sample size was relatively small and collected over a two-year period, further study is needed to understand how geographic and habitat variation affects the relationship between paternal care and extra-pair paternity; we encourage others to explore these behaviors across a species' distribution.

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