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Reprinted from THE AUK
Vol. 105, No. 4, October 1988

Nonparental Attendants in a North-temperate Migrant

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Nonparental attendants (NPAs) are recorded in 46 of the 304 (15%) North American passerines (Skutch 1961). With a few well-studied exceptions (e.g. Tree Swallows [*Tachycineta bicolor*; Lombardo 1985], and Barn Swallows [*Hirundo rustica*; Crook and Shields 1987]), accounts are often anecdotal especially for migratory species (Skutch 1961). We observed juvenile and adult NPAs in a migratory population of the Grasshopper Sparrow (*Ammodramus savannarum*), a small emberizine (17 g) that is a common summer resident of North American grasslands.

We observed (1981–1984) Grasshopper Sparrows provisioning 23 nests for a total of 251 h on Arapaho Prairie, a mixed-grass prairie in the Sandhills of Nebraska. We used a spotting scope in a blind 5 m from the nest to note the number of trips, prey type, number of prey, and prey size. We checked nests every 1–2 days and calculated nestling survival probabilities (Mayfield 1975). Grasshopper Sparrows double brood and nestlings fledge at 6–8 days (Kaspari unpubl. data).

When possible, birds were color-banded and sexed in the hand based on brood patch and cloacal protuberance (Pyle et al. 1987). In most cases the males were sexed initially from territorial song and distinguished from females on individual plumage features (lore color, median line, and missing feathers). The tendency for males to sing after visiting the nest allowed us to regularly verify these identifications. Juveniles were distinguished from adults by their streaked breast.

We observed NPAs (defined as birds bringing food to the nest) at 4 of the 23 nests (17.4%). No NPAs were observed in 1981 (2 nests) and 1982 (5 nests). One of six nests in 1983 and three of ten nests in 1984 had NPAs (Table 1). Juvenile NPAs occurred twice early in the breeding season (June); adults from adjacent territories were NPAs later in the season (July). Three of the nests had single NPAs, and two juveniles were observed in a single day at one nest. NPAs made from 9–50% of daily provisioning trips. Parents were tolerant and often facilitated provisioning by stepping out of the nest. At 2 nests a juvenile and adult Grasshopper Sparrow approached the nest without food. These birds were vigorously driven away by both parents. An adult female NPA at 4G14 also brooded young after provisioning the nestlings. This bird lost a nest to predation the previous day. We observed no hostility by NPAs toward parents or young.

Nests did not differ significantly in young fledged with and without NPAs (with NPA: $\bar{x} = 2.50$, s = 2.08; without NPA: $\bar{x} = 3.00$, s = 1.88; Mann-Whitney $U_{4,19} = 45.5$, $P > 0.05$). Total provisioning rates (trips per nestling per minute) did not vary significantly with NPAs (95% confidence intervals) for any of the 5 nestling ages observed. There was no uniform trend across all nesting ages.

We compared prey size, prey type, and prey number per trip between parents and NPAs, splitting each variable into 2 categories (prey size: <2 cm or >2 cm; prey type: acridids or nonacridids; prey number: 1 or >1). Parents and NPAs at all 4 nests tended to return the same distribution of prey types, prey sizes, and load sizes. All 12 comparisons were not significant ($P > 0.05$, using 95% binomial confidence intervals).

NPAs did not affect the frequency of adult female provisioning trips when calculated daily for each nest (with NPAs: $\bar{x} = 59.6\%$, s = 14.26; without NPAs: $\bar{x} = 54.03\%$, s = 20.65; Mann-Whitney $U_{5,4,8} = 0.5099$, $P = 0.4752$). Male parents at nests with NPAs provisioned significantly less frequently (with NPAs: $\bar{x} = 20.11$, s = 11.18; without NPAs: $\bar{x} = 45.97$, s = 20.65; Mann-Whitney $U_{5,4,8} = 11.574$, $P = 0.0007$).

We found no evidence of between-year philopatry in this population. Of 85 Grasshopper Sparrow adults and juveniles banded on Arapaho Prairie from 1982–1984, none was recaptured through 1985. Adult NPAs were unlikely to be related to the parents they assisted. Furthermore, juvenile NPAs occurred too early in the season in the study area to have attended their own parent's nests.

The rarity of NPAs in this population of Grasshopper Sparrows introduces the possibility of Type II statistical error. Hence, we suggest that the NPAs are likely a case of misdirected parental care. Price et al. (1983) came to similar conclusions in 2 *Geospiza* finch populations, where the male NPAs occurred in a year when a high percentage went unmated. Misdirected parental care presumably resulted from highly canalized responses to feeding stimuli (the extra female at 4G14 was an NPA shortly after losing her own nest) and because "Selection against helping may be weakened because of possible maladaptive consequences for parental behavior" (Price et al. 1983: 194).

Crook and Shields (1987) showed a low frequency of NPAs in Barn Swallows, low relatedness between parents and NPAs, and no differences in nest success with respect to NPAs. Both Barn Swallows and Tree

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TABLE 1. Summary of NPA behavior at 4 nests of the Grasshopper Sparrow.

Nest	Nestling ages observed[1]	Min observed	NPA age	Nestling age with NPA[2]	No. NPA trips/ total
3G1	3–7	1,140	Juvenile	7	7/46
4G9	2–3	439	Juvenile	2	2/22[3]
				3	8/34
4G12	3–5	662	Adult	4	3/30
4G14	2–5	1,234	Adult	3	10/20
				4	8/19
				5	10/28

[1] Nestling ages (in days) in which observations were made.
[2] Nestling ages in which NPAs participated.
[3] Two juvenile NPAs, 1 trip each.

Swallows may potentially usurp nest sites (Crook and Shields 1987, Lombardo 1985). Such an explanation does not appear to hold for the Grasshopper Sparrows. Nest sites are abundant on the open prairie (Kaspari unpubl. data) and NPAs, which consist of both adults and juveniles, apparently are not harmful to nestlings. Grasshopper Sparrows also appear to screen nest visitors on the basis of provisioning abilities.

NPAs may decrease parental males' provisioning responsibilities. An alternate explanation is that this "neglect" facilitates the undisturbed approach of the NPAs (see also Price et al. 1983). Lack of philopatry in migratory populations may prevent the evolution of kin-based altruism among adults. Similarly, high juvenile mortality in the Grasshopper Sparrow (eggs have only a 0.38 probability of producing a fledgling; Kaspari unpubl. data) reduces the likelihood of juvenile help by reducing the pool of kin available to help with the second brood.

NPAs appear to be fairly common among bird populations, but occur at low frequency within populations. Such behavior may be a precursor to both altruistic associations (i.e. "helping"; Woolfenden and Fitzpatrick 1984) and exploitative interactions (e.g. intraspecific brood parasitism; Brown 1984). We encourage the documentation of NPAs at nests of other migratory birds. Collectively, such long-term studies should increase our understanding of intraspecific interactions in the breeding season.

We appreciate discussions with many of the faculty and graduate students at the University of Arizona. We gratefully acknowledge the support of A. Joern, J. Janovy Jr., the Cedar Point Biology Station, The Nature Conservancy, and grants from the School of Biological Sciences of the University of Nebraska.

LITERATURE CITED

BROWN, C. R. 1984. Laying eggs in a neighbor's nest: benefits and costs of colonial nesting in swallows. Science 224: 518–519.

CROOK, J. R., & SHIELDS, W. M. 1987. Non-parental nest attendance in the Barn Swallow (*Hirundo rustica*): helping or harassment? Anim. Behav. 35: 991–1001.

LOMBARDO, M. P. 1985. Mutual restraint in Tree Swallows: a test of the TIT FOR TAT model of reciprocity. Science 227: 1363–1365.

MAYFIELD, H. F. 1975. Suggestions for calculating nesting success. Wilson Bull. 87: 456–466.

PRICE, T., S. MILLINGTON, & P. GRANT. 1983. Helping at the nest in Darwin's finches as misdirected parental care. Auk 100: 192–194.

PYLE, P., S. N. G. HOWELL, R. P. YUNICK, & D. F. DESANTE. 1987. Identification guide to the North American passerines. Bolinas, California, Slate Creek Press.

SKUTCH, A. F. 1961. Helpers among birds. Condor 63: 198–226.

WOOLFENDEN, G. E., & J. W. FITZPATRICK. 1984. The Florida Scrub Jay: demography of a cooperatively breeding bird. Princeton, New Jersey, Princeton Univ. Press.