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Simultaneous Incubation By Two Females And Nestling Provisioning By Four Adults At A Savannah Sparrow Nest

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Simultaneous Incubation by Two Females and Nestling Provisioning by Four Adults at a Savannah Sparrow Nest

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ABSTRACT.—We present the first observations of misdirected parental care by Savannah Sparrows (*Passerculus sandwichensis*) including a rare occurrence of simultaneous incubation. Two females simultaneously incubated eggs, brooded, and fed nestlings, and two males fed nestlings in one nest. These behaviors may have been prompted by strong parental instincts in combination with a stressful breeding environment mediated by hayfield management, as any genetic benefits were unlikely. *Received 1 September 2007. Accepted 24 October 2007.*

Cooperative breeding, in which care for young is provided by individuals other than the breeding pair, is estimated to occur in only 9% of avian species (Cockburn 2006). Cooperative breeding is thought to evolve when the additional help allows for greater production of young or increased survival of adults through reduced breeding effort (Brown 1978, Crick 1992). Helpers may receive resource benefits from being a member of a group or may enhance future breeding opportunities. Furthermore, helpers that are closely related to the breeders they assist gain indirect genetic benefits from raising kin (Hamilton 1963, 1964). Alternatively, Jamieson (1986, 1991) hypothesized that helping is a behavioral response to the presence of begging young. This ''misdirected parental care'' (Price et al. 1983: 192) may explain rare cases of feeding or incubation by individuals which do not appear to receive resource or genetic benefits.

Avian incubation is usually performed by only one individual at any given time regardless of the parental care system. Incubation and brooding by more than one bird simultaneously has rarely been documented for temperate species (Forbush 1929, Howell 1942, Bellrose 1943, Hawksley and McCormack 1951, Brackbill 1952, Fuller and Bolen 1963). We present observations of misdirected parental care by the Savannah Sparrow (*Passerculus sandwichensis*), a ground-nesting songbird with a mixed-mating strategy and biparental care (Wheelwright and Rising 1993). We describe simultaneous incubation, brooding, and provisioning of young by two females, and provisioning young by two males.

METHODS

We captured and uniquely banded (U.S. Geological Survey [USGS] metal band and three colored leg bands) all breeding adult Savannah Sparrows in 2002–2007 on a 10.5-ha managed hayfield (44° 39′ N, 73° 27′ W) in Shelburne, Vermont, USA. We located Savannah Sparrow nests (n = 515) and monitored them every 1–3 days until they fledged or failed, and banded nestlings (USGS band only) on post-hatch day 6–7 (Perlut et al. 2006).

OBSERVATIONS

On 12 July 2007 we found a nest containing four eggs being incubated by a female Savannah Sparrow with two orange bands on the left leg and a yellow and metal band on the right leg (hereafter referred to as the primary female). On the same day, we discovered another nest containing four eggs being incubated by a female with metal and blue bands on the left leg and orange and red bands on the right leg (hereafter referred to as the secondary female). These nests, 73 m apart, were on adjacent territories. Both females were still incubating four eggs on 13 July. By 16 July, the secondary female's nest had failed, while the primary female was still incubating four eggs. On 17 July, two birds flushed ~0.5 m from each other from the area of the primary female's nest. One of these birds was identi-

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fied as the secondary female. The secondary female's nest had recently failed and no further attempts to follow this bird were made as it was too soon for her to have renested. On 20 July, two birds flushed directly from the primary female's nest. The rim of the nest was flattened on one side, making the nest cup atypically wide. Within minutes, both primary and secondary females returned to the nest. We flushed the birds two more times to reconfirm these observations, flushing from within 1 m of each other and directly from the nest together. We searched the area extensively for a second nest, but none was located.

On 20 July, at 1000 hrs EDT the nest had four eggs, one of which appeared damaged with a small indentation. We videotaped the nest using a small ($9 \times 3 \times 3$ cm) wide angle lens at 1325 hrs, at which time the nest contained one nestling and three unhatched eggs. We made two recordings, one of 30 min and one of 17 min; both females were observed incubating simultaneously as well as singly. They sat together on the nest for 11 min during one period with the primary female in a normal incubating posture and the secondary female sitting partially on the back of the primary female and partially on the rim of the nest. Both birds were facing roughly the same direction. This simultaneous incubation ended when we approached the nest to remove the camera. On six occasions a bird forced itself underneath the other already incubating bird to begin incubating the nest itself. During one 22-sec period, this forceful exchange occurred three times.

We recorded (4.5 hrs) the nestling stage at post-hatch 4–5 days. Additional aggressive behavior between the two females beyond the forceful incubation exchanges occurred. When a female was on the nest and the other female approached, it would often do so with one or both wings raised and give aggressive squealing and chattering calls. During one interaction, while the primary female was brooding, the secondary female arrived at the nest with both wings raised and made a squealing vocalization. The two birds faced each other with bills agape for 1 min as the primary female remained on the nest. The interaction ended when the primary female pecked at the secondary female, causing the secondary female to retreat. These vocalizations and displays were notably different from those observed when one female and one male interacted at the nest. Despite these aggressive interactions, the primary female tolerated the secondary female, as evidenced by simultaneous incubation, brooding, and provisioning of young.

Two of the four eggs hatched and the two damaged or infertile eggs were removed by 23 July. Both females continued to brood and provision the nestlings. Two males also were observed provisioning nestlings. The male which frequently brought food was the social male associated with the primary female's two previous nesting attempts. The second male was the social male associated with the secondary female's previous nesting attempts. This second male visited the nest and fed nestlings only once during the recordings. The nestlings fledged on 29 July.

DISCUSSION

Our observations represent the first documented case of misdirected parental care occurring naturally at a Savannah Sparrow nest. Weatherhead and Robertson (1978, 1980) describe a case of helping induced artificially and a second case where clutches were laid simultaneously by two females in the same nest. Why did the secondary female (and her mate) help at the nest rather than initiate another nesting attempt? We have no reason to suspect intraspecific brood parasitism, as both females had active nests simultaneously, and the number of eggs in the primary female's nest remained at four throughout the incubation period. Paternity assignment of 109 broods in a related study revealed no evidence of egg dumping (N. G. Perlut, unpubl. data); Savannah Sparrows on Kent Island, New Brunswick show no evidence of egg dumping (C. R. Freeman-Gallant, pers. comm.). We do not know whether the two birds were related, as both were first banded as adults on 15 May 2007. It seems improbable the secondary female had any direct genetic investment in the nest despite this uncertainty.

We suspect the secondary female discovered the primary female's nest while foraging and her maternal instinct was to incubate the eggs. Females likely monitor the breeding status of their neighbors, as the field is densely populated (2 females/ha in 2007) and individuals commonly interact. Other females at this site initiated renests around the date the nest of the secondary

female failed; some females have laid up to six clutches in a year, fledging as late as 24 August. Thus, there were sufficient resources and time with which to renest. The sight of eggs in a nest may have stimulated hormones that led to an incubation response. This effect was perhaps similar to the response of adults to nestlings of brood parasites, in which parental instincts and mistaken identity cause a maladaptive response to feed nestlings (Price et al. 1983). Similarly, the secondary male likely provisioned young simply because his mate was caring for the nest.

Stress, mediated by the effects of hayfield management, likely contributed to this unusual behavior. The secondary female had attempted three previous nests. The field was cut twice during the nesting season, each cutting followed by manure application; all active nests failed as a result of haying. These sources of nest failure, in addition to failure from natural causes, may have placed these birds under high stress. It is possible these factors contributed to the secondary female's ''decision'' to attend this nest rather than initiate another clutch.

The secondary female and her mate assisted in incubation and in provisioning nestlings. However, whether these birds helped rather than hindered development of the young is debatable. For instance, only two young reached the fledgling stage, whereas the average number of fledged young from successful post-second harvest nests was 3.0 (n = 10) in 2007. Of the two young that survived, one nestling's leg was splayed to the side. This could have been a genetic defect, but was more likely an injury sustained in the nest, possibly during an interaction between the two females.

Our observations of simultaneous incubation and provisioning of young by Savannah Sparrows are highly unusual and may have been prompted by misguided parental instincts in combination with a stressful breeding environment.

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