An Apparent Case of Between-Brood Sibling Competition in Chestnut-collared Longspurs, *Calcarius ornatus*

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I report observations consistent with the interpretation that a Chestnut-collared Longspur (*Calcarius ornatus*) fledgling from a first brood begged for and received food from its parents at a their second brood nest. All five nestlings in the second brood subsequently died and starvation appeared to be the major factor contributing to their deaths. This is the first reported case of apparent between-brood sibling competition in a passerine species and it fits the criteria of a parent-offspring conflict.

Key Words: Chestnut-collared Longspur, *Calcarius ornatus*, sibling competition, parent-offspring conflict, multiple broods.

Within-brood sibling competition is common among birds. Death of younger or smaller offspring often is attributed to larger or older siblings through competition for food, trampling, ejection of siblings from the nest, or overt aggressive attacks (reviewed by Mock et al. 1990). Debate persists as to whether sibling competition represents the phenotypic expression of an underlying genetically based, parent-offspring conflict (Trivers 1974), or whether the outcome of such competition is in keeping with the brood-reduction strategies of parents (Drummond 1993; Forbes 1993). Siblings compete with one another for food by begging, which involves vocalizing, jockeying for position within the nest, gaping, and stretching their necks towards the parents. Mock and Forbes (1992) suggested that, in order to demonstrate that nestling begging is a manifestation of parent-offspring conflict, it must be shown that begging induces parents to invest in offspring at levels detrimental to their own fitness. Here, I report the first observation of apparent between-brood sibling competition in a passerine species that appears to fit those criteria.

Chestnut-collared Longspurs (*Calcarius ornatus*) are small (20 g) grassland passerines that breed in the native short- and mixed-grass prairie regions of North America. Longspurs nest from the end of April to the beginning of August and typically raise two broods within the same breeding season (Hill and Gould *in press*). Females build a new nest for each clutch, and the broods overlap such that fledglings from first broods are still dependent on their parents for food when second clutches are initiated (Fairfield 1968). The male provides the majority of fledgling care while the female prepares for the second clutch (Harris 1944; Hill and Gould *in press*). Pair-bonds persist throughout the breeding season (Harris 1944; Hill and Gould *in press*), and young remain on their natal territory well past independence (Hill and Gould *in press*).

Individually colour-banded longspurs were observed within a 600 m × 700 m grid located in the Remount Community Pasture near Bindloss, Alberta (50° 40′ N, 110° 10′ W). I found nests by dragging a 30-m rope over the pasture to flush incubating females and by observing female longspur behaviour. Once located, nests were visited daily until the young left the nest or the nest failed. Young were weighed, measured, and banded with a unique combination of three plastic coloured leg bands and a numbered aluminium U.S. Fish and Wildlife band. As part of a larger study examining parental care, hour-long focal nest observations were conducted on nestling day 6 (from day 1 = hatch day).

On 1 May 1994, a banded female initiated her first clutch, which contained four eggs. Three of the eggs hatched 16 May and the fourth 18 May. Young were banded 23 May when the largest nestling had a wing length of 33 mm (siblings' measurements ranged from 30 to 32 mm) and a mass of 13 g (siblings' masses were 12 g, 13 g, and 13 g). On 26 May, all four young left the nest. On 3 June, the female initiated her second clutch, which ultimately contained five eggs. Her banded mate was observed feeding two of the first-brood fledglings on 11 June while the female was incubating the second clutch. At that time, both fledglings were observed pecking at the ground and one, the largest at banding, successfully caught an insect.

Four eggs from the second clutch hatched on 18 June and the fifth hatched 19 June. By that time there was no evidence that the male was still feeding the first-brood fledglings. Typically, offspring are fed for up to 14 days after leaving the nest (Harris 1944). The longest I have observed a male feeding a fledgling is 22 days after leaving the nest, while his mate was incubating the second brood (unpublished data). In three years of study, I have never observed

longspur parents feeding first-brood young up to the time their second brood hatched (N = 35 second broods), although they still uttered alarm calls when fledglings were approached by humans. Furthermore, parents often responded aggressively to begging fledglings once young were present in the second-brood nest (personal observation).

A focal nest observation conducted at the second-brood nest on 23 June was unusual for two reasons. First, loud begging vocalizations were heard from the vicinity of the nest, which is atypical because, although Chestnut-collared Longspur fledglings often beg loudly, day 6 nestlings are generally inaudible from the 20-40 m distances from which nest observations were conducted. Secondly, the combined hourly number of feeding trips made by the parents during that observation was much higher than the average: 21 compared to a mean of 11.6 (± 4.5 SD; N = 52 focal nest observations). At the end of the observation period, the nest was approached and one of the first-brood fledglings, the largest from the first brood, flushed from beside the nest. The following day, the second brood young were banded. Their masses were typical for day 7 nestlings (7-13 g) and no external parasites were found on any of the young. The smallest nestling (7 g) was found dead in the nest 25 June and the next smallest (10 g) died 26 June. These two deaths were not completely unexpected given that those nestlings were the smallest two in the brood and brood reduction is fairly common in this species (personal observation). There is no indication that brood reduction is more common in second than in first broods, and brood size on day 6 was similar in first and second broods (unpublished data). However, on 29 June, 11 days after hatching, when most Chestnut-collared Longspur young leave the nest (Harris 1944; Fairfield 1968), the remaining three young were found dead.

Bodies of those three nestlings were collected and autopsy revealed that their crops were empty and their gizzards contained only small quantities of grasshopper legs. Because I monitored nests daily, the young could not have been dead more than 24 hours. Masses of the dead young at collection were only 5 g, 5 g, and 4 g, which represents an approximate 60% reduction from their masses attained five days previously at banding on 24 June. Although some of the mass loss probably resulted from desiccation, the autopsies suggest that despite the high number of feeding trips made by the parents during the 23 June nest observation, the young were not fed for several days and subsequently starved. Both parents were observed on the territory up to the day the nestlings were found dead. No evidence of injury was found on any of the young.

The dead nestlings were examined for ectoparasites. The nestling that had the highest parasite load had six *Protocalliphora metallica* (order: Diptera, family: Calliphoridae) blowfly larvae on its wings and back. One other nestling had two of these larvae and the other had none. *Protocalliphora* larvae feed intermittently on nestling blood (Bennett and Whitworth 1991). Cases of these parasites causing nestling death are rare and are usually attributed to a combination of stresses including starvation or dehydration (Gold and Dahlsten 1983). Gold and Dahlsten (1983) found that the blowfly larvae themselves survive better in nests that successfully fledge young and suggested that it would be maladaptive for *Protocalliphora* to kill its nestling hosts. This strongly suggests that parasites alone did not kill these nestlings and that starvation was the principal factor in their deaths. Of 254 nests monitored in three years, this was the only nest at which starvation of an entire brood was observed. Furthermore, the observations made during the focal nest watch suggested that the first-brood fledgling was begging at the second-brood nest and, thus, at least attempting to compete with its second-brood siblings. Assuming that some of the feedings by adults were received by that fledgling, it is likely that this contributed to the deaths of the second brood chicks.

Ricklefs (1966) was among the first to suggest that begging represents competition between siblings, as well as communication between parents and offspring. Trivers (1974) proposed that there is a genetic basis for parent-offspring conflict because parents should value all of their offspring equally whereas each offspring should value itself more than its siblings. Thus, it has been suggested that begging is a phenotypic manifestation of the underlying genetically based, parent-offspring conflict (e.g., Harper 1986). However, parental birds appear to promote brood reduction through incubation regimes that create size and age hierarchies within broods. Therefore, it is unclear whether within-brood sibling competition complements or conflicts with parental fitness (Mock and Forbes 1992; Drummond 1993; Forbes 1993).

In contrast, between-brood sibling competition clearly represents a parent-offspring conflict. I suggest that my observations are consistent with the explanation that the first-brood fledgling, although capable of feeding itself, manipulated its parents to continue feeding it by begging at the second-brood nest and thus "posed" as a nestling. Although this behaviour is rare, it suggests that double-brooded avian species, particularly those with brood-overlap, may prove valuable subjects in unravelling the complexities of begging competition and its relationship to parent-offspring conflict.

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