

GENERAL NOTES

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Distribution of food within broods of Barn Swallows.—The delivery of food by parent birds and its distribution among nestlings of a brood are important determinants of nestling survival. Despite the role of parental distribution of food among nestlings in the process of brood reduction and subsequent evaluations of fitness, direct observations of parent-offspring interactions in the nest are rare (Löhrl 1968, Best 1977, Rydén and Bengtsson 1980, Reed 1981). Field observations have shown that older and larger nestlings are more likely to survive than are their smaller siblings (Howe 1976, O'Connor 1978a, Richter 1982). This could result from parents selectively feeding larger nestlings (Ricklefs 1965, Dawkins 1976) or from the superior competitive abilities of larger nestlings (Löhrl 1968, Richter 1984). Clearly, both processes can operate simultaneously.

If parent birds are capable of preferentially feeding some nestlings, then they must be able to distinguish among the nestlings of their brood. Such perceptual capabilities are in stark contrast to what many species seem to possess; for example, consider the inability of many passerines to distinguish Brown-headed Cowbird (*Molothrus ater*) and other social parasitic nestlings from their own offspring (Rothstein 1982). Beecher and his co-workers (Beecher et al. 1981a, b; Stoddard and Beecher 1983) have shown that in colonial Cliff (*Hirundo pyrrhonota*) and Bank (*Riparia riparia*) swallows, parental recognition of individual young occurs when the young are mobile enough to intermingle. Individually distinctive "signature calls" develop in chicks at about 15 days posthatch. Their observations show that the subtle differences among conspecific nestlings in the nest are unnoticed by parents.

Inter-nestling competition is aggressive in raptors (O'Connor 1978b, Stinson 1979) but relatively passive in passerines (Skutch 1976). Within a passerine brood, larger nestlings can gape higher and command more favorable positions within the nest than their smaller siblings (Löhrl 1968, Rydén and Bengtsson 1980). A size differential among nestlings often results in the early death of the smallest nestlings (Richter 1984); however, the size of a nestling is not always correlated with the proportion of feedings it receives. For instance, Best (1977) in Field Sparrows (*Spizella pusilla*) and Reed (1981) in Song Sparrows (*Melospiza melodia*) determined that the sequence of feedings was essentially random. Rydén and Bengtsson (1980) observed that increased begging rates and movement toward favored nest positions enhanced the feeding rate of small nestlings.

Methods.—The observations we report on here are of the interactions between parental Barn Swallows (*Hirundo rustica*) and nestlings at six nests, three each in 1980 and 1981. The study was conducted in Jefferson County, Kansas, on the Nelson Environmental Studies Area of the University of Kansas, Lawrence. In previous years, Barn Swallows built their nests on the underside of a loft in a barn on the study area. During the fall of 1979, we cut a 7.6-cm diameter hole through the planks above 13 nests that had been active in the past summer, and then filled the hole with a wooden plug.

Nest contents were checked regularly until the appearance of the first egg, after which checks were made daily. On the first hatch day, the wooden plug was replaced with a glass plate. Nestlings were marked for individual recognition by painting nail polish on their crowns; marks were replaced periodically as needed. The nesting pair was given a day to adjust to the plate before observations began on day one posthatch. We observed the birds' behavior through the glass plate over each nest. Upon our arrival at a nest, parent swallows were momentarily agitated, but quickly habituated to our presence. We did not record data until the birds were calm. We recorded the time of each feeding, which nestlings gaped as the parents arrived at the nest, which nestling was fed, and various nestling behavioral

TABLE 1
PROPORTION OF FEEDINGS GIVEN TO EACH NESTLING AS A FUNCTION OF NESTLING RANK

Year	Nest number	Nestling rank						CI*
		1	2	3	4	5	6	
1980	1	0.35 (200) ^b	0.37 (212)	0.27 (154)				(0.29–0.37)
	2	0.29 (91)	0.35 (111)	0.36 (113)				(0.28–0.38)
	3	0.19 (41)	0.11 (24)	0.16 (34)	0.15 (31)	0.17 (36)	0.21 (45)	(0.12–0.22)
1981	4	0.22 (16)	0.30 (22)	0.27 (20)	0.22 (16)			(0.15–0.35)
	5	0.32 (33)	0.33 (34)	0.35 (36)				(0.24–0.42)
	6	0.28 (51)	0.32 (53)	0.20 (37)	0.22 ^c (40)			(0.19–0.31)

* 95% confidence interval around expected random distribution.

^b Number of feedings.

^c House Sparrow nestling.

patterns such as preening and defecation. It was impossible to keep track of nestling gaping at Nest 3 in 1980 because it contained six nestlings.

To test parental recognition of nestlings, a House Sparrow (*Passer domesticus*) nestling was added to Nest 6 in 1981 on day two posthatch. Its weight (4.5 g) was equal to that of the lightest Barn Swallow nestling. Two other House Sparrow nestlings were added to two other Barn Swallow nests (not monitored as part of the main study) in 1981 on day nine posthatch and the reaction of the adult and nestling swallows to the intruders noted.

Quantitative data reported here are based on 1450 feedings of the nestlings at the six nests. Nestlings were weighed to the nearest 0.5 g with a 25-g Pesola scale every second or third day beginning within one day of hatch (except Nest 3 where nestlings were first weighed on day four). Weighings were discontinued after day 12–15, as nestlings approached fledging, to avoid causing premature departure from the nest. Weights on other days were estimated by linear extrapolation between known weights; we assumed a constant age-specific growth rate between consecutive weighing days. This approach has been used by Crossner (1977) to estimate parameters of logistic growth curves. For our purposes, we needed only to be able to rank the nestlings by weight. Nest 1 had the greatest weight difference between highest and lowest ranked nestlings (5 g on day three, increasing to a maximum of 10 g on day seven, but reduced to 1 g on day 17). By comparison, the other five nests showed maximum weight differentials of 3.0, 7.5, 2.5, 4.5, and 5.0 g, respectively.

Results.—Our main interest was in determining whether the rank of a nestling (where nestlings were ranked by weight) influenced the nestling's probability of receiving food from parents. To that end we addressed the following questions:

(1) Did all nestling ranks receive an equal proportion of the feedings? Because a nestling's rank sometimes changed during the nestling period, the data for a particular rank included

TABLE 2
CORRELATIONS BETWEEN BARN SWALLOW BROOD AGE AND PROPORTION OF DAILY FEEDINGS GIVEN TO NESTLINGS OF HIGHEST AND LOWEST RANK

Year	Nest number	Nestling rank	
		Highest	Lowest
1980	1	-0.85 ^a (12) ^b	0.70 ^a (12)
	2	0.07 (10)	-0.19 (10)
	3	0.07 (8)	-0.33 (8)
1981	4	-0.76 ^c (7)	0.14 (7)
	5	-0.30 (11)	0.63 ^c (11)
	6	0.16 (9)	-0.09 (9)

^a Spearman rank correlation coefficient is significantly different from 0.0 at $P < 0.01$.

^b Number of days observed.

^c Spearman rank correlation coefficient is significantly different from 0.0 at $P < 0.05$.

observations from several nestlings. We compared the proportion of total feedings given to each nestling rank against the null hypothesis of an equal distribution to each rank using a *t*-test for proportions (Walpole and Myers 1978). Only for Nest 1 did any of the proportions exceed the approximate 95% confidence interval around the expected random distribution of feedings to all nestling ranks (Table 1). Hence, based solely on total feedings, high rank does not seem to confer an advantage to nestlings.

(2) Does the potential value of high rank change with nestling age? Due to asynchronous hatching, the within-brood coefficient of variation of nestling weight can be high, but it drops for surviving broods as weights of nestlings converge near fledging. Hence, the relative weight difference between the highest and lowest ranked nestlings in a brood usually decreases as nestlings age. To determine whether the significance of high or low rank to feeding probabilities changed with nestling age, we looked at the correlation between nestling age and the proportion of total daily feedings received for the nestlings of highest and lowest rank in each brood. Again at only one nest, Nest 1, does the importance of rank clearly change with age (Table 2). Here, the highest ranked nestling received a high proportion of the feedings at an early age with the lowest ranked receiving progressively more as the brood aged. Similar trends occurred in nests 4 and 5 in 1981.

(3) A nestling has to gape to be fed, but a gape does not guarantee a feeding. Does rank confer an advantage such that a nestling of high rank will be fed a greater proportion of times following a gape than one of low rank? Using ANOVA, we compared the average conditional probability of a nestling being fed given that it gaped (total number of feedings/total number of gapes) among groups of nestlings ranked by weight. To keep the ANOVA balanced, and in order to include all nests where gapes were recorded, only nestlings ranked one through three were compared. To avoid bias due to absolute feeding rate or food abundance differences, proportions were expressed as deviations from the mean for each brood. Even the highest ranking nestling was passed over from 40 to 52% of the times it gaped for food (Table 3). The ANOVA summary shows that the mean probability of a nestling being fed following a gape is different between ranks (Table 3). The standardized group means are similar for ranks one and two, whereas the mean is lower for nestlings of Rank 3 ($\bar{x}_1 = 0.028$, $\bar{x}_2 = 0.033$, $\bar{x}_3 = -0.06$). Hence, there is some indication that, compared to high-ranked individuals, lower-ranked nestlings were less likely to be fed when they gaped.

TABLE 3
PROBABILITY OF A NESTLING BEING FED FOLLOWING A GAPE

Year	Nest number	Nestling rank*			
		1	2	3	4
1980	1	0.57	0.45	0.32	
	2	0.56	0.56	0.32	
1981	4	0.48	0.59	0.55	0.50
	5	0.60	0.68	0.60	
	6	0.49	0.52	0.37	0.43 ^b

* Difference among ranks 1 to 3 is significant by ANOVA at $P < 0.01$; Mean Square Ranks/Mean Square Error = 0.0379/0.00117 = 32.3 = $F_{2,12}$.

^b House Sparrow nestling.

(4) Can defecation influence feeding probabilities? Even at one day after hatching, each nestling oriented its cloaca toward the outside of the nest prior to defecating. Initially, this facilitated parental removal of the fecal sacs as defecation occurred in the presence of an adult. Later, the nestling defecated over the front of the nest. This turning was very rapid and took place even on top of the other nestlings. Surprisingly, an equally rapid return to a forward-facing position was not observed until nestling day 12. Once oriented to the rear of the nest, the nestlings gradually returned to a forward-facing position, but up to 30 min elapsed before a return was achieved. Whatever the mechanism, the consequence was that, regardless of size, no nestling could maintain an advantageous position in the nest as defecation removed it temporarily from the front of the nest. To determine whether defecation reduced the probability of a nestling being fed, we compared, for each brood, the average probability a nestling would be fed given that it just defecated, to the null hypothesis of a random distribution of feedings. A paired comparison t -test was used to compare the two sets of probabilities. The probability of being fed following defecation was significantly lower than the average probability of a feeding (Table 4).

(5) Are House Sparrow nestlings rejected? All three of the House Sparrow nestlings were fed by their foster parents, despite their different appearance, calls, and gaping behavior. Two reached weights (22.5 g and 29.0 g) consistent with expectations for normally fledged House Sparrows in the Lawrence area (Murphy 1977). On four occasions beginning on day seven at Nest 3 and on day 10 and 14 at one of the unmonitored nests, the House Sparrow nestling was found on the ground below the nest. Both nestlings were fed by their foster parents following replacement in the nest.

Discussion.—Reed (1981) concluded from his study of a single Song Sparrow brood that although feedings were randomly distributed among nestlings, a dominant nestling could receive a higher proportion of the feedings by maintaining a position in the nest near the parents' arrival point. In his study, nestling position shifted in association with feeding bouts, and no nestling was dominant. Our observations showed that the total distribution of food items to nestling Barn Swallows was generally independent of nestling rank. High rank, however, increased the probability that a nestling would be fed, given that it gaped. In Nest 1, the feedings were not randomly distributed among the nestlings, and the difference was most pronounced at young nestling ages (Table 2).

We found, unlike Reed (1981), that the reordering of nestling position following defecation changed the probability that particular nestlings would be fed. Like Reed (1981), we feel

TABLE 4
EFFECT OF DEFECATION ON FEEDING PROBABILITIES

Year	Nest number	Mean probability of being fed	Probability of being fed following defecation ^a
1980	1 (46) ^b	0.33	0.22
	2 (10)	0.33	0.10
	3 (10)	0.17	0.10
1981 ^c	4 (9)	0.25	0.22
	6 (13)	0.25	0.15

^a Average difference between probabilities is significantly different from 0.0, $\bar{d} = 0.128$, $S_d = 0.07$, $t = 4.08$, $df = 4$, $P < 0.05$.

^b Number of observed defecations.

^c No defecations were observed at Nest 5.

that the periodic change of nestling position could result in an even distribution of food to all nestlings in a brood if the nestlings are of about equal weight.

The feeding of the House Sparrow nestlings implies that Barn Swallow parents cannot distinguish their own nestlings from those of a different species. Burt (1977) showed that Barn Swallow parents distinguish their own offspring from other conspecific young only after fledging. Adults behave aggressively toward alien fledglings that are soliciting feedings. There is good evidence that in colonial swallows parental recognition of nestlings does not occur until chicks are mobile enough to leave the nest (Beecher et al. 1981a, b). Stoddard and Beecher (1983) suggest that individual chick facial patterns may facilitate recognition in the Cliff Swallow. As our nestlings were individually marked for our recognition, they might have appeared distinctive to their parents. Our observations ended prior to fledging, however, and the distribution of feedings did not suggest any within-nest discrimination by parents.

As parent Barn Swallows cannot distinguish among their nestlings, they are not capable of actively manipulating brood size following hatch. Brood-size changes are likely the result of differing competitive abilities among nestlings. Despite the general acceptance of this concept, studies of nestling feeding have found only a weak relationship between nestling size and proportion of feedings received (Best 1977, Rydén and Bengtsson 1980, Reed 1981). However, larger nestlings tend to receive a higher proportion of first feedings and need to gape less for food (Löhr 1968, Rydén and Bengtsson 1980). In times of food shortage, larger nestlings may force the starvation of their smaller siblings, but this has yet to be demonstrated empirically.

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Species-area relationship of migrants in isolated woodlots in east-central Illinois.—Many species of birds use woodlots temporarily for resting and foraging while on migration (Martin 1980, Graber and Graber 1983), and the loss of forest habitat and its fragmentation into isolated patches may adversely affect these birds (Graber and Graber 1983). Isolated patches of forest may be important particularly to migrants in highly disturbed landscapes where