

## NESTLING FEEDING-SPACE STRATEGY IN ARABIAN BABBLERS

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**ABSTRACT.**—Maintaining individual space is a foraging tactic widely used by many adult animals. However, this behavior has not been described for altricial nestling birds. In this study, nestling Arabian Babblers (*Turdoides squamiceps*) defended individual spaces around themselves and obtained food in relation to the size of these spaces. Each nestling created two circular feeding zones around itself: (1) an internal one (termed exclusive space), within which it usually succeeded in preventing nest mates from obtaining food; and (2) an external one (shared space), within which the nestling competed for food with siblings according to its relative strength. The first indication of the imminent death of a nestling was when siblings began receiving food inside its exclusive feeding space. Stability of feeding spaces was tested by adding a fifth nestling to the nest. None of the exclusive feeding spaces decreased, and feeding rates within them remained constant. In contrast, feeding rates in the shared feeding spaces diminished as a consequence of their reduction in size. It seems that a nestling's survival depends on its ability to defend its exclusive feeding space. This tactic may enable Arabian Babbler nestlings to obtain food and survive in their cooperative as well as competitive nest environment in a relatively nonaggressive manner. Received 22 December 1997, accepted 13 November 1998.

AVIAN BROOD REDUCTION has been the subject of much empirical and theoretical research since the appearance of O'Connor's (1978) seminal paper. So-called altruistic behaviors, as well as selfish ones, were explained through brood reduction using a wide range of theories such as inclusive fitness, the handicap principle, parent-offspring conflict, and honest signaling.

Unlike its theoretical explanations, the mechanisms of brood reduction have attracted less attention. In nonpasserines, sibling aggression is very common and leads to both uneven food distribution and brood reduction (Cash and Evans 1986, Mock et al. 1987, Anderson 1990, Forbes 1991, Drummond 1993, Ploger 1997). In passerines, however, aggressive interactions among nest mates are rare. Although nonaggressive brood reduction has been widely documented (Magrath 1989, Teather 1992, McRae et al. 1993, Kacelnik et al. 1995, Price and Ydenberg 1995, Leonard and Horn 1996, Ostreiher 1997), its mechanisms are still enigmatic. Begging calls (Harper 1986, Smith and Montgomerie 1991), jockeying for a better position (Gottlander 1987, McRae et al. 1993), body postures (Kilner 1995), or a combination of these behaviors (Kacelnik et al. 1995, Kilner 1995) have been considered as the main manifesta-

tions of sibling competition. All of these behaviors, however, seem to be directed toward the feeding adults. In the Blue-footed Booby (*Sula nebouxi*; Drummond and Garcia Chavelas 1989), Great Blue Heron (*Ardea herodias*; Mock 1985, Mock and Parker 1986), Great Egret (*Ardea alba*; Mock 1984, 1985), American Kestrel (*Falco sparverius*; Anderson et al. 1993), Arabian Babbler (*Turdoides squamiceps*; Ostreiher 1997), and others, food distribution among nest mates is determined by the outcomes of nestling interactions. It seems unlikely that in passerines, no direct interactions have been developed among the nest mates during the evolution of nestling competition.

Arabian Babblers are cooperative breeders (Zahavi 1990). The modal clutch size is four, and incubation usually starts after the last egg has been laid such that broods hatch almost synchronously, with only 6 to 34 h passing between hatching of the first and last chicks. Feeding rate is negatively correlated with hatching order, nestlings compete for food, and brood reduction is frequent (Ostreiher 1997). Pecking among the nestlings has never been seen (based on more than 1,100 h of observation from hatching to fledging in 42 nests), but nest mates may struggle by pushing each other. The aim of the current research was to study mechanisms of sibling rivalry used by Arabian Babbler nestlings.

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## METHODS

The study was carried out at the Shezaf Nature Reserve in the Arava Valley and around the Hazeva Field Study Center, about 30 km south of the Dead Sea, in southeastern Israel. These babblers are part of an ongoing study that was started in 1971 (Zahavi 1990). The current study was conducted over the five breeding seasons from 1 February to 1 June, 1992 to 1996.

The study area contained about 35 groups comprising more than 240 individuals. The birds are accustomed to human presence and tolerant of close observations. Each group was observed at least twice a week, and groups that had started nest building were observed daily. Nests were visited every day, and each egg was marked to establish laying order. During the last two days of the 14-day incubation period, nests were checked every hour and were observed continuously from first to last hatching. Each nestling was marked with a colored dot immediately after hatching. A colored collar was fitted to its neck and a colored wire to one leg on day 4 after hatching. The collars were exchanged among nestlings at the end of each observation to prevent possible feeding bias associated with certain colors. Each nestling was banded with a four-color combination at 9 or 10 days old, and the collar was removed on day 12 or 13, one or two days before fledging.

Observations of nests were made from 0.5 to 2 m distance. Many groups became so habituated that most or all of the adults did not mob experimenters as they handled nestlings. Daily 3-h observations, starting at first light, were made at 42 nests in which four nestlings had hatched. Data presented here are of 285 observation hours on days 8 to 12 posthatching for 19 nests containing four nestlings that successfully fledged. An additional 65 observation hours were carried out for five nests in which one nestling died.

Activity in the nest was recorded with a SVHS video camera located vertically above the nest. Videos were downloaded to a computer using Fast Movie Machine Pro hardware and software and analyzed in slow motion to an accuracy of 1/25 s. At each nest, a glass with a grid of squares (each square  $0.5 \times 0.5$  cm) was placed briefly on the nest surface when the adults were away. One video frame taken with the glass grid in place was used as a reference to locate in the computer an overlapping transparent grid, made in Corel Draw software, above the nest surface. The locations of all feedings were then mapped on the nest surface using coordinates of the grid.

Nestlings received food only when in a static posture, not while moving. The center of the open beak while receiving food was determined as a reference point. Each transfer of a prey item from feeder to nestling contributed one reference point. The geometric center of all reference points was considered

as the nestling's feeding-space center. Distance from each square in which a food item was obtained to all four nestling feeding-space centers was measured in mm from the square's center to the feeding-space center.

Each nestling's ability to control the nest surface around itself was measured by counting the squares within which food was obtained. Each square on the nest surface was scored for each nestling into three categories: (1) squares within which it received food exclusively; (2) squares in which both it and one or more siblings received food; and (3) squares within which it did not receive food. This division was valid as long as the nestling stayed in the same location. When a nestling changed its place, the classification of squares also changed. Accordingly, I prepared separate maps for each place in which at least one feeding was received. Each nestling's feeding maps were placed one above the other, keeping the feeding-space center and nestling direction constant. Each nestling thus accumulated reference points with every feeding event around a constant point. Combining all of the reference points enabled the mapping of each nestling's feeding space. Squares that were not used, but were surrounded on all four sides by squares belonging to a single category, were assigned to that same category.

To examine the flexibility of feeding spaces, a foreign nestling, which was older than the nest inhabitants by one or two days, was introduced into each of 10 different four-nestling nests. The experiment was carried out in 10 of the original 19 nests, on the ninth or tenth day posthatching, following the 3-h morning observation period. Feeding rate was recorded for 3 h, beginning 1 h after the nestling introduction. The five nestlings' feeding spaces were measured and compared with their feeding spaces prior to the experiment. At the end of each trial, the foreign nestling was returned to its natal nest. Each trial involved a different foreign nestling. Adding a fifth nestling for 4 h did not change the feeding rates on the next morning because feeding rates during 3 h on the following morning did not differ between the 10 experimental and 9 nonexperimental (same-aged nestlings) nests (Wilcoxon two-sample test,  $n_1 = 10$ ,  $n_2 = 9$ ,  $U = 42.5$ ,  $P = 0.21$ ).

When an adult landed on the nest rim, the nestlings rose, turned their beaks upward, gaped, and called. In the course of this extension, they often pushed each other so that some individuals were forced to subside or even lose their balance and readiness to be fed. Extensions and pushing events sometimes occurred independent of adult landings. I measured pushing efficiency of individual nestlings as the proportion of pushes that were followed by feedings to the pusher. A feeding was considered to be a consequence of a push if the sequence of feeder landing, nestling push, and pusher fed was not interrupted by feeding of another nestling. Usually,

TABLE 1. Number of feedings in exclusive and shared squares relative to hatching order of nestling Arabian Babblers;  $n = 19$  for each of the hatching orders.

Hatching order	Exclusive squares	Shared squares	Total
First	1,036	1,271	2,307
Second	896	849	1,745
Third	994	453	1,447
Fourth	931	272	1,203
Total	3,857	2,845	6,702

such events happened within 0.5 to 4.5 s after the feeder landed.

Statistical analyses were conducted in SPSS 7.5 for Windows. Friedman's method for randomized blocks, Wilcoxon signed-rank tests, Wilcoxon two-sample tests, and Spearman rank correlations were used as nonparametric tests following Sokal and Rohlf (1981). All  $F$ -tests were repeated-measures ANOVAs in which 4 nestlings and 5 days were used as factors, and 19 nests as replicates, except for two analyses noted in the text.

## RESULTS

*Food distribution to nestlings.*—The mean number of feedings per nest was  $352.7 \pm \text{SD}$  of 17.3 ( $n = 19$ ) and did not differ significantly among nests ( $F = 1.01$ ,  $df = 4$  and 18,  $P = 0.48$ ). In contrast, the mean number of feedings differed among days ( $F = 154.1$ ,  $df = 3$  and 4,  $P < 0.001$ ) and nestlings ( $F = 55.2$ ,  $df = 3$  and 4,  $P < 0.001$ ). Nestlings that hatched earlier obtained more feedings than their siblings that hatched later ( $r_s = -0.87$ ,  $n = 76$ ,  $P < 0.001$ ).

*Food distribution on the nest surface.*—Each square within which food was obtained was categorized as an exclusively used square or a shared square (Table 1). Mean distances from nestling feeding centers were  $0.96 \pm 0.55$  cm,  $2.40 \pm 0.44$  cm, and  $6.30 \pm 2.25$  cm, respectively. Exclusively used squares were significantly closer to feeding centers than were shared squares ( $F = 320.4$ ,  $df = 1$  and 3,  $P < 0.001$ ).

*Exclusive vs. shared feeding spaces: Food distribution and size.*—During the sampling period, each nestling obtained an average of  $51.4 \pm 7.9$  feedings ( $n = 76$ ) within its exclusive feeding space and  $36.8 \pm 23.6$  feedings within its shared feeding space. The average size of exclusive feeding spaces was  $7.9 \pm 0.9$  cm<sup>2</sup>, and



FIG. 1. Number of pushes per Arabian Babbler nestling ( $\bar{x} \pm \text{SD}$ ) in exclusive and shared feeding spaces in relation to hatching order.

the size of exclusive feeding spaces did not differ significantly among siblings ( $F = 2.23$ ,  $df = 3$  and 4,  $P = 0.095$ ). Shared feeding spaces averaged  $4.8 \pm 2.3$  cm<sup>2</sup>, and their size differed significantly among siblings ( $F = 93.93$ ,  $df = 3$  and 4,  $P < 0.001$ ). Specifically, the size of shared feeding spaces decreased significantly with hatching order ( $r_s = -0.92$ ,  $n = 76$ ,  $P < 0.001$ ).

Nestlings obtained similar numbers of feedings within exclusive feeding spaces ( $F = 2.61$ ,  $df = 3$  and 4,  $P = 0.089$ ). However, the number of feedings obtained in shared feeding spaces differed significantly among nestlings ( $F = 75.34$ ,  $df = 3$  and 4,  $P < 0.001$ ) and was negatively correlated with hatching order ( $r_s = -0.92$ ,  $n = 76$ ,  $P < 0.001$ ).

*Defense of feeding spaces.*—On average,  $57.0 \pm 7.3$  pushes per nest ( $n = 19$ ) and  $14.2 \pm 4.6$  ( $n = 76$ ) pushes per nestling occurred within exclusive feeding spaces, and the number of pushes per nestling was weakly correlated with hatching order ( $r_s = 0.24$ ,  $n = 76$ ,  $P = 0.024$ ; Fig. 1). Pushing efficiency averaged  $61.8 \pm 3.1\%$  ( $n = 76$ ) and was similar among nestlings (Friedman's method,  $\chi^2 = 3.0$ ,  $df = 3$ ,  $P = 0.36$ ; Table 2). Within shared feeding spaces, there were  $136.4 \pm 16.4$  pushes per nest ( $n = 19$ ) and  $34.1 \pm 25.9$  pushes per nestling ( $n = 76$ ), and the number of pushes per nestling was negatively correlated with hatching order ( $r_s = -0.90$ ,  $n = 76$ ,  $P < 0.001$ ). Pushing efficiency was  $43.8 \pm 11.3\%$  ( $n = 76$ ) and was negatively correlated with hatching order ( $r_s = -0.88$ ,  $n = 76$ ,  $P < 0.001$ ).

*Food stealing from exclusive feeding spaces.*—In addition to 3,857 feedings that were provided to nestlings within their exclusive feeding spaces, 104 feedings (2.7%) were given to invading nestlings that suddenly extended into

TABLE 2. Pushing efficiency by nestling Arabian Babblers in exclusive and shared feeding spaces.

Hatching order	No. of pushes	No. of feedings after a push	Pushing efficiency (%)
<b>Exclusive feeding spaces</b>			
First	251	172	68.5
Second	244	149	61.1
Third	286	165	57.7
Fourth	302	183	60.6
Total	1,083	669	61.8
<b>Shared feeding spaces</b>			
First	1,281	658	51.4
Second	816	329	40.3
Third	322	115	35.7
Fourth	173	34	19.6
Total	2,592	1,136	43.8

the exclusive feeding space of a sibling, received food, and then immediately withdrew from the space. In contrast to ordinary feedings, where several feedings may have occurred in the same feeding space, no invader ever obtained two consecutive feedings in a foreign exclusive feeding space. Of 76 nestlings, 17 (22.4%) were observed to steal food (Table 3). I found no relationship between hatching order and the tendency to steal food ( $\chi^2 = 2.89$ ,  $df = 3$ ,  $P = 0.41$ ) or to have food stolen ( $\chi^2 = 2.78$ ,  $df = 3$ ,  $P = 0.43$ ).

*Changes in feeding-space size with nestling growth.*—As the nestlings grew, they controlled larger exclusive feeding spaces; the change was similar for all siblings ( $F = 2.27$ ,  $df = 3$  and  $4$ ,  $P = 0.102$ ; Fig. 2). In contrast, the increase in size of shared feeding spaces with nestling age depended on hatching order ( $F = 63.5$ ,  $df = 3$  and  $4$ ,  $P < 0.001$ ), being largest for first-hatched nestlings and virtually absent for last-hatched nestlings (Fig. 2).

TABLE 3. Food stealing by nestling Arabian Babblers (first-, second-, third-, and fourth-hatched) from exclusive feeding spaces. Sample sizes are in parentheses.

Owner	Thief					Total (17)
	First (5)	Second (2)	Third (4)	Fourth (6)	Total	
First (6)	—	5	9	11	25	
Second (5)	10	—	6	7	23	
Third (8)	7	10	—	8	25	
Fourth (7)	13	10	8	—	31	
Total (22)	30	25	23	26	104	

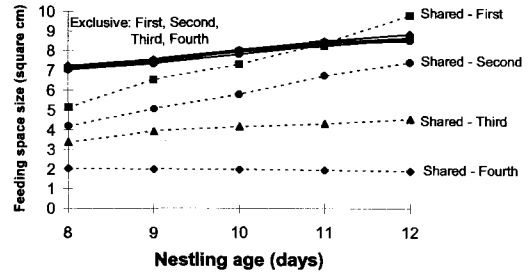


FIG. 2. Changes in size of mean exclusive and shared feeding spaces with nestling age for the first-, second-, third-, and fourth-hatched Arabian Babbler nestlings.

*Loss of feeding space.*—Of 168 hatched nestlings in 42 nests, 40 died before fledging. The feeding spaces of five nestlings that died between the 10th and the 12th day posthatching were estimated by measuring all feedings in their nests for 3 h each day. The first indication that a nestling would die was the success of its siblings in obtaining food in its exclusive feeding space. Subsequently, the size of its exclusive feeding space decreased (Fig. 3), its share in the general feedings diminished, and it eventually lost its exclusive feeding space completely. A decrease in the size of exclusive feeding spaces was observed only in nestlings that died.

*Adding a fifth nestling to a nest.*—The addition of an older foreign nestling into nests with four nestlings ( $n = 10$ ) had no significant influence on the size of exclusive feeding spaces (Wilcoxon signed-rank test,  $T = 368$ ,  $n = 40$ ,  $P = 0.76$ ), nor on feeding rates ( $T = 315$ ,  $n = 40$ ,  $P = 0.70$ ), compared with before the experiment. All five nestlings were fed equally within their exclusive feeding spaces (Friedman's method,  $\chi^2 = 1.51$ ,  $df = 4$ ,  $P = 0.82$ ). In contrast, after the addition of a foreign nestling, the size of shared feeding spaces of the four original nestlings de-

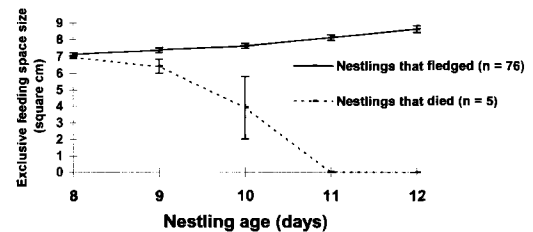


FIG. 3. Size of exclusive feeding space ( $\bar{x} \pm SD$ ) of Arabian Babbler nestlings that fledged relative to that of nestlings that died.

clined ( $T = 9.5$ ,  $n = 40$ ,  $P < 0.001$ ), their feeding rates decreased ( $T = 9.9$ ,  $n = 40$ ,  $P < 0.001$ ), and feeding rates were negatively correlated with hatching order ( $r_s = -0.85$ ,  $n = 50$ ,  $P < 0.001$ ).

#### DISCUSSION

Aggressive interactions among nestlings are a well-known factor in brood reduction among nonpasserines (e.g. O'Connor 1978, Braun and Hunt 1983, Mock 1985). In studies of brood reduction in passerines, however, relationships among siblings have been almost completely ignored. Instead, these studies have focused on begging behavior, which illuminated many interesting questions but left the mechanisms of brood reduction unclear. These results concur with previous findings in that early hatched chicks had higher survival than their later-hatched nest mates (e.g. Mock 1985, Cash and Evans 1986, Anderson 1990), and they reveal how, without direct aggression, young nestlings may starve to death.

Arabian Babblers nestlings defined two feeding spaces around themselves and defended them, when necessary, by pushes. Within exclusive feeding spaces, which were equal in size, all four siblings obtained similar amounts of food. In contrast, within shared feeding spaces, feeding rates were positively correlated with feeding-space size and negatively correlated with hatching order. Preventing nest mates from obtaining food by defending a feeding space that moves with the nestling actually is an individual-distance (space) defense (Conder 1949, Emlen 1952), a behavior heretofore known only for adult birds.

When a fifth nestling was introduced into the nest, none of the exclusive feeding spaces decreased, and feeding rates remained constant. In contrast, feeding rates in the shared feeding spaces decreased as a consequence of their reduction in size. Under the heavy pressure of an older foreign nestling, resident nestlings gave up part of their shared feeding spaces, but not their exclusive ones. These findings suggest that a nestling's ability to obtain food depends on its ability to defend a feeding space around itself, and that the difference in feeding rates among nestlings derived mainly from the difference in their ability to enlarge and control their shared feeding spaces. Nestling compe-

tion is not a struggle over every piece of food, but a more sophisticated system, based on long-term interactions among nest mates. The different behavior of nestlings in the two feeding spaces implies that each space has a different function. I suggest that a basic amount of food is necessary for nestling survival, and that this basic amount is obtained in the exclusive feeding space.

The first indication that a given nestling was likely to die was food being consistently obtained inside its exclusive feeding space by invading siblings. Unlike food stealing, which happened occasionally and harmed the owner only by the loss of one item, invading nestlings usually obtained several consecutive feedings inside a sibling's exclusive feeding space without being ejected by that sibling. Thus, the exclusive feeding space gradually became shared. Exclusive feeding spaces never decreased for nestlings that successfully fledged, but only for those that died before fledging. In contrast, decreases in the size of shared feeding spaces (fourth-hatched nestlings in Fig. 2) apparently caused loss of feedings but did not lead to death. It seems that the ability of a nestling to survive depended on its ability to defend an exclusive feeding space. Measuring feeding spaces enabled us to predict which nestling would die several days before the event actually happened.

Empirical studies have found that nestlings express their needs honestly and do not manipulate their provisioners (Kilner 1995, Cotton et al. 1996, Leonard and Horn 1996, Kilner and Johnstone 1997, Iacovides and Evans 1998). For begging to be a reliable signal of need, it should be costly (Zahavi 1987; Godfray 1991, 1995). However, because the cost of begging is low (Leech and Leonard 1996, McCarty 1996, Bachman and Chappell 1998), parents cannot use it as a reliable indicator of need. This conflict of evidence may be solved by a nestling feeding-space strategy. Expensive efforts are not invested in begging, but in establishing conditions for begging by controlling feeding spaces. Parents accept begging as an honest signal because it is based on a system of feeding spaces that apparently are costly to maintain.

Aggressive interactions require high expenditure of energy, expose nestlings to injury, reduce the benefit from available food (Lamey and Mock 1991), and also restrict the ability of

nestlings to collaborate in begging, which reduced food intake. The feeding-space strategy of Arabian Babbler nestlings, and possibly other passerine nestlings, enables them to obtain food and survive in their cooperative but competitive environment in a relatively nonaggressive way.

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