

# The Ontogeny of Antiphonal Calling in European Starlings

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The ontogeny of antiphonal calling was studied in free-living European starlings. Nestlings participate in three types of vocal exchanges: (1) Broodmates exchange calls while the parents are away; (2) parents and nestlings exchange calls during feeding; (3) nestlings exchange calls with parents approaching from a distance. Analysis of the temporal patterning of vocal interactions revealed call alternation and avoidance of acoustic overlap in exchanges of the first and third types. The antiphonal exchanges between parents and young develop shortly before fledging and appear to help family groups maintain contact after the young have left the nest. Early antiphonal exchanges between broodmates are as smooth as later ones between parents and chicks, suggesting that chicks quickly attain proficiency at antiphonal interactions and do not rely on an adult partner to maintain the pattern. There are parallels with the development of vocal turn-taking in human infants.

Antiphonal vocalizing, in the sense of either alternating vocalizations or avoiding acoustic overlap, has been described in a wide range of taxa. It often occurs among members of a pair or group seeking to establish or maintain contact—e.g., between mated quail (*Colinus virginianus*, *Lophortyx californicus*, and *L. gambelii*, Stokes & Williams, 1968), between mother and infant horseshoe bats (*Rhinolophus ferrumequinum nippon*, Matsumura, 1981), and among groups of bowhead whales (*Balaena mysticetus*, Clark, Ellison, & Beeman, 1986). Antiphony also occurs in the context of territorial and courtship displays—e.g., among Hylid treefrogs (Arak, 1983; Forester & Harrison, 1987; Wells, 1977; Zelick & Narins, 1982, 1985), between pairs of lar gibbons, *Hylobates lar* (Raemaekers & Raemaekers, 1985), and among many songbird species (Kroodsma, 1979; Todt, 1981). Taking turns is a key feature of human communication (Feldstein & Welkowitz, 1978; Jaffe & Feldstein, 1970), underlying many aspects of social interaction (Bruner, 1974/75; Hay & Rheingold, 1983). The relative simplicity of the antiphonal pattern, in the sense that it lends itself to quantitative treatment, affords a good opportunity to address questions about the development of interactive aspects of communication. Its widespread occurrence invites a comparative approach. Little is known about the ontogeny of antiphonal patterning in nonhuman vocal ex-

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been obtained. Recordings ended after the birds remained silent for a minimum of 15 seconds. Observations on the location and behavior of parents and nestlings accompanied all recordings.

Vocal interactions were categorized according to the behavioral contexts in which they were recorded, although the call types involved could also be identified on the basis of acoustic structure. The recordings included vocal interactions of three types—chirp exchanges between broodmates, snarl/beg exchanges between parents and chicks, and cheet exchanges between parents and chicks. Chirp exchanges and snarl/beg exchanges occur in approximately the second week after hatching, and cheet exchanges at the end of the third week (Chaiken, 1986).

For the analysis, good recordings were selected in which two birds gave at least four calls each, and interactions involving more than two birds were excluded. These criteria, in addition to facilitating analysis, achieved a degree of standardization across behavioral contexts necessary for comparisons between them.

The temporal boundaries of an interaction were defined by examining frequency distributions of the intervals between calls by the two participants in each type of interaction. Intervals from parent to chick calls and from chick to parent calls were examined separately. In all cases, the distributions peaked below 1 second and trailed off by about 5 seconds. There was a gap in the combined distributions between 5.3 and 8.5 seconds. Thus all intervals less than 5.3 seconds were considered to occur within an interaction and intervals above 8.5 were considered to occur between interactions. Sometimes a nestling would continue to vocalize after its partner had flown away or fallen silent for the duration of the call sequence, and in these cases an interaction was considered to have ended after the first two of a series of three or more unanswered calls.

To ensure the independence of observations for each type of interaction, only one exchange of each type was used from each family. When more than one good recording of a snarl/beg or chirp sequence was available from the same family, recordings were chosen so as to match ages of chicks in the two samples as closely as possible. Age ranges for the samples were 7–18 days posthatch for chirp exchanges, 10–16 days for snarl/beg exchanges, and 19–22 days for cheet exchanges. Thirty-two call sequences from 30 families were used in the analysis, with 10–11 sequences of each type and an average of 24 calls per sequence.

Most studies of antiphonal vocalizing have focused on interactions between two individuals; in cases where the investigation was extended to more complex situations it was found that the results obtained for two participants could be generalized to interactions among three or more (Puerto Rican treefrogs, *Eleutherodactylus coqui*, Brush & Narins, 1989; Peking ducklings, *Anas platyrhynchos*, Christopher Evans, personal communication). The sample of two-bird exchanges used in this study represents a subset of normal vocal interactions among starling parents and nestlings in that many exchanges involve more than 2 participants (29% of the chirp exchanges I recorded, 71% of snarl/beg exchanges, and 53% of cheet exchanges). As a check on the typicality of this sample with respect to antiphonal patterning, I examined a second sample of 32 call sequences selected at random from among the remaining recordings, including sequences that consisted of as few as 2 calls per bird and segments of 3-bird exchanges in which only 2 birds were calling. For each call sequence in each sample, I calculated the percentage of calls that began before the preceding call had ended, that is, the

order in which the birds called, the durations of the calls, and the intercall intervals were determined for each sequence.

## Results

### Vocal Interactions Among Starlings Chicks and Parents

Starling chicks and their parents engage in three types of vocal interaction while the chicks are in the nest (Figs. 2 and 3 show sound spectrograms of the calls involved): (1) **“Chirp exchanges” between broodmates.** While the parents are away the nestlings utter a series of chirps, referred to as “distant begging calls” by Hartby (1969) and Van Elsacker, Pinxten, and Verheyen (1986), and described as a soft “churr” by Feare (1984). (2) **“Snarl/beg exchanges” between parents and chicks.** When a parent arrives at the nest the chicks utter loud and raucous begging calls (see Feare, 1984; Hartby, 1969), which differ significantly from chirps in duration and frequency structure (Chaiken, 1986). Begging calls are often interspersed with the parents’ “snarl,” which they utter before entering their nest holes once the young have hatched (Bent, 1950; Chaiken, 1986) and also direct at predators as part of an aggressive display (Chaiken, 1986; DeBruyn & Verheyen, 1985; Feare, 1984; Hartby, 1969). (3) **“Cheet exchanges” between parents and chicks.** Shortly before fledging, parents begin to utter “cheets” for the first time in that reproductive cycle, and chicks respond with a juvenile version of the same call. Cheet exchanges are typically initiated as the parent approaches the nest from a distance, and become the predominant vocalizations after the young have fledged. The acoustic structure of juvenile cheets shows developmental continuity with adult cheets (Hartby, 1969) and also with both early begs and early chirps (Chaiken, 1986). I classify these juvenile calls as cheets in view of their structural and functional continuity with the adult calls. There is some inconsistency among investigators in the classification of chick calls given around the time of fledging. The “distant begging calls” of Hartby (1969) and Van Elsacker et al. (1986) correspond to both my chirps and pre-fledging cheets. Hartby’s “flock call” and Schüz’s (1942) “shrä” may correspond to my post-fledging cheets. The “adult location call” of Van Elsacker et al. corresponds to my parent cheets. The classification of juvenile cheets is not critical to the purposes of the present study; it is sufficient to note that “cheet exchanges” constitute a distinct behavioral context for calling.

### Order of Calling

The identity and order of the callers in the joint sequences were determined for each pair of successive calls, or “call pairs” (see Fig. 1). There are four possible types of call pairs in any sequence of calls by two birds, say birds A and B: AA, AB, BA, and BB. If the birds called at random, a call sequence would contain an approximately equal number of call pairs of each type. If they alternated calls, there would be an equal number of AB and BA call pairs and no AA or BB call pairs. Figure 4 shows the mean proportion of call pairs of each type in the three kinds of vocal exchanges. Chi-square values were computed for each call sequence and these values were added to obtain a total for each kind of vocal exchange (Fleiss, 1973).

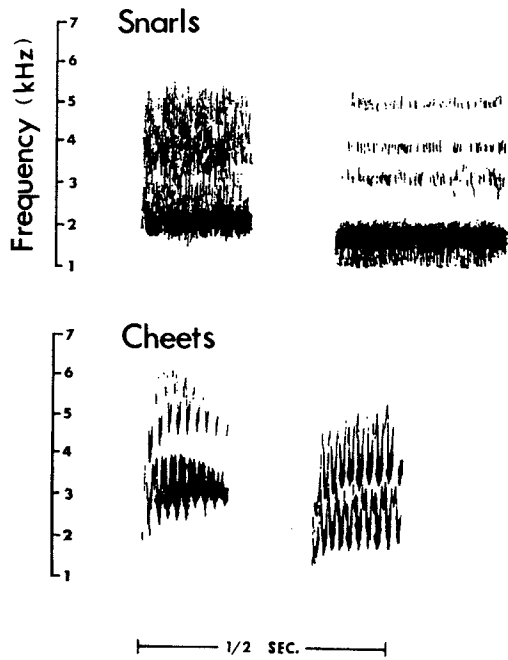


Fig. 3. Sound spectrograms of parent calls. Above: snarls of two adults. Below: cheets of two adults.

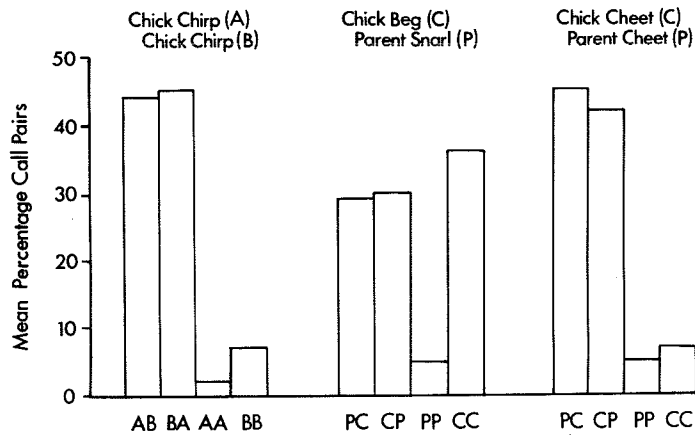


Fig. 4. Order of calling by partners during vocal exchanges. In a vocal exchange between two birds, say A and B, there are four possible combinations of callers for any pair of successive calls: AA, AB, BA, BB. The figure shows the mean percentage of call pairs that fall into each of these categories for three kinds of vocal exchanges.

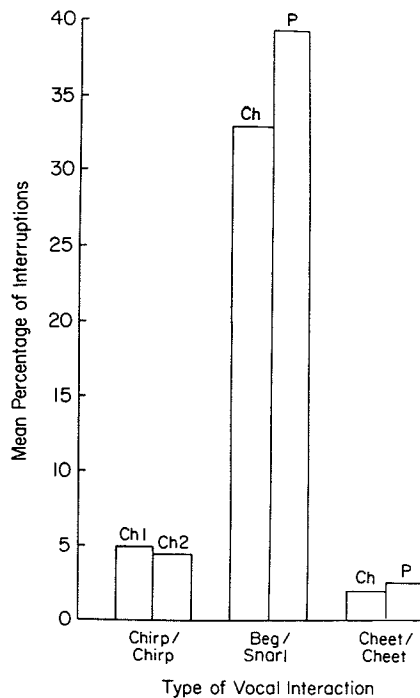


Fig. 5. Percentage of interruptions during vocal exchanges. The percentage of times a bird (A) interrupts its partner (B) in a vocal exchange is calculated as the percentage of BA call pairs (successive calls by B and A) in which A starts calling before B has finished.

### Developmental Comparisons

One would predict that call exchanges between broodmates during the second week would run less smoothly than exchanges with parents at the end of the third week if the chicks' proficiency improved with age or if the adult participant compensated for any lack of facility on the part of the chicks. I calculated the proportion of times each bird interrupted its partner in chirp and cheet sequences (See Fig. 5). The proportion of times a bird (A) interrupted its partner (B) in a given exchange is calculated as the proportion of BA call pairs in which A started calling before bird B had finished. Chicks did not interrupt their partners significantly more often in chirp sequences than in cheet sequences (Student's *t*-test, two-tailed,  $T = .07$ ,  $df = 21$ ,  $P > .05$ ). Moreover, in cheet sequences chicks interrupted their parents slightly less often than parents interrupted their chicks.

As for the order of calling, chicks did not call out of turn more often in chirp exchanges with each other than in later cheet exchanges with their parents. In cheet exchanges chicks called out of turn about as often as their parents (refer to Fig. 2). When chicks did call out of turn, they never waited less than their average length of time for an answer, whereas parents failed to do so 16% of the time.

Thus in their second week the chicks seem as proficient in antiphonal calling as the adults, without relying on adult partners to help maintain the pattern.

it has been suggested that competition between males to be the first to answer a female's vocalization leads to the male's overlapping the female's signal.

Antiphonal calling among broodmates in the nest is more difficult to explain as an adaptation to the conditions of early life, particularly since the communicative significance of the chicks' chirps is unclear. The maintenance of contact hypothesis may apply if the nestlings' calls are directed jointly at their parents. Antiphonal calling among two or more individuals may make them easier for another party to locate, either separately or as a group—for instance, antiphonal calling among male treefrogs appears to aid in their localization by females (Arak, 1983; Forester & Harrison, 1987; Littlejohn & Martin, 1969), and alternation of distress calls by ducklings may aid in maternal retrieval of young (Gaioni, 1982; Gaioni & Evans, 1986). Still, it seems unlikely that starling parents would need auditory cues to locate their nestlings. More general advantages may accrue to antiphony in bouts of joint calling addressed to the parents: Gaioni and Evans suggest that in addition to preventing mutual masking, antiphonal calling within a group may permit the participants to continue signaling for longer periods by allowing them to share the energetic costs of calling.

Another possibility is that early exchanges of chirps between broodmates prepare the chicks for subsequent exchanges of cheets with their parents (see Beer, 1979, on the possibility of such a preparatory function in early vocal exchanges between laughing gull, *Larus atricilla*, parents and young). Whether the starlings' antiphonal pattern of calling involves a skill that can be improved or maintained by practice is an open question. It is not clear that practice is in general necessary for the establishment of precisely timed patterns of vocal exchange, even in cases of elaborate dueting. Pairs of buff-breasted wrens (*Thryothorus leucotis*; Farabaugh, 1982) and bay wrens (*T. nigricapillus*; Levin, 1983) begin to sing complex duets from the moment they begin their association, although it is possible that they learned their parts before pairing. On the other hand, duets between a pair of captive bou-bou shrikes (*Lanarius ferrugineus*) took shape over a period of weeks (Thorpe & North, 1966).

In the present study, starling chicks were proficient at antiphonal calling in their earliest interactions with each other, and no effect of practice was apparent in the initial establishment of the pattern. However, antiphonal exchanges with parents present new challenges for the chicks—the parents, unlike broodmates, call from a range of distances and directions and the chicks appear more highly aroused. The early experience with broodmates could help the chicks reestablish the antiphonal pattern under these more demanding conditions. There is some indication that the transition may be less seamless than the present study suggests. When Van Elsacker et al. (1986) induced cheet exchanges at an earlier age than I was able to observe them under natural conditions (starting at 13 days posthatch as distinct from 19 days for my sample), they found that calling and answering between parents and young “runs more smoothly as the young grow older.” They also found that the smoothness of the interaction could be related to the success of the parents in locating their displaced broods, which suggests an adaptive advantage for any mechanism promoting the early establishment of the antiphonal pattern in cheet exchanges.

In summary, starlings attain a high level of proficiency at antiphonal interactions well before they have acquired an adult repertoire of vocal signals. The

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