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Acoustic Interactions in Broods of Nestling Birds

Andrew G. Horn and Marty L. Leonard Dalhousie University

Studies of acoustic interactions in animal groups, such as chorusing insects, anurans, and birds, have been invaluable in showing how cooperation and competition shape signal structure and use. The begging calls of nestling birds are ideal for such studies, because they function both as a cooperative signals of the brood's needs and as competitive signals for parental allocation within the brood. Nonetheless, studies of acoustic interactions among nestlings are rare. Here we review our work on acoustic interactions in nestling tree swallows (*Tachycineta bicolor*), especially how calls are used in competition for parental feedings. Nestlings attracted parental attention and responded to acoustic interference mainly by increasing call output. However, nestlings also gave more similar calls when they called together and decreased their call bandwidth when exposed to elevated noise. We suggest that these competitive uses of calls might intensify the cooperative brood signal, affecting both parental provisioning and vocal development. Given their tremendous variation across species, begging calls offer promising opportunities for developmental and comparative studies of acoustic signaling.

Keywords: begging, acoustic interactions, acoustic signaling, vocal development, ambient noise

Studies of acoustically signaling groups of animals have been instrumental in showing how cooperation and competition shape the structure and use of signals (Gerhardt & Huber, 2002; Greenfield, 2002; Todt & Naguib, 2000). Studies of birds, for example, have shown how group breeders signal cooperatively by using intricately coordinated joint songs (e.g., Hale, 2006) and how territorial songbirds interact competitively through the timing and patterning of their song exchanges (e.g., Naguib, 2005). Despite extensive research on such vocal interactions, one of the most widespread and striking examples of acoustic signaling in groups, begging by nestling birds, has received very little attention.

Nestling birds beg for food from their parents with loud calls, accompanied by a visual display that includes stretching upward, waving wings, and gaping. In contrast to more extensively studied group vocalizations, begging calls combine cooperative and com-

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petitive functions, offering a unique opportunity to see how both affect acoustic signaling. Specifically, begging calls function both as a joint signal of the brood's hunger, which parents use to regulate their overall provisioning rate, and as individual, competitive signals, which parents use to decide which nestling to feed on a given visit (Horn & Leonard, 2002, 2005). Detailed studies of acoustic interactions among nestlings are needed to clarify how these two contrasting functions are reconciled in the structure and use of calls.

Such studies would be useful and interesting for several reasons. First, an understanding of how nestlings interact acoustically would help clarify competitive interactions among nest mates, which have been studied extensively but are still poorly understood (as discussed in Royle, Hartley, & Parker, 2004). Second, in many species, nestling calls develop into important adult signals such as contact calls and advertising song (reviewed in Sharp & Hatchwell, 2006), and acoustic interactions among nestlings might affect this development. Finally, across species, begging call structure varies tremendously (Popp & Ficken, 1991), and an understanding of how call structure relates to acoustic interactions might help to explain this variation.

In this article, we review our work on acoustic signaling within broods of our main study species, the tree swallow (*Tachycineta bicolor*). First, we briefly review evidence that parents regulate provisioning rate based on calling by the brood as a whole. Because this function has been widely studied (Hinde & Kilner, 2007), we focus most of our review on the more controversial role of calling in competition for parental food distribution within the brood. We then show how acoustic interference among competing nest mates might affect call structure and use and suggest how those changes, in turn, affect the brood level signal. Finally, we briefly suggest how further studies of acoustic interactions among nestlings might relate to vocal development and interspecific variation in call structure.

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HORN AND LEONARD

Study Species

The tree swallow (T. bicolor) is a common North American passerine. Like the great tit (Parus major) and pied flycatcher (Ficedula hypoleuca) of Europe, the tree swallow has become a model organism for field ornithology (Jones, 2003), largely because it nests readily in artificial nest boxes. Nest boxes not only facilitate studies of breeding biology but, for our purposes, also provide experimental chambers in which a nestling's acoustic environment is easily recorded and manipulated in both field and lab. A nestling placed in a warmed nest box in the lab experiences very similar conditions to a nestling in the field and can usually be stimulated to beg when a recorded adult provisioning (contact) call is played back(Leonard, Fernandez, & Brown, 1997).

The breeding cycle of tree swallows is typical of most temperate passerines (Robertson, Stutchbury, & Cohen, 1992). Young hatch naked and completely reliant on parents for food and warmth. Parents arrive at the nest with food about every 10 minthroughout the day, feeding one nestling on each trip with a bolus of insects they have collected in flight near the nest. The female parent broods the nestlings regularly until they can thermoregulate, when nestlings are 7-10 days old. Typically, young leave the nest about 21 days after hatch, following the parents for about a week thereafter before feeding independently (Robertson et al., 1992).

Growth during the nestling period is accompanied by dramatic changes in the structure of nestling begging calls, from unmodulated, brief, high whistles that appear shortly after hatching to highly variable, frequency modulated and sometimes harmonically structured calls in the second week after hatching (see Figure 1; Leonard & Horn, 2006; Robertson et al., 1992). By Day 15, these calls, now usually given in pairs or triplets, have a complex pattern of frequency modulation that is stereotyped within the individual and, to some extent, distinctive between broods (Leonard, Horn, Brown, & Fernandez, 1997). After fledging, these same calls are used to beg and to maintain contact with the parents, and eventually they become the contact calls of adults (Brown & Brown,

1995). Adult contact calls are used in a broad range of contexts, including provisioning young, coordinating nest visits between members of the pair (Leonard, Fernandez, & Brown, 1997), copulation (in females), and as one of several call types that make up male song (Sharman, Robertson, & Ratcliffe, 1994). The origin of the approximately 12 other adult vocalizations (Robertson et al., 1992) is unknown; presumably they first appear after fledging.

Signaling by the Brood

Our review of the cooperative and competitive influences on calling begins with a brief review of how calling is a joint signal of brood hunger. The main evidence that calling is a joint signal of need is that, in a wide range of species, begging by the brood increases when parents provisioning rate decreases, and parents deliver more food to the brood in response (Budden & Wright, 2001; Wright & Leonard, 2002).

In tree swallows, calling by the brood encodes information on hunger. Specifically, the duration of calling by the brood at each parental visit increases the longer the parent has been away from the nest and when food availability is low (Hussell, 1988; Leonard & Horn, 1996, 2000; Thomas & Shutler, 2001). In turn, parent tree AQ:1 swallows use this variation in calling to regulate how often they return to the nest with food. Specifically, parents deliver food more frequently when nestlings call longer at each parental visit (Hussell, 1988) and when nestlings give more intense visual begging displays (Leonard & Horn, 1996), which correlate with higher calling rates (Leonard & Horn, 2001a). Also, playback of begging calls increases parental visitation rates, relative to control playbacks of background sounds (Leech, 1996). Thus, as in many other species, begging calls in tree swallows form a joint signal of the need of the brood as a whole that signals to the parents how often to provision the brood. It is unclear whether nestlings coordinate their calls to achieve this function, although this possibility is indirectly addressed by our work on how calling affects food allocation within the brood, which is discussed next.

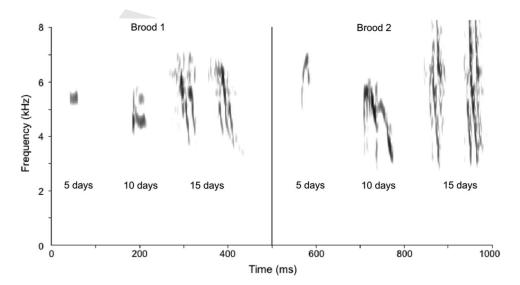


Figure 1. Spectrograms (bandwidth 761 Hz; resolution 1 ms, 23 Hz) of tree swallow nestlings from two different broods (left and right sides of graph), with one call from each of three ages (5, 10, and 15 days posthatch; Day 15 call has two notes).

F1

ACOUSTIC INTERACTIONS IN NESTLINGS

Signaling by Individuals Within the Brood

In contrast to their function as a joint signal of brood need, the function of begging calls as individual signals affecting which nestlings are fed has rarely been demonstrated (Forbes, 2007). Such evidence is, of course, key to understanding the effect of competitive interactions on begging calls. Three pieces of evidence support this function in tree swallows: (a) the calls of individual nestlings vary with individual need, so a parent could use them to gauge each nestling's needs and direct feedings accordingly; (b) nestlings use calls in situations in which calling is a particularly effective way to attract the parent's attention; and (c) calls affect parental feeding decisions.

The first of these points, that a nestling's calls advertise its hunger, has been shown in several species (e.g., Kilner, Noble, & Davies, 1999; Price & Ydenberg, 1995; Sacchi, Saino, & Galeotti, 2002). In tree swallows, for example, calling rate and length increase with nestling hunger throughout the nestling period, and amplitude and frequency range also increase with hunger in older nestlings (Leonard & Horn 2001a, 2006). The second two points, however, have rarely been demonstrated, so we explain the evidence in more detail.

Are Calls Used to Attract Parental Feedings?

If calls are used to attract parental feedings, one would expect nestlings to call more when their ability to catch the parent's attention is compromised, for example, when their visual display is obscured or when other nestlings are closer to optimal feeding locations within the nest. The first of these situations has been created experimentally by dimming illumination within nest boxes (Heeb, Schwander, & Faoro, 2006). Such experiments have not examined the effect of lighting on calling but do show that this manipulation is a promising approach.

In our work, we took the second approach, manipulating the position of nestlings within the nest. Parents preferentially feed nestlings near the entry hole at the front of the nest box (Leonard & Horn, 1996; Whittingham, Dunn, & Clotfelter, 2003), so we used Plexiglas partitions to prevent nestlings from approaching this optimal feeding location (Leonard, Horn, & Parks, 2003). In experimental nests, two nestlings were confined to the back of the nest; in control nests, nestlings were free to move to the front of the nest, toward the parent. We predicted that nestlings that were prevented from approaching the parent would call more to compensate for their poor position in the nest.

Indeed, confined nestlings called at nearly double the rates of unconfined nestlings. Moreover, among the control, unconfined nestlings, those that remained in the back of their nests called more than those that chose to move forward toward the parent. Thus calls were indeed used in ways that might help to draw the parent's attention toward nestlings that are farther away. Calling rate and hunger, as measured by the time since the parent's previous visit, were not correlated in this experiment (Leonard, Horn, & Parks, 2003), despite their strong correlation in our other work (e.g., Leonard & Horn, 2001a, 2006). Thus, in certain contexts, the use of calls to signal hunger might be superseded by their use in attracting the parent's attention, highlighting the competitive, as opposed to cooperative, dimension of calling.

Do Parents Use Calls to Allocate Feedings Within the Brood?

Of course, the most fundamental requirement for calls to be used competitively to affect food allocation is that parents actually use nestling calls to select which nestling to feed. In the experiment just described, parents did indeed preferentially feed nestlings that called more, and partial correlations showed that this preference was independent of their strong preference for nestlings that had more intense visual begging displays (Leonard, Horn, & Parks, 2003). Similar correlational evidence exists in a few other species (Kilner et al., 1999; Price & Ydenberg, 1995; Sacchi et al., 2002). A more direct approach, however, would test for a preference with no cues other than the vocal signal.

We conducted such a experiment by placing small speakers on either side of a nest box, next to a nestling that we had thoroughly satiated by hand feeding so that it would not move or call during the experimental trial (Leonard & Horn, 2001b). When a parent arrived at the nest, we played the calls of a deprived versus a fed nestling and video recorded which nestling the parent attempted to feed. Parents preferentially directed feeding attempts to calls played back at higher rates (Leonard & Horn, 2001b), showing that, in the absence of visual cues, parents did use calls to deliver feedings to particular nestlings. Similar results, using similar paradigms, have been reported in two other species (Kilner, 2002; R. Brandt, personal communication, August 2000). In contrast, muting red-winged blackbird (Agelaius phoeniceus) nestlings did not reduce parental feedings to those nestlings (Glassey & Forbes, 2002), but this may be because parents switched to visual cues when acoustic cues were not available. Indeed, although the influence of visual cues on parental feedings is well established (albeit mainly from correlational rather than experimental studies), the interaction between visual and acoustic cues is virtually unexplored and deserves more study (Kilner, 2002).

How Do Nestlings Overcome Acoustic Interference From Nest Mates?

Having shown that calls function to influence food allocation within the brood, we now consider how competition for parental feedings shapes call structure and use. The most obvious form this competition might take is acoustic interference among nest mate calls, so we would expect calling by individual nestlings to show features that circumvent this masking. To identify these features, we have used two approaches that have yielded different, but complementary, results. The first and most obvious was to expose nestlings to calling nest mates and see how the nestlings changed their calls.

How Do Nestlings Respond to Interference From Nest Mate Calls?

Following from studies of call interference in better studied systems, that is, chorusing insects, anurans, and adult songbirds, we could think of three main ways that nestlings might call to reduce interference. Specifically, nestlings might alternate calls, give individually distinctive calls, or simply increase the output, that is, the rate, length, or amplitude, of their calls. To test these alternatives, we deprived nestlings of food for an hour and then

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stimulated them to beg either alone or with another nestling undergoing the same treatment behind an opaque partition (Leonard & Horn, 2001c). We performed the test at two ages (Days 7–8 and Day 13) and tried all combinations of the largest and smallest nestling from each brood.

We found no significant relationships in the timing of nest mates' calls as measured by their phase relationships analyzed with circular statistics (Klump & Gerhardt, 1992). Nestlings did, however, increase their call rate in response to calling nest mates by nearly 50% (see also Leonard & Horn, 1998). Otherwise, we found no consistent changes in call amplitude, length, frequency, or bandwidth, although one marginally nonsignificant effect (p = .06) suggested that small nestlings may have increased the amplitude of their calls by 3 dB when they were calling with a larger nestling.

The most surprising result, however, was the thorough contradiction of our prediction that nestlings would increase the distinctiveness of their calls to overcome masking. When nestlings called together, the structure of their calls, as measured by crosscorrelation, did not diverge but instead converged; that is, nestling calls were more similar when nestlings called together than when they called alone (Leonard & Horn, 2001c). Whether this convergence is a response to competition per se is uncertain. As nestling tree swallows age, their calls become more similar to those of brood mates and less similar to those of other broods, partly, perhaps, to facilitate parent–offspring recognition after fledging (Leonard, Horn, et al., 1997). Thus perhaps the increase in call rate in response to nest mates coincidentally yielded more calls that matched the brood's typical call structure.

Certainly the nestlings' responses to competing calls increasing call rate and call similarity—would seem to increase rather than decrease acoustic interference. These acoustic interactions appear to be competitive scrambles to capture the parent's attention and perhaps to mask competing signals rather than more intricate exchanges that would reduce interference overall. That said, tests in other contexts or at other ages might well yield more sophisticated forms of interaction. For example, shortly before fledging, nestlings do appear to alternate their calls (personal observation), as experimentally shown in the closely related bank swallow (*Riparia riparia*; Beecher & Beecher, 1983) and in starlings (*Sturnus vulgaris*; Chaiken, 1990; see also Muller & Smith, 1978; Price & Ydenberg, 1995). Further work, for example, studies that use playbacks of calls, would be worthwhile.

How Do Nestlings Respond to Interference From Ambient Noise?

An alternative approach to studying how nestlings effectively transmit their calls despite noise from nest mates is to present nestlings with sound that can mask their calls but is neutral in content, such as white noise. Given that nest mates are the main source of acoustic interference within the nest, whatever calling strategies nestlings use in elevated noise presumably evolved partly to cope with noise from nest mates. Thus this approach uses neutral noise as a surrogate for noisy nestlings. A caveat to this approach, of course, is that nestlings might actually respond differently to such noise than to noise from nest mates, so the results should be interpreted cautiously. In particular, noise from ambient sources such as wind and running water has more energy in low frequencies than nestling noise, so one strategy for circumventing noise, raising call frequency (see later discussion), might be ineffective for dealing with nestmate calls.

Recently, we conducted several experiments testing how nestlings change their calls in the presence of 65 dB (sound pressure level [SPL]) white noise that is synthesized to cover the frequencies from 0 to 22 kHz, that is, encompassing the frequency range of nestling calls (approximately 2-10 kHz). We predicted that nestlings might show some of the same adjustments documented in other acoustic signalers exposed to elevated noise. Specifically, nestlings might simply increase call amplitude so that it remains high relative to the noise amplitude, a widespread strategy known as the Lombard effect (Brumm & Slabbekoorn, 2005). They might also increase call redundancy through an increase in call length or rate (Brumm & Slabbekoorn, 2005). Finally, they might change the frequency structure of calls. They might increase the lowest frequency of calls, which raises the calls above the low frequencies that predominate in most ambient environmental noise (Slabbekoorn & Peet, 2003) albeit not necessarily the higher frequency noise that comes from nest mates. Alternatively, however, they might decrease call bandwidth, which concentrates signal energy into a narrow frequency so that the call is easier to detect in any broadband noise (Lohr, Wright, & Dooling, 2003), including noise from nest mates. These vocal adjustments are usually studied as responses to abiotic and heterospecific noise; but because they are responses to acoustic interference per se, they might well apply to the acoustic interference from nest mates that interests us here.

Our experiments showed some of these responses, but the particular response varied depending on the time scale of the noise exposure. During 1 or 2 hours of exposure in the lab or field, nestlings did not change the length or frequency of their calls but did elevate call amplitude by approximately 10 dB (SPL; Leonard & Horn, 2005, 2007b). Thus, as in virtually every acoustic signaler tested to date (Brumm & Slabbekoorn, 2005), nestlings simply increased their call amplitude in response to elevated ambient noise. We tested whether this amplitude increase improved reception by parents by presenting parent tree swallows in the field with the same choice between different call rates as we used in the choice tests described previously, except that white noise was played at 60 dB (SPL) within the nest box and the sets of calls that parents had to choose between were played at either low (55 dB) or high (65 dB) SPLs. As in the earlier choice tests, parents preferentially directed feedings toward higher call rates but only when the calls were played back at the higher levels. Thus, noise interfered with parents' responses to calls, and raising call amplitude was an effective strategy for overcoming that interference.

These experiments tested nestlings' responses to short periods of elevated noise, simulating the short-term elevations in noise levels that might occur, for example, when the whole brood is hungry and thus calling loudly. If noise persisted for longer periods, however, as in a nest with a particularly large brood, nestlings might respond differently. In particular, even if begging is energetically cheap, as in tree swallows (Leech & Leonard, 1996; Leonard, Horn, & Porter, 2003), delivering louder calls at a higher rate might be marginally more expensive or riskier in attracting predators (Leech & Leonard, 1997) than calling more quietly. Thus nestlings might use a different strategy to respond to noise levels that are sustained over days rather than the hour or less used in the experiments described previously. ACOUSTIC INTERACTIONS IN NESTLINGS

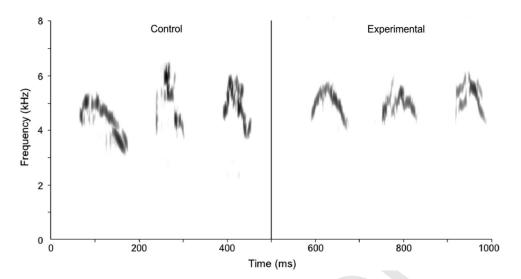


Figure 2. Spectrograms (bandwidth 761 Hz; resolution 1 ms, 23 Hz) of calls of nestlings after 48 h of ambient noise playback at 55 dB (sound pressure level [SPL]; control, left three calls) or 65 dB (SPL; experimental, right three calls). Each call is from one of the three broods whose changes in call bandwidth were the closest to the median for that treatment.

To test the responses of nestlings to noise over longer time periods, we played back white noise at nests in the field for 48 hours and compared several call characteristics at the end of the noise exposure (Leonard & Horn, 2007b). Out of call length, amplitude, emphasized frequency, and frequency range, the only call variable that showed a significant effect was call frequency range, which decreased in experimental relative to control nestlings (see Figure 2). Call structure changes quite rapidly during the nestling period (Leonard & Horn, 2006), so even this difference sustained over just 2 days might have a more persistent effect on call development. Indeed, we have since extended the experiment by playing white noise from Day 3 to Day 15 of the nestling period (Leonard & Horn, 2007a). Preliminary results suggest that nestlings at nests with elevated ambient noise again produce calls of narrower bandwidth, and the difference persists through the nestling period to at least 2 days after the noise is turned off, consistent with a more permanent, developmental change in call structure. Neither experiment showed any detectable effect of elevated noise on parental feeding rates or nestling growth.

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These results are consistent with our expectation that nestlings might use more efficient strategies than simply increasing call amplitude to deal with noise over the long term. Higher minimum frequencies and narrower frequency ranges are both call features that have been cited as adaptive responses to elevated noise (see earlier discussion). Thus nestlings might adaptively shift the frequency structure of their calls to deal with noise, which is perhaps a cheaper strategy than sustaining the high call amplitudes they showed in the short-term lab experiment. Alternatively, the shift in frequency could be a nonadaptive by-product of disrupted auditory feedback, although previous studies of auditory feedback have applied much more intense sound levels or deafening with variable results (e.g., Heaton & Brauth, 1999; Watanabe, Eda-Fujiwara, & Kimura, 2007).

Whether the frequency changes we observed were adaptive adjustments to noise or not, the results do show that ambient noise at the nest can affect call structure and perhaps call development. In turn, given that nest mates are the predominant source of acoustic interference in the nest, the results suggest that acoustic interactions might affect not only call output (rate and amplitude) on the short term but also, over a developmental time scale, the frequency structure of nestling calls.

Summary and Conclusions

We have shown that calling by nestling birds is both a group signal, which influences parental feeding rate, and a collection of individual signals, which influence food allocation within the brood. Here we summarize how these two contrasting functions of calling might account for the structure and use of begging calls.

The competitive function of calling has been our main focus. Our experiments show that nestlings increase call rate when nest mates call and increase call amplitude when ambient noise levels increase. These results suggest that the main effect of the competitive use of calls on call structure is an increase in overall call output. It may also affect the frequency patterning within calls; nest mates that call together tend to converge on a shared call structure, and nestlings exposed to moderate levels of elevated noise give calls with narrower bandwidths.

These results also have implications for the cooperative function of calling. Most obviously, nestlings' increase in call output in response to acoustic interference presumably intensifies the signal of the brood as a whole, more than it would if nestlings avoided interference, for example, by alternating calls. Thus, although nestlings' responses to interference appear inefficient, they might be compensated at the brood level by increased provisioning rates to the brood (Royle et al., 2004). Indeed, what seem to be escalations between nest mates may actually be cooperative efforts to amplify the signal of the brood as a whole (Forbes, 2007; Wilson & Clark, 2002; see also Bell, 2007; Mathevon & Charrier, 2003). Our finding that calls became more similar when nestlings called together fits well with this possibility.

Clearly, the results suggest an interplay between signaling by and within the brood that might have important effects on how calls regulate provisioning. In this respect they contribute to the increasing evidence from a wide range of signaling systems that competitive interactions within groups can benefit individuals by increasing the signal output of the group as a whole (Bell, 2007). For example, the competitive interactions within choruses of frogs and toads create a collective signal that attracts females more effectively than lone females (Wells & Schwartz, 2006).

Nestling calling is unique among the systems studied to date, however, in that the interplay between competition and cooperation may affect signal development. For example, convergence in call structure during acoustic interactions among nest mates might account for how calls become more similar within but more distinctive between broods in many species, including tree swallows (Leonard, Horn, et al., 1997). Similarly, changes in the frequency range of calls in response to ambient noise might partly account for interbrood variation in call structure. Especially given that nestling calls often develop into adult vocalizations (Sharp & Hatchwell, 2006), the effect of acoustic interactions on call development deserves more study.

How cooperative and competitive acoustic interactions among nestlings relate to signal design is likely to vary widely among species. Nestling calls display an enormous range of variation across species, from abrupt, broadband calls to long whistles (Popp & Ficken, 1991). Even within species, nestling calls can be diverse in structure and function (Sharp & Hatchwell, 2006), such as the whistles and whines given between and during feedings, respectively, by nestling white-browed scrubwrens(*Sericornus frontinalis*; Maurer, Magrath, Leonard, Horn, & Donnelly, 2003).

This variation, especially between species, might relate partly to variation in nest structure or resource competition within the nest (see discussions in Horn & Leonard, 2002, 2005), but ultimately they are bound to affect, and be affected by, acoustic interactions among nest mates. For example, several studies suggest that the calls of cavity nesting species, such as woodpeckers, have more abrupt onsets and offsets and broader frequency ranges than the calls of open nesting species (Horn & Leonard, 2002). If so, then cavity species might tend to compete via strategic timing of calls, compared to open nesting species that might tend to vary the frequency structure of their calls.

Detailed studies of nestling calls are so few that such specific predictions are probably premature. Nonetheless, the few existing descriptions of acoustic interactions among nestlings suggest they are indeed more diverse than implied by the relatively simple interactions we report here for tree swallows. For example, unlike tree swallows, barn owl (*Tyto alba*) chicks engage in complex vocal interactions that appear to determine which chick will get the next feeding from the parent (Roulin, 2002). Similarly, individual field sparrow (*Spizella pusilla*) nestlings call at different frequencies when calling with nest mates, perhaps to avoid overlap in call frequency (Popp & Ficken, 1991)—a response we predicted but did not observe in tree swallows.

Like the better understood choruses of male birds, anurans, and insects, begging nestlings illustrate how cooperation and competition affect acoustic signaling. Moreover, nestling calls have a developmental dimension not found in the more thoroughly studied systems. Given their tremendous variation across species, begging calls clearly offer promising opportunities for developmental and comparative studies of acoustic signaling.

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