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Nestling responses to adult food and alarm calls: 1. Species-specific responses in two cowbird hosts

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Begging by nestlings can prove costly, either through energy expenditure if food-bearing parents are not present, or through increased predation risk. Therefore, parents may provide cues to modulate begging. We investigated responses of 7-day old nestlings of eastern phoebes, *Sayornis phoebe*, and red-winged blackbirds, *Agelaius phoeniceus*, to various adult calls. Phoebes begged strongly to playback of conspecific food calls but not to other vocal stimuli, and only weakly to manual stimulation. They had no specific response to phoebe alarm calls. We suggest that phoebe alarms, which were given mainly when a partner was nearby, at both egg and chick stages, function primarily to warn mates. Red-winged blackbirds begged most readily to manual stimulation and ceased begging, and crouched, specifically to conspecific alarm calls. Therefore, in phoebes begging is 'switched on', and in red-winged blackbirds it is 'switched off', by parental calls. We suggest that for species like red-winged blackbirds, which nest on flexible substrates, nestlings readily beg to vibrational cues such as nest movement, so parent alarms are important to switch off begging at inappropriate times. For species like phoebes, which nest on rigid substrates, food calls induce begging in the absence of vibrational stimuli, and may replace the need for alarm calls to nestlings. The marked differences seen in these hosts of the brown-headed cowbird, *Molothrus ater*, raises the question of whether nestlings of this generalist brood parasite can eavesdrop on such diversity in host cues, a problem we address in our companion paper.

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The loud and rapid begging calls of nestling birds signal their hunger and stimulate parental provisioning (Kilner et al. 1999). However, broods that beg more intensely may suffer increased predation (Redondo & Castro 1992) and experimental playbacks from artificial nests have confirmed that increased calling can indeed attract more predators (Haskell 1994; Leech & Leonard 1997; Dearborn 1999). This predation cost is likely to be an important selection pressure on begging signals because comparative studies show that species with more vulnerable nests have less conspicuous nestling begging calls (Redondo & Arias de Reyna 1988; Briskie et al. 1999; Haskell 1999).

Parents could reduce this cost in two ways. First, they could alert noisy chicks by giving alarm calls when predators are near the nest. Many field studies have reported that nestlings cease begging and crouch when their parents give alarm calls in response to a predator (East 1981; Duckworth 1991; Halupka 1998), and in some

species playback experiments have shown that parent alarms can reduce chick begging (Greig-Smith 1980; Knight & Temple 1986; Platzen & Magrath 2004; but see Maurer et al. 2003). However, only one study has shown that nestlings respond specifically to their own species' alarm calls (Davies et al. 2004). Furthermore, in some species, parental alarms do not lead to a reduction in chick begging (J. R. Madden & N. B. Davies, personal observation) and may function instead to distract predators away from the nest (Greig-Smith 1980) or alert mates (East 1981; Yasukawa 1989) rather than warn nestlings.

Second, parents could give calls as they arrive at the nest to signal to the chicks that food is about to be delivered and it is safe to beg. Several studies involving video recordings at nests have reported that parents give 'food calls', especially to young chicks, and that these apparently rouse their chicks to beg, whereas older chicks beg more in response to tactile and visual cues from the parent (Bengtsson & Rydén 1981; Khayutin 1985; Clemmons 1995). Only two studies have used experimental playbacks to confirm that nestlings beg directly in response to food calls (Leonard et al. 1997; Maurer et al. 2003).

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Given the paucity of evidence that nestlings react specifically to the calls of their parents, our aim was to test the responses of nestlings of two North American passerines that are commonly parasitized by the brown-headed cowbird, *Molothrus ater*: the red-winged blackbird, *Agelaius phoeniceus*, and the eastern phoebe, *Sayornis phoebe*. In our companion paper (Madden et al. 2005), we tested whether the parasitic chicks of the brown-headed cowbird tune in to the parent-offspring communication systems of these two hosts.

METHODS

Study Area

In April and May 2003, we monitored 81 eastern phoebe and 18 red-winged blackbird nests in Tompkins County, New York, U.S.A., during egg laying to predict day of hatching.

Natural Levels of Phoebe Calls

We recorded the number of alarm calls given by one phoebe parent in 1 min, immediately after our arrival within 3 m of the nest. Nests were visited during both the egg and chick stages. We searched for signs of a partner and, if we could not see it within that minute, we scored it as absent. Repeated measures were made at 19 of the 37 nests surveyed. To avoid problems of pseudoreplication, we considered only a single alarm count from each nest, consistently selecting the last count made.

To record natural usage of food calls, we set up a miniature (26.7 × 16.65 × 17.4 mm) security camera (Millennium wide-angle colour camera from Rapid Electronics, Colchester, U.K.) and a tie-clip microphone (Electret condenser mini tie-clip microphone from Rapid Electronics) within 30 cm of nest cups. These were connected via 10 m of cabling to a Canon MV500i Digital Video Camcorder, and 90 min of action at the nest was filmed. Adults typically returned to the nest within 5 min of our departure and seemed unperturbed by the camera. We analysed the last 60 min of videotape.

Box Experiments

Chicks were temporarily removed from their nests 7 days after hatching and transported to a quiet test site in a heated old nest of their own species. We put replacement chicks into the nest during the temporary absence of the usual chicks to prevent parents deserting. Test chicks were then left in the experimental nest for at least 80 min before testing. We tested nestlings from six different phoebe and six different blackbird nests with a maximum of three per brood. All nestlings were tested singly. All 12 red-winged blackbird chicks tested came from unparasitized nests. Six of the 11 eastern phoebe nestlings tested came from nests that contained a brown-headed cowbird nestling.

Prior to the recording, we put the experimental nest into the test box: a Sterilite Ultra 40l white plastic bin. This was equipped with a Canon MV500i video camera and a tie-clip microphone, both suspended above the nest, and had a hole in the side to allow access to the nest. A Sony SRS-A27 speaker was placed next to the box for call playback. Calls were broadcast directly from WAV files on a laptop computer, via the Sony speaker. Volume levels were set constant.

Alarm experiment

We tested the effect of three different vocalizations on chick begging behaviour. We classified two vocalizations as alarms, because they were given by parent eastern phoebes and red-winged blackbirds in response to a predator near the nest. We could record these by acting as a potential predator, approaching a nest and recording vocal responses of adults. The alarm calls of phoebes (Fig. 1a) are very simple, short (<0.02 s) 'chips' that rapidly decline in both strength and pitch, whereas, the alarms of red-winged blackbirds (Fig. 1b) are much longer (>0.4 s) 'sees' which retain pitch and strength for the duration of the call after an initial lowering of pitch. We also played a simple control vocalization, a contact call of rose-breasted grosbeaks, *Pheucticus ludovicianus*, recorded on territories in the study area (Fig. 1c). This 'chink' call is short and retains a fairly constant pitch, with at least three overtones.

We examined how the presentation of a call affected a chick's begging behaviour, compared to its baseline begging. Chicks of both species begged in response to manual stimulation, so we induced begging for 3 s to measure a baseline begging response. We could stimulate red-winged blackbirds to beg by tapping their bill lightly with a pair of forceps. Phoebes required more vigorous stimulation, in the form of a knock on the side of the test box. We then played the two alarm call types and the control vocalization, accompanied by manual stimulation every 3 s, for a further 18 s.

Every chick was subjected to all three types of vocalization. We used three recordings of each alarm call type each taken from a different adult. Each of these was edited to produce a 6-s cut, containing five calls. The choice of which of the three exemplars of each alarm type was used in each experiment, and the order in which the two alarm call types and the control vocalization were presented, were selected at random. The chick was left undisturbed for 1 min between each experimental sequence. We subsequently scored chick behaviours from the videos, noting the total number of calls and duration (s) of gaping during each experimental period. We measured two aspects of begging. Time spent gaping was observed directly. The number of calls was highly correlated with time spent gaping (Pearson correlation, $r_{61} = 0.58$, $P < 0.001$), so to provide an independent measure of response we also calculated the number of calls made per second spent gaping. Results are presented as baseline begging minus begging during the playback period. For simplicity, they are subsequently referred to as 'gape' and 'calling'. A general reduction in begging during the playback,

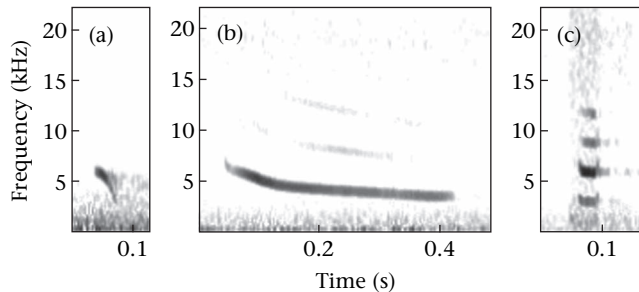


Figure 1. Sonograms of typical individual calls used in the alarm experiment. (a) Eastern phoebe alarm. (b) Red-winged blackbird alarm. (c) Rose-breasted grosbeak contact call.

compared to the baseline levels, might be expected if the chick became fatigued or habituated to repeated manual stimulation with no reward. Our analyses therefore focus on differences in response to the three playbacks.

Food call experiment

Each chick experienced the food call experiment 5 min after the end of the alarm experiment, having spent the intervening period undisturbed in the test equipment. We used four vocalizations in this experiment: the phoebe food call, given by parents as they approached the nest with food (collected from our videos); the phoebe song (taken from Elliot et al. 1997); the red-winged blackbird food call (taken from Elliot et al. 1997), described by Yasukawa (1989) as a call given by parents visiting the nest containing chicks, a context similar to that of the phoebe food call; and house wren, *Troglodytes aedon*, song (taken from Elliot et al. 1997), which acted as a complex control vocalization from a bird found in the local area. Phoebe song (Fig. 2a) is a two syllable ‘fee-bee’. The food call of phoebes is a complex ‘chatter’, made up of many different syllables which themselves are structurally complex and comprise several overtones (Fig. 2b) and so shares similarities with the song of the house wren (Fig. 2c). Conversely, the red-winged blackbird food call is a much simpler series of ‘chits’, consisting of repetitions of similar syllables, which are themselves structurally simple and consist of only fundamental frequencies (Fig. 2d). We used two different cuts of 2 s of each vocalization. Cuts for phoebe food calls and house wren songs comprised a single chatter or song phrase. Phoebe song cuts comprised three repetitions of fee-bee. Cuts for red-winged blackbird food calls included four repeated series of twitters. Cuts of the three vocalizations taken from Elliot et al. (1997) came from an unknown number of adults, while those we recorded on the study site came from different adults. One cut (chosen randomly) was used during the playback treatment, and the second during the playback and stimulation treatment. We switched the assignment of cut to the two experimental treatments between chicks.

We tested each chick with all four types of vocalizations, presented in random order. Before each test there was a control period of 10 s, during which the chick made no calls or gapes. For each vocalization the test then involved three treatments presented in random order: stimulation,

gentle brushing of the chick’s bill and nest edge with forceps for 6 s; playback, three repeats of the 2-s cut; playback and stimulation, these two stimuli presented simultaneously. Chick behaviour was filmed as described above, and we recorded total number of calls and total duration of gaping. Recording persisted until the chick had settled back into a state of rest when no calls or gapes were made. This usually took a few seconds. The next 10-s control period started 1 min after the end of each treatment. Time spent gaping (s) and number of calls per second spent gaping were obtained for each chick. One phoebe and one red-winged blackbird chick could not be induced to beg for at least one of the alarm experiments, so could not be included in a repeated measures analysis. They were omitted from the alarm analysis, but did respond during the food call experiments, and so were included in those results as they had experienced the same alarm stimuli in previous trials as all the other birds.

Statistical Analyses

The two independent variables, gape and calling, were analysed separately. For analysis of the alarm experiment, we used a repeated measures design, initially considering one within-subjects factor, Call (grosbeak control call, eastern phoebe alarm call, red-winged blackbird alarm call) and one between-subjects factor, Nest (to account for the fact that some chicks shared rearing environments).

For analysis of food call experiments, we again used a repeated measures design, analysing gaping and calling separately. We considered three fixed factors: Stimulus, presence or absence of manual stimulation; Playback, presence or absence of playback stimulation; Call, four types of vocalization. For comparisons between species, a between-subjects factor Species was included. Nest was initially included as a factor, but did not have a significant effect in any of the analyses and so was dropped from the model. The strongly non-normal distribution of data, caused by a large number of zero response scores, required us to perform 10 000 randomizations in order to calculate appropriate significance values, depending on the proportion of randomly derived F values that exceeded the F value derived from the original data. We achieved this using R (R Development Core Team 2003) to produce P values appropriate to the error structure of our data. All P values given are two tailed. Given the small sample sizes involved, some of our negative results should be treated with caution. All other analyses were conducted using SPSS v11 (SPSS Inc., Chicago, IL, U.S.A.).

Ethical Note

The work was conducted under state and federal permits held by D. W. Winkler, and the protocols were approved by the Institutional Animal Care and Use Committee at Cornell University. We temporarily removed chicks from their nests (under licence), placed them in an old conspecific nest, and took them to the laboratory, keeping them warm in transit using a hot water-bottle placed under the nest. We ensured that some chicks remained in the natural

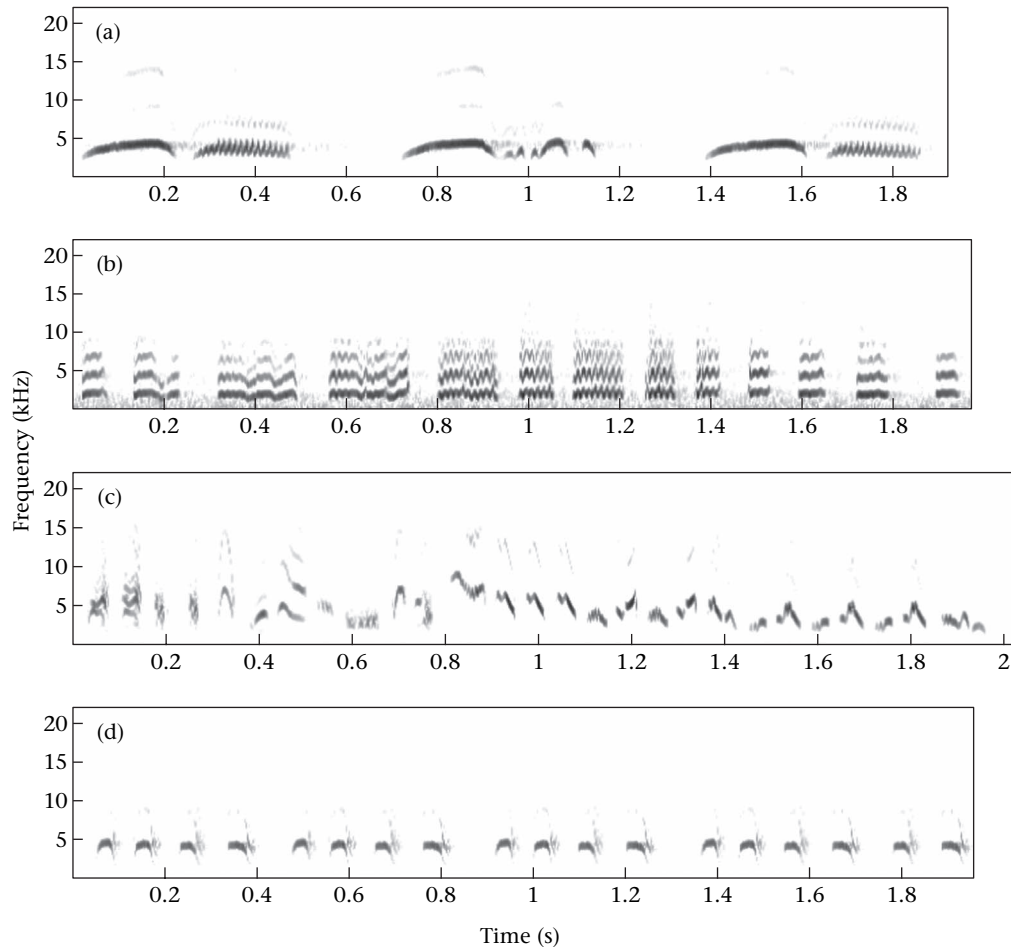


Figure 2. Sonagrams of typical individual calls used in the food call experiment. (a) Eastern phoebe song. (b) Eastern phoebe food call. (c) House wren song. (d) Red-winged blackbird food call.

nest (using similarly aged replacements where necessary) so that parents would not desert. In the test box, the nest was supported by a wooden stand and heated from below with an insulated jar of regularly renewed warm water, following the methodology of Kilner & Davies (1998). The temperature of the nest was monitored continuously with a thermistor probe in the nest (with a digital readout) and maintained at a natural temperature of 25–30°C. At the end of testing, chicks were fed with minced beef to satiation prior to being returned to their nests. No chicks died while removed from the nests, no adults deserted nests from which chicks had been taken and visits to the nest up to 2 days after testing conducted as part of a separate study revealed that all returned chicks survived at least that long.

RESULTS

Field Observations of Phoebe Calls

Alarms

We counted alarms given in response to human presence at 37 nests. We found no difference between the number of alarm calls/min given by eastern phoebes at

the egg stage and nestling stage (ANOVA development stage effect: $F_{1,36} = 0.78$, $P = 0.38$; Fig. 3). However, there were dramatically more calls when in the presence of another adult phoebe than when alone (ANOVA presence/absence effect: $F_{1,36} = 40.45$, $P < 0.001$; Fig. 3), a situation apparently unaffected by developmental stage (interaction: $F_{2,35} = 2.26$, $P = 0.14$). These results suggest that phoebe alarms might function to warn partners from

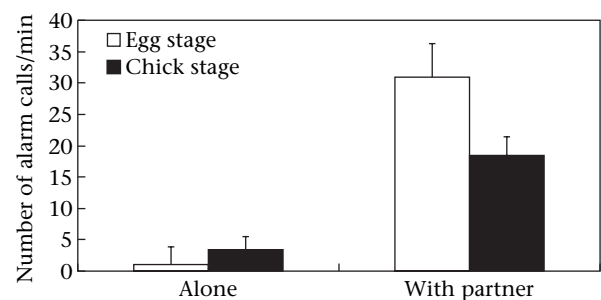


Figure 3. Number of alarm calls/min given by eastern phoebes in response to human presence at the nest at differing nest stages and in differing social situations. Sample sizes from left to right are: 10, 19, 3, 9. Means + SE are shown.

approaching the nest and so revealing its location, rather than to warn noisy nestlings.

Food calls

Eleven nests were filmed twice, when chicks were 4 and 8 days old. The proportion of visits at which food calls were given did not vary between days 4 and 8 (paired t test: $t_{10} = 0.54$, $P = 0.60$). A further 20 nests were filmed at either 4 or 8 days. Phoebes gave food calls on approach to their nests at an average 26.7% of visits (range 0–100%, $N = 31$ nests). It was not possible to confirm that the parent was bringing food to the nest at each visit.

Box Experiments

Alarm Experiment

Neither eastern phoebes nor red-winged blackbirds differed significantly in baseline begging, measured either as time spent gaping or calls per time spent gaping, prior to any of the three alarm playbacks (Friedman tests: eastern phoebe: gape: $\chi^2_2 = 0.88$, $N = 8$, $P = 0.65$; call: $\chi^2_2 = 0.82$, $N = 8$, $P = 0.66$; red-winged blackbird: gape: $\chi^2_2 = 0.67$, $N = 10$, $P = 0.72$; call: $\chi^2_2 = 0.91$, $N = 10$, $P = 0.63$).

Eastern phoebes. Ten phoebe chicks were tested. They did not respond differently to any of the three calls in their gaping (Call: $F_{2,8} = 0.68$, $P = 0.53$; Fig. 4a). There was also no significant difference in their calling rate response (Call: $F_{2,8} = 3.80$, $P = 0.07$; Fig. 4b), although there was a hint of a stronger reduction in calling rate during the two alarm playbacks. There were no significant interactions between Call and Nest for either gaping or calling (Call \times Nest: gaping: $F_{10,8} = 1.88$, $P = 0.19$; calling: $F_{10,8} = 2.82$, $P = 0.08$). We conclude that eastern phoebe chicks showed no clear selective response to adult conspecific alarm calls for either measure of begging.

Red-winged blackbirds. Eleven red-winged blackbirds were tested. They reduced both gaping and calling more in response to red-winged blackbird sees alarms (Call: gape: $F_{2,10} = 10.53$, $P = 0.003$; calling: $F_{2,10} = 17.48$, $P = 0.0005$; Fig. 5). There was no significant difference in response to phoebe alarms compared with grosbeak contact calls (post hoc least significant difference, LSD, tests: gape: $P = 0.09$; calling: $P = 0.30$), but response to red-winged blackbird alarm calls was significantly stronger than to both these other vocalizations (post hoc LSD tests: gape: both $P < 0.04$; calling: both $P < 0.004$). Rearing environment had a significant effect in the case of gaping (Nest: $F_{5,5} = 5.20$, $P = 0.05$), but this did not affect the way that the chicks responded to different calls (Call \times Nest: $F_{10,10} = 1.74$, $P = 0.20$). Conversely, there was a significant interaction between nest and response in the case of calling (Call \times Nest: $F_{10,10} = 11.29$, $P = 0.0003$), but responses did not differ across nests (Nest: $F_{5,5} = 3.14$, $P = 0.12$).

In addition to these quantitative differences, we observed marked qualitative differences in behaviour. Six of the red-winged blackbirds (four different nests) crouched

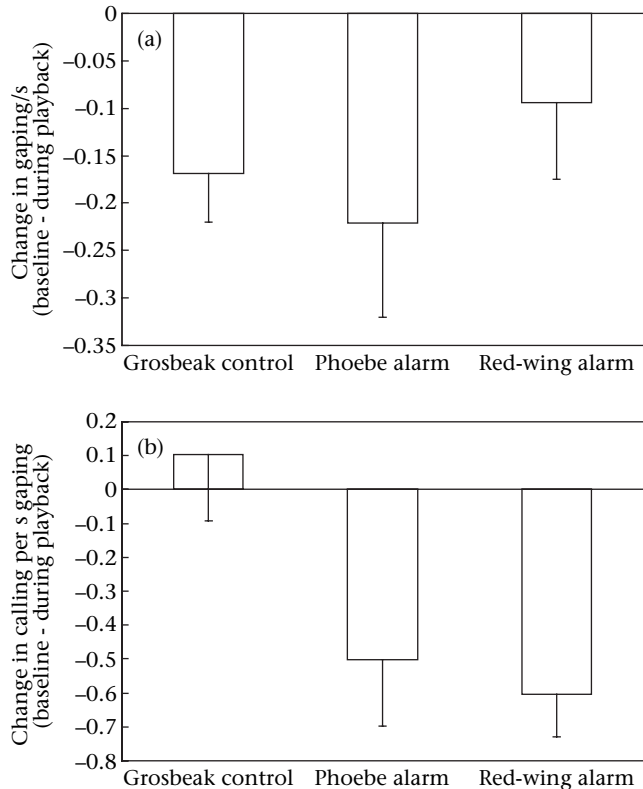


Figure 4. Change from baseline begging levels in begging responses of 10 phoebe nestlings during playback of a conspecific alarm call, a heterospecific alarm call (red-winged blackbird) and a control call (rose-breasted grosbeak). (a) Duration of gaping (s). (b) Number of calls given per second spent gaping. Means + SE are shown.

immediately in response to red-winged blackbird alarms whereas none crouched to the other two vocalizations. The proportions crouching to different alarm calls were significantly different ($\chi^2_2 = 14.4$, $P < 0.001$). We conclude that red-winged blackbird chicks respond most strongly to playback of conspecific sees alarms by reducing their begging behaviour. Six of the 11 blackbirds crouched when alarmed by conspecific calls, compared with none of the 10 phoebes (Fisher's exact test: $P = 0.012$).

Food call experiment

Eastern phoebes. Eleven phoebe chicks were tested, including all 10 from the alarm experiment. The effects of call type were dramatic, with higher levels of both gaping and calling to eastern phoebe chatter food calls than to any of the other calls (Call: gape: $F_{3,27} = 20.17$, $P < 0.001$; calling: $F_{3,27} = 10.94$, $P < 0.001$; post hoc LSD tests: phoebe food calls versus all other calls: $P < 0.01$; comparisons between all other calls: $P > 0.1$; Fig. 6). Phoebe chicks gaped more when manually stimulated (Stimulus: $F_{1,29} = 10.32$, $P = 0.01$) and when a call of any type was present (Playback: $F_{1,29} = 17.5$, $P < 0.001$), than when such stimuli were absent. However, the form of stimulation did not affect their calling rates. We conclude that phoebe chicks begged most strongly in response to conspecific food calls. Although they also responded to

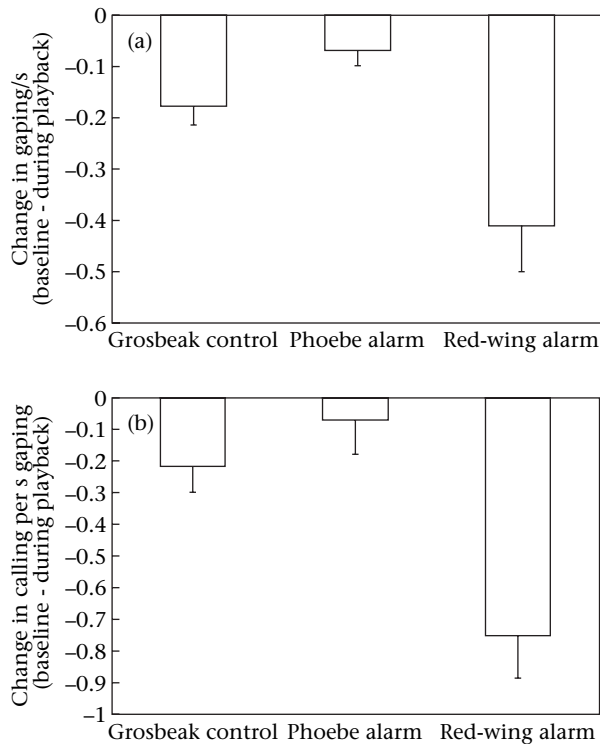


Figure 5. Change from baseline begging levels in begging responses of 11 red-winged blackbird nestlings during playback of a conspecific alarm call, a heterospecific alarm (eastern phoebe) call and a control call (rose-breasted grosbeak). (a) Duration of gaping (s). (b) Number of calls given per second spent gaping. Means + SE are shown.

manual stimulation, this did not enhance their response to playback of food calls.

Red-winged blackbirds. Twelve red-winged blackbirds were tested, including all 11 from the alarm experiment. They gaped and called more when stimulated manually (Stimulus: gape: $F_{1,35} = 40.6$, $P < 0.001$; calling: $F_{1,35} = 15.67$, $P < 0.001$; Fig. 7). They also begged differently in response to different playbacks. They gaped more to phoebe chatter food calls than to others (Call: $F_{3,33} = 5.68$, $P < 0.001$; Fig. 7). We conclude that red-winged blackbird chicks responded most strongly to manual stimulation. They elevated their begging, specifically gaping, a little when subjected to conspecific chit food calls, but there was a stronger gape response to the chatter food calls of eastern phoebes. In contrast to the phoebe, calls did not enhance begging when manual stimulation was applied. For example, the level of gaping induced by playback with manual stimulation was almost identical to that induced by manual stimulation alone.

DISCUSSION

Two common hosts of brown-headed cowbirds, eastern phoebes and red-winged blackbirds, differed in the way that vocal and tactile cues from the parents modulated chick begging behaviour. Adult phoebes effectively 'switch

on' nestling begging behaviour, with chicks showing very strong selective responses to conspecific food calls given when the parent approaches the nest. Levels of manual stimulation, which are known to induce begging in many other species, such as gentle brushing of the bill or side of nest (e.g. Davies et al. 2004), were ineffective for the phoebes, which instead usually required a knock to the side of the box containing the experimental nest.

Our observations of adult behaviour at nests revealed that food calls were given in only around a quarter of visits. We suggest that, although such calls are very efficient at provoking begging, chicks may also pay more attention to visual cues, such as the arrival of the adult at the nest, which were not considered in this study. We propose a hierarchy of cues which provoke begging in the phoebe chicks. Visual cues are likely to be a primary motivation since they seem sufficient to induce begging in about three-quarters of all nest visits. Under conditions when these are ineffective, such as low light or early in life before the eyes are open, vocal cues then might exert the strongest effect. Vibrational cues appear to be much less effective in the eastern phoebe.

The response of red-winged blackbirds to food calls was much less clear. Red-winged blackbird nestlings readily begged to manual stimulation, both with and without playbacks. With such a strong response to vibrational stimulation, an accompanying specific food call by approaching parents may be less necessary. Although the nestlings did respond to conspecific food calls, they responded more strongly to food calls of phoebes. We suggest that phoebe food calls share some similarities with red-winged blackbird food calls, namely many short syllables produced rapidly with short intersyllable intervals, but with more complex syllable structure and more numerous overtones. Thus, the phoebe food call may appear to red-winged blackbird nestlings as a supernormal red-winged blackbird food call and so provoke a stronger response. We propose that the hierarchy of cues that provoke begging by red-winged blackbird nestlings is headed by vibrational cues (and possibly visual cues, which we did not test). Red-winged blackbird food calls appear to be less important in inducing chicks to beg. Rather than using vocalizations to induce begging, red-winged blackbird adults instead switch off nestling begging with alarm calls at the approach of a predator to the nest. Red-winged blackbird nestlings greatly reduced their levels of gaping and calling when a conspecific alarm was played, and in several cases crouched in the nest.

We suggest that across species, whether parental calls switch on or switch off nestling begging could depend on features of their nesting ecology. Our study manipulated two cues that could influence nestling begging behaviour, namely vibrational cues and adult vocalizations. Vibrational stimuli may often be effective because movement of the nest can indicate that a parent has arrived bearing food. An immediate response would have obvious fitness payoffs if chicks that begged early obtained a greater proportion of the food brought to the nest (Dearborn 1998). Selection might then favour increased sensitivity of response, as in red-winged blackbirds, where the lightest brushing of the nest rim induces begging. However, nest

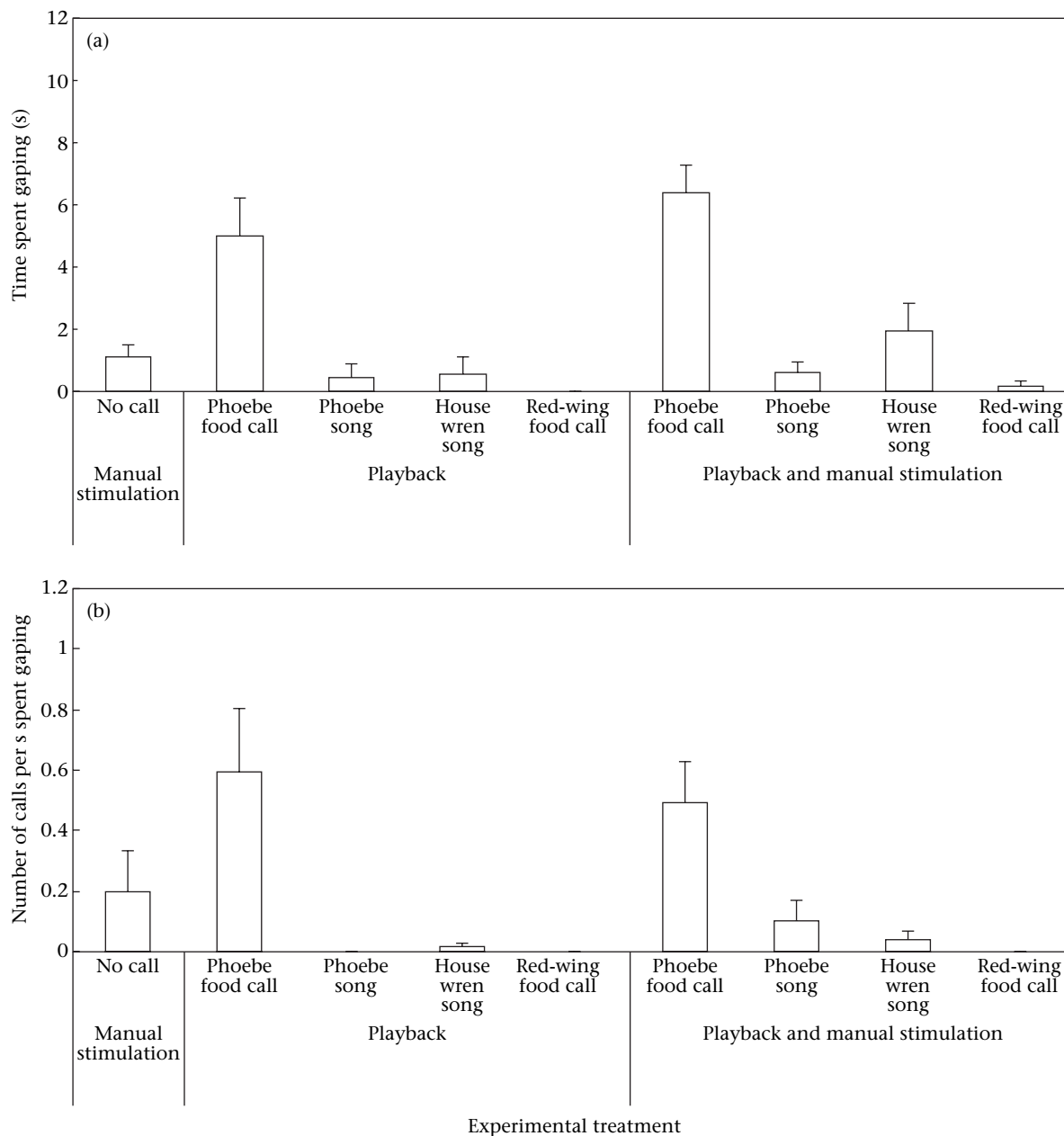


Figure 6. Responses of 11 phoebe nestlings in the food call experiment: (a) gaping or (b) calling while gaping. Two cues were used to provoke begging: manual stimulation and playback. Means + SE are shown.

movement may be caused by factors other than provisioning parents (e.g. a gust of wind), so a sensitive begging response imposes costs both energetically (Chappell & Bachman 2002) and in increased predation risk (Redondo & Castro 1992; Haskell 1994, 1999). Therefore, switching off begging at inappropriate times by means of parent alarm calls becomes beneficial.

We predict that other species that nest on flexible substrates, for example reeds, grass or branches, and whose chicks respond to vibrational stimulation, will also possess an effective alarm system that suppresses begging. This is the case for those species that we are aware of where nestlings respond to alarms: European robin, *Erithacus rubecula*, dunnoek, *Prunella modularis*, reed

warbler, *Acrocephalus scirpaceus* (Davies et al. 2004), American goldfinch, *Carduelis trisis* (Knight & Temple 1986), red-winged blackbird (this study) and white-browed scrubwren, *Sericornis frontalis* (Platzen & Magrath 2004).

For species nesting in more rigid environments such as cavities or on the ground, vibrational cues may become less viable as the nest moves much less on the arrival of the parent. Visual cues may also be less reliable for cavity nesters than for open nesters, because nestlings have a more restricted view; a shadow at the nest entrance could be a passing predator rather than a parent. We suggest that under such circumstances nestlings should target other cues indicating the imminent arrival of food. We predict that in species nesting in cavities, on the

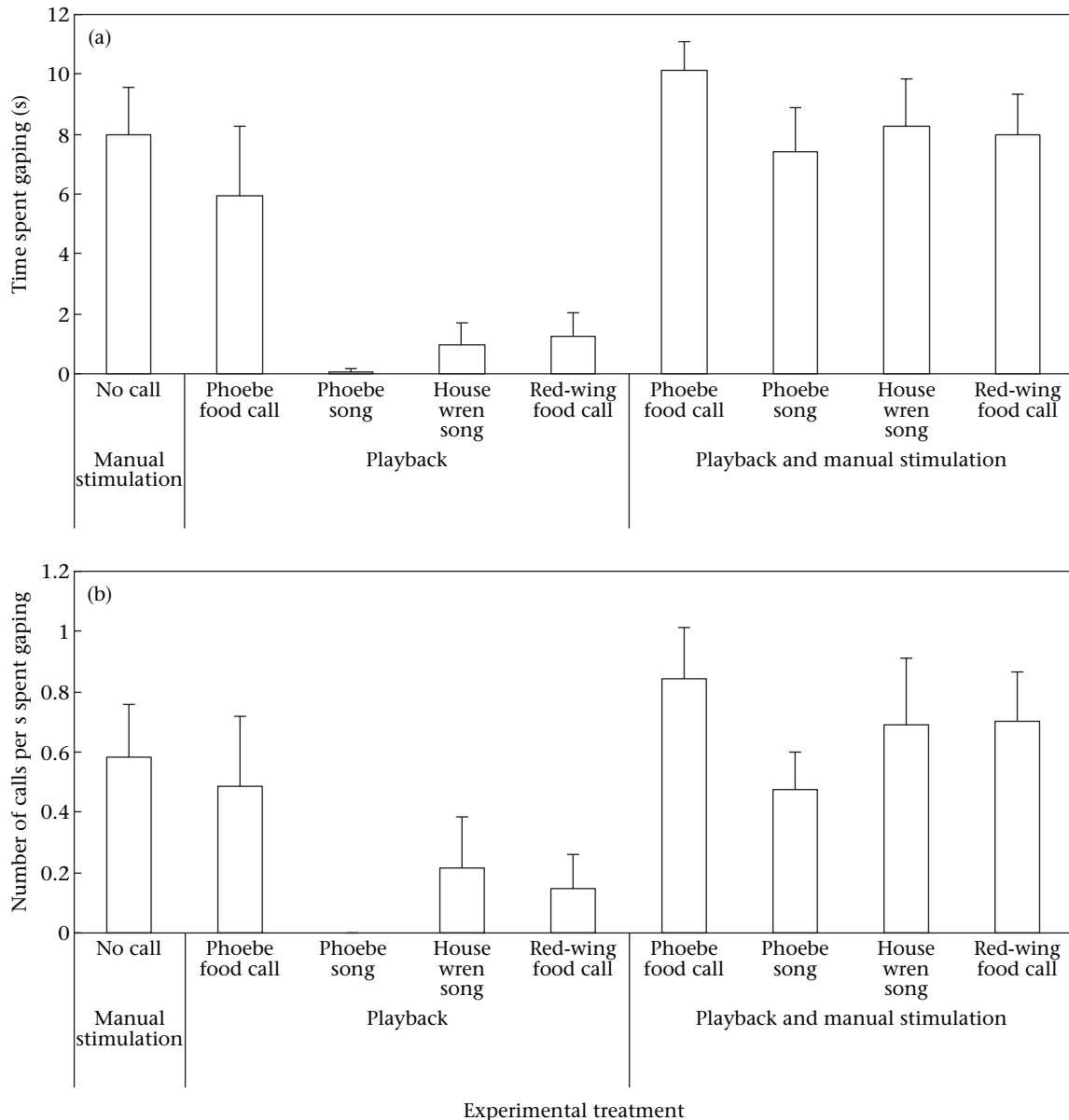


Figure 7. Responses of 12 red-winged blackbird nestlings in the food call experiment: (a) gaping or (b) calling while gaping. Two cues were used to provoke begging: manual stimulation and playback. Means + SE are shown.

ground or in other rigid sites, adults should induce begging with vocal cues. Species that we know of that have effective food calls all nest in such sites. Tree swallows, *Tachycineta bicolor* (Leonard et al. 1997), great tits, *Parus major* (Bengtsson & Rydén 1981; Khayutin 1985), black-capped chickadees, *Poecile atricapilla* (Clemmons 1995), and pied flycatchers, *Ficedula hypoleuca* (Bengtsson & Rydén 1981) are all cavity nesters, whereas eastern phoebes (this study) nest on ledges under cliffs or eaves and alpine accentors, *Prunella collaris*, nest in crevices (N. B. Davies, personal observation). White-browed scrub-wrens, which have food calls as well as alarm calls that silence their chicks, nest either on or near the ground (Platzen & Magrath 2004), so may benefit from both a switch-on and a switch-off system. However, it is too early to draw comparative conclusions; further studies are needed.

When food calls are used to induce begging, inappropriate begging becomes less likely, so an alarm call directed at chicks may be less important. Instead adults may use alarm calls to warn their partners not to visit the nest and so reveal its location when a predator is nearby. Therefore, we predict that, across species, parental calls will function either to switch on or switch off begging, and their primary function will depend on nesting ecology. Although vibrational and vocal cues both induced begging in red-winged blackbirds and phoebes, one or the other effectively became redundant when both were presented simultaneously, so that combining cues did not elevate the begging response to levels above those provoked by one cue in isolation.

We conclude that two common hosts of brown-headed cowbirds vary dramatically in the form and function of

their parent–offspring communication systems. If such cues mediate fitness payoffs to nestlings by increasing food acquisition or reducing the risk of attracting predators, then parasitic cowbird chicks are expected to eavesdrop on such signals and respond appropriately. Our study of just two potential host species has revealed wide variation in both the signal used by adults to modulate begging, and in the response shown by their nestlings. Brown-headed cowbird nestlings, which may develop in the nest of over 100 different host species (Ortega 1998), face a formidable challenge if they are to respond to the variety of host parent–offspring communication systems they are likely to encounter. We explore whether these brood parasites eavesdrop on these signals in our companion paper (Madden et al. 2005).

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