

Available online at www.sciencedirect.com

Nestling responses to adult food and alarm calls: 2. Cowbirds and red-winged blackbirds reared by eastern phoebe hosts

J. R. MADDEN, R. M. KILNER & N. B. DAVIES
Department of Zoology, University of Cambridge

(Received 27 February 2004; initial acceptance 5 May 2004;
final acceptance 18 November 2004; published online ■ ■ ■; MS. number: 8029)

We tested whether nestlings of a generalist brood parasite, the brown-headed cowbird, *Molothrus ater*, had special adaptations for tuning into host parent food and alarm calls. We compared the responses of 7-day-old cowbird nestlings reared by eastern phoebes, *Sayornis phoebe*, with those of a related, nonparasitic icterid, the red-winged blackbird, *Agelaius phoeniceus*, reared experimentally in phoebe nests. Cowbirds begged readily to manual stimulation but not to playbacks of either phoebe or red-winged blackbird food calls, irrespective of whether they had been reared alone, or together with phoebe nestlings (and so had experience of nestmates which responded strongly to phoebe food calls). Red-winged blackbirds reared by phoebes did not differ from those reared by conspecifics. They responded as readily as cowbirds to manual stimulation, but also (surprisingly) begged most strongly to phoebe food calls, whose rapid chatter might act as super-normal red-wing food calls. Both cowbirds and red-winged blackbirds reared alone by phoebes reduced begging most to red-winged blackbird alarms, suggesting that they share an innate icterid response, although this selective response was less marked in cowbirds reared alongside phoebe young. We conclude that cowbirds do not tune into phoebe host parent vocalizations. Given the problem of attending to such a variety of host species food and alarm calls, it may be most adaptive for generalist brood parasites simply to respond to general vibrational or visual cues likely to be encountered across all hosts.

© 2005 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

About 1% of bird species are obligate brood parasites; they lay their eggs in the nests of other species which serve as hosts, incubating the parasite's eggs and then rearing the parasitic young to independence (Rothstein 1990; Davies 2000). Parasitic young seem to behave unusually selfishly compared with the young of normal nesting species. This may take the extreme form of always ejecting or killing the host young, so the parasite chick is reared alone in the nest (some cuckoo species, honeyguides: Davies 2000). In other cases, the parasite chick tolerates the host young and is reared alongside them, but it begs more vigorously and often outcompetes its nestmates (e.g. some cuckoo species, cowbirds). This more vigorous parasite begging includes being quicker to beg, stretching higher when the host parents arrive with food, and more loud and rapid calling than the host young (cuckoos: Redondo 1993; Soler et al. 1995; Redondo & Zuniga 2002; cowbirds: Briskie et al. 1994; Dearborn 1998; Lichtenstein & Sealy 1998; Lichtenstein 2001). Even when the parasite is reared alone, it may

have exaggerated begging calls. For example, common cuckoo, *Cuculus canorus*, nestlings have extraordinarily rapid calls which sound like many host young (Davies et al. 1998; Kilner & Davies 1998; Kilner et al. 1999).

The consequence of an increase in begging calls is likely to be increased predation (Haskell 1994; Leech & Leonard 1997; Dearborn 1999). The more exuberant calls of nestling common cuckoos certainly make it easier for human observers to find the host nest, compared to nests with host young (personal observation). The loud calls of nestling brown-headed cowbirds, *Molothrus ater*, are likely to contribute to the increased predation of parasitized indigo bunting, *Passerina cyanea* nests (Dearborn 1999), although other factors may be involved too, such as more frequent nest visits by the host parents (Martin et al. 2000). In addition to costs of predation, begging imposes energetic costs (Kilner 2001; Chappell & Bachman 2002). Given their exaggerated begging calls, it should be especially advantageous for parasite chicks to tune into any host parent signals that might inform them when it is safe to beg or when begging is most likely to result in reward. These include alarm calls, produced when a predator is near the nest, which in some species cause

Correspondence: J. R. Madden, Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, U.K. (email: jrm54@cam.ac.uk).

the host chicks to cease begging, and food calls, which can prompt the host chicks to start begging when the parent approaches with food (Madden et al. 2005 and references therein).

The brown-headed cowbird is a generalist brood parasite which regularly parasitizes over a 100 North American host species (Ortega 1998). Parasitized nests usually contain a single cowbird chick, which is often reared alongside the host young. However, when the cowbird chick has a marked size advantage (small host species) or a head start in hatching and growth (hosts with long incubation periods), then the host chicks may all starve to death early in the nestling period, leaving the cowbird to be reared alone (Lorenzana & Sealy 1999; Hauber 2003a; Kilner 2003). One common host is the eastern phoebe, *Sayornis phoebe*, currently parasitized at about 20–30% of nests, and likely to be an old host because its habitat includes forest edges in the ancestral range of the cowbird (Hosoi & Rothstein 2000).

In our companion paper (Madden et al. 2005), we showed that parent food calls had a marked effect in 'switching on' the begging of the phoebe chicks, but that there was no specific effect of adult alarm calls on 'switching off' begging. Here, we tested whether cowbird chicks tune in to phoebe alarm and food calls, and investigated whether sharing the nest with host young influences the cowbird's response, by comparing cowbirds reared alone from hatching with those reared together with phoebe young. We also experimentally parasitized phoebe nests with the eggs of a closely related non-parasitic species from the same family as the cowbird (Icteridae), namely the red-winged blackbird, *Agelaius phoeniceus*. A molecular phylogeny shows that *Agelaius* is the sister genus of *Molothrus* (Johnson & Lanyon 1999). This allowed us to test whether any responses by the cowbird to host alarm and food calls are a special adaptation for a generalist brood parasite, exposed to a wide variety of alarm and food calls from their many host species, or a more general property shared by other (nonparasitic) icterids.

METHODS

General Methods

In April and May 2003, we monitored 81 eastern phoebe and 10 red-winged blackbird nests in Tompkins County, New York, U.S.A, during egg laying. We arranged that 20 phoebe nests were parasitized with a single cowbird egg taken from phoebe ($N = 17$), house finch, *Carpodacus mexicanus* ($N = 2$), and song sparrow, *Melospiza melodia* ($N = 1$), nests. At 10 of these nests, we manipulated the clutch so that the cowbird nestling would be reared alone. At the remaining 10 nests, we manipulated clutches so that two phoebe nestlings, which hatched either on the same day as the cowbird chick ($N = 18$) or a day later ($N = 2$) were reared alongside the cowbird. Phoebe young were introduced from a different nest on the day of hatching, except in two cases where hosts reared their own young with the cowbird. Molecular

sexing (Griffiths et al. 1998) later revealed that we had assigned equal numbers of male and female cowbird nestlings to the two treatments by chance. Nests were randomly assigned to each treatment, with no significant difference in hatch date between treatments (unpaired $t_{18} = 0.69$, $P = 0.500$). In addition, we experimentally parasitized a further eight phoebe nests with a single red-winged blackbird egg, manipulating clutches so that the red-winged blackbird was reared alone. We compared their responses with those of 12 red-winged blackbird chicks that were reared by their parents, to act as controls (see Madden et al. 2005).

Box Experiments

Chicks were moved and treated as described in Madden et al. (2005), and tested in the box equipment described in that paper. Chicks were tested in old nests of the same species by which they had been reared.

Alarm experiment

This experiment followed the protocols described in Madden et al. (2005). All nestlings were tested singly, at 7 days after hatching, with playbacks of alarm calls of eastern phoebes ('chips') and red-winged blackbirds ('sees'), as well as a control contact call ('chinks') of the rose-breasted grosbeak, *Pheucticus ludovicianus*. 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 at the start of each experiment, we induced chicks to beg by lightly tapping their bill for 3 s. This produced a baseline response. We then played the call, accompanied by manual stimulation every 3 s, for a further 18 s.

The creation of alarm exemplars and their selection and order of playbacks are described in Madden et al. (2005). 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 of gaping (s) during the 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: $r_{103} = 0.58$, $P < 0.001$), 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, compared to baseline levels, might be expected simply because 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 alarm experiment. This ensured that all nestlings had experienced the same alarming stimuli. We followed

protocols described in Madden et al. (2005), presenting four vocalizations: eastern phoebe food call ('chatter'), eastern phoebe song ('fee-bee'), red-winged blackbird food call ('chits') and house wren, *Troglodytes aedon*, song. We compiled two different cuts of 2 s of each type of vocalization, comprising either a single phrase (phoebe food call and house wren song) or two repetitions (phoebe song and red-winged blackbird food call). One cut (chosen randomly) was used during the playback treatment, and the other during the playback and stimulation treatment.

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 with no stimulation, during which the chick made no calls or gapes. For each vocalization the test then involved three treatments presented in random order: manual stimulation for 6 s (gentle brushing of the chick's bill and nest edge with forceps), playback for 6 s (three repeats of the 2-s cuts) and 6 s of playback with manual stimulation. Chick behaviour was filmed and we recorded the total number of nestling calls and total duration of gaping. From this, we calculated the number of nestling calls per time spent gaping. Recording continued until the chick had settled back and stopped gaping or calling, which usually took a few seconds. The next 10-s control period started 1 min after each treatment.

Statistical Analyses

The two independent variables, gaping 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, Treatment (rearing treatment: in the case of cowbirds, either alone or alongside two phoebe chicks; for red-winged blackbirds, either by red-winged blackbirds or phoebes).

For the food call experiment, we again used a repeated measures design, and considered three fixed factors: Stimulus: presence or absence of manual stimulation; Playback: presence or absence of playback stimulation; Call: four types of vocalizations. For comparisons between species, a between-subjects factor Species was included. A between-subjects design was also used to test the influence of rearing conditions on response. The factor Treatment refers to the conditions in which the subject was reared, in the case of cowbirds either alone or with two phoebe chicks, or for red-winged blackbirds, either by conspecifics or by eastern phoebes. This was a between-subjects factor, just like Species, although these two factors were never entered into the same model. The strongly non-normal distribution of data, caused by large numbers 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

For general licensing and ethical issues pertaining to chick care and testing, see Madden et al. (2005). We arranged artificial broods by removing and relocating eggs or chicks. In natural phoebe nests, cowbirds usually hatch several days before their host's offspring, causing the host eggs to die through exposure as the parents cease incubating in order to feed the cowbird (Hauber 2003a). Therefore, in our experimental nests, all unhatched eggs were removed from phoebe nests within 5 days of the cowbird hatching. External inspection confirmed that these eggs were not viable and they were destroyed. If host and parasite young hatched simultaneously, all excess phoebe chicks removed from manipulated nests were fostered with other broods of conspecifics, or were added to nests with cowbirds in order to provide two equal-aged nestmates. This did not induce any desertions and any subsequent mortality was the result of complete brood predation.

RESULTS

Alarm Experiment

Neither cowbirds nor red-winged blackbirds reared in phoebe nests differed significantly in either their gape or call response during the baseline period prior to any of the three alarm playbacks (Friedman tests: cowbird: gape: $\chi^2_2 = 2.24$, $N = 15$, $P = 0.33$; call: $\chi^2_2 = 1.70$, $N = 15$, $P = 0.43$; red-winged blackbird: all gaped continuously so no difference; call: $\chi^2_2 = 3.92$, $N = 8$, $P = 0.14$).

Cowbirds

We failed to induce begging from four of the 20 cowbirds, so these were excluded. Thus, 16 cowbirds were tested in the alarm experiment: nine were reared alone and seven with host young. Rearing treatment affected how cowbirds gaped to different calls (Call \times Treatment: $F_{2,28} = 10.01$, $P < 0.001$; Fig. 1a). Cowbirds reared alone showed the strongest reduction in gaping during playback of red-winged blackbird sees alarms (post hoc least significant difference, LSD, tests: phoebe versus grosbeak: $P = 0.66$; red-wing versus phoebe: $P = 0.006$; red-wing versus grosbeak: $P = 0.003$). By contrast, cowbirds reared with phoebes showed no significant difference in response to any of the three vocalizations (post hoc LSD tests: phoebe versus grosbeak: $P = 0.18$; red-wing versus phoebe: $P = 0.84$; red-wing versus grosbeak: $P = 0.86$).

By contrast, rearing treatment had no effect on calling behaviour, and there was no significant interaction (Call \times Treatment: $F_{2,28} = 0.70$, $P = 0.50$; Treatment: $F_{1,14} = 2.47$, $P = 0.14$). Regardless of treatment, red-winged blackbird alarm calls had the strongest effect on switching begging off (Call: $F_{2,28} = 4.09$, $P = 0.028$; post hoc LSD tests: calling: phoebe versus grosbeak: $P = 0.41$;

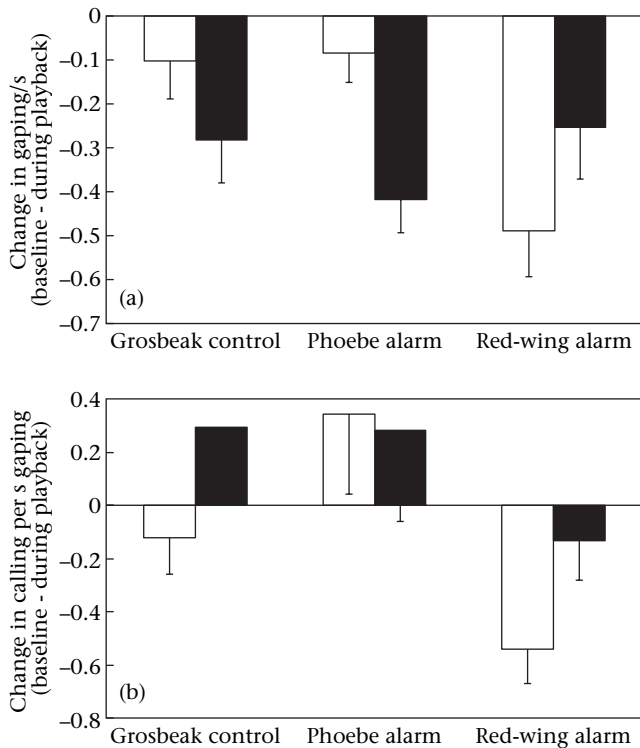


Figure 1. Change from baseline begging levels in begging responses of 16 cowbird nestlings, reared either alone by phoebes (□; $N = 9$) or alongside two host young (■; $N = 7$), when exposed to alarm calls of eastern phoebes or red-winged blackbirds and a grosbeak control call. (a) Duration of gaping. (b) Number of calls given per second spent gaping. Means + SE are shown.

red-wing versus phoebe: $P = 0.027$; red-wing versus grosbeak $P = 0.007$; Fig. 1b). In addition to these qualitative differences in response, three of the cowbirds crouched after playback of red-winged blackbird alarms, but none did so after any of the other alarms.

We conclude that cowbirds respond strongly to the alarms of the closely related red-winged blackbird if they have been reared alone by phoebe foster parents. However, their gaping response appears to be sensitive to rearing conditions, so if reared alongside phoebe nestlings, such a selective response is less marked.

Red-winged blackbirds

We compared the responses of eight red-winged blackbirds reared by phoebes with those of 12 red-winged blackbirds reared by red-winged blackbird parents (detailed in Madden et al. 2005). Red-winged blackbirds reared by phoebes did not differ significantly from those reared by conspecifics in their levels of either gaping or calling response, and there were no significant interactions between responses to different calls and rearing treatment (Call \times Treatment: gape: $F_{2,34} = 0.58$, $P = 0.56$; calling: $F_{2,34} = 0.45$, $P = 0.64$; Treatment: gape: $F_{1,17} = 3.70$, $P = 0.071$; calling: $F_{1,17} = 0.75$, $P = 0.40$). Regardless of treatment, they responded selectively to different vocalizations, reducing their gaping most during playback of red-winged blackbird sees alarm calls (Call: $F_{2,34} = 7.41$, $P = 0.002$; post hoc LSD tests: phoebe versus

grosbeak: $P = 0.42$; red-wing versus phoebe: $P = 0.009$; red-wing versus grosbeak: $P = 0.007$; Fig. 2a). They did not respond differently in terms of reduction in their calling rate while gaping (Call: $F_{2,34} = 1.48$, $P = 0.24$; Fig. 2b).

We conclude that, in contrast to cowbirds, the alarm response of red-winged blackbird nestlings is insensitive to rearing condition. They have a strong, unlearned response to conspecific alarm calls.

Cowbirds reared alone by phoebes did not differ significantly in their alarm responses from red-winged blackbirds also reared alone by phoebes. There was no significant interaction between species and call type (Call \times Species: gape: $F_{2,30} = 2.79$, $P = 0.080$; calling: $F_{2,30} = 0.034$, $P = 0.86$).

Food Call Experiment

Cowbirds

Four of the original 16 cowbirds that were tested with the alarm experiment either continually crouched or had to be returned to their nests for logistical reasons. Thus, 12 cowbirds were tested, all of which were previously tested in the alarm experiment. Of the 12 successfully tested, six were reared alone by phoebes and six alongside two phoebe chicks. Rearing treatment had no significant effect on the cowbird's response (Treatment: gape: $F_{1,23} = 1.81$, $P = 0.21$; calling: $F_{1,23} = 0.38$, $P = 0.55$). Instead, regardless of rearing

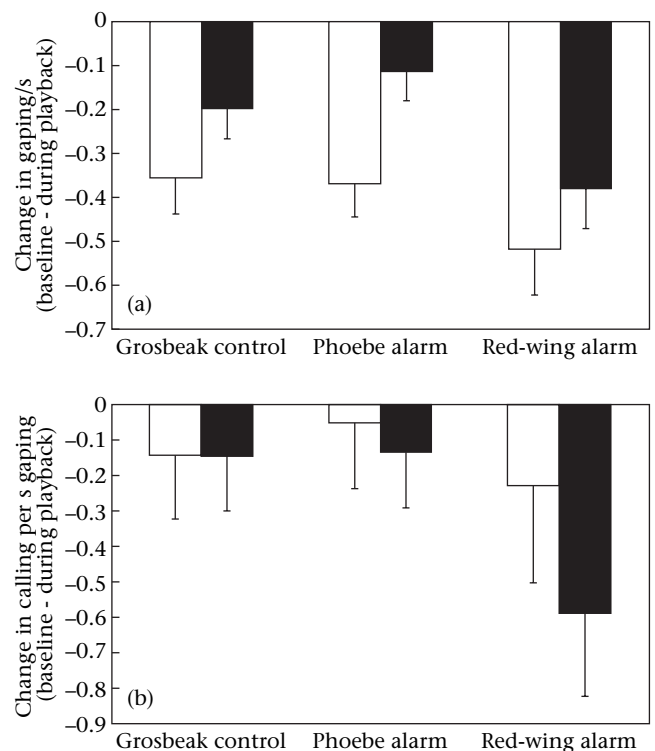


Figure 2. Change from baseline begging levels in begging responses of 20 red-winged blackbird nestlings, reared either by conspecifics (■; $N = 12$) or alone in nests of eastern phoebes (□; $N = 8$), during playback of two types of alarm calls and one control call. (a) Duration of gaping. (b) Number of calls given per second spent gaping. Means + SE are shown.

treatment, cowbird nestlings gaped more and called more rapidly during gaping when manually stimulated (stimulus: gape: $F_{1,23} = 85.6$, $P < 0.001$; calling: $F_{1,23} = 5.09$, $P = 0.05$; Fig. 3). The magnitude of the cowbird's response was not increased when food calls were broadcast during manual stimulation (Fig. 3). Furthermore, playback of food calls unaccompanied by manual stimulation almost always failed to elicit any begging behaviour from these chicks. We conclude that cowbirds ignore the food calls given by their phoebe host parents, even if they experience the strong begging response shown by companion host nestlings (Madden et al. 2005). Instead, they possess a general response to manual stimulation, begging vigorously following the slightest disturbance.

Red-winged blackbirds

All eight red-winged blackbirds reared by phoebes that were tested in the alarm call experiment were also tested in the food call experiment. Again, we compared their responses with those of 12 red-winged blackbirds reared by conspecifics. No interactions involving treatment were

significant, suggesting that rearing conditions did not alter begging responses (Fig. 4). Regardless of rearing treatment, nestlings gaped and called more vigorously when stimulated manually or with playbacks (stimulus: gape: $F_{1,18} = 61.78$, $P < 0.001$; calling: $F_{1,18} = 26.03$, $P < 0.001$; playback: gape: $F_{1,18} = 13.82$, $P = 0.002$; calling: $F_{1,18} = 6.32$, $P = 0.02$; Fig. 4). Their begging response also differed, depending on the call used in the playbacks, gaping and calling significantly more in response to playback of phoebe chatter food calls (Call: gape: $F_{3,54} = 20.19$, $P < 0.001$; calling: $F_{3,54} = 7.87$, $P < 0.001$; post hoc LSD tests: gape: phoebe food call versus all others: $P < 0.009$; all other pairwise comparisons: $P > 0.40$; calling, phoebe food call versus all others: $P < 0.0007$; all other pairwise comparisons: $P > 0.14$).

When cowbirds reared alone by phoebes were compared with red-winged blackbirds also reared alone by phoebes, we found no differences in the effect of manual stimulation in inducing begging by the two species (Stimulus \times Species: gape: $F_{1,12} = 2.6$, $P = 0.13$; calling: $F_{1,12} = 0.054$, $P = 0.82$). However, red-winged blackbirds begged significantly more than cowbirds when stimulated by aural cues

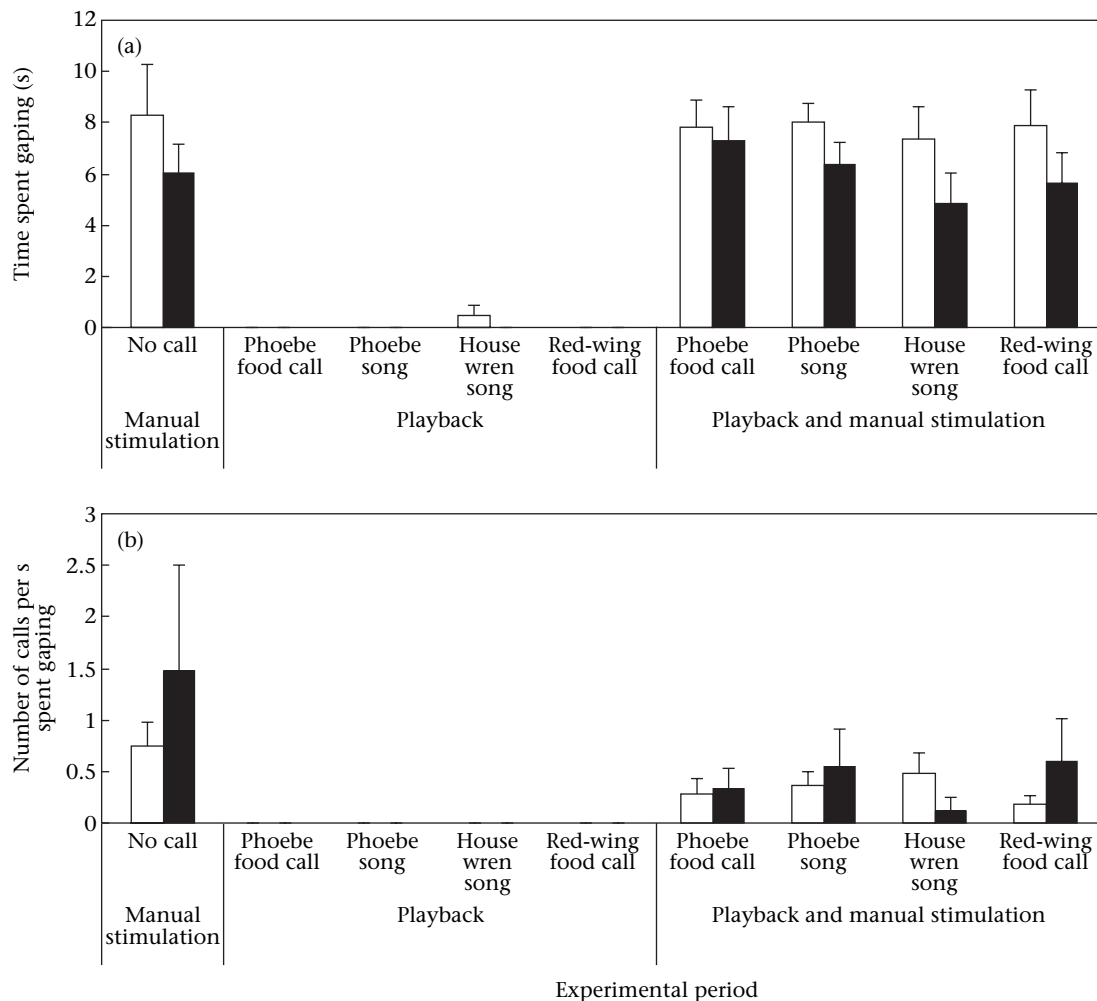


Figure 3. Food call experiment responses of 12 cowbird nestlings, reared by eastern phoebes either alone (\square ; $N = 6$) or with two host chicks (\blacksquare ; $N = 6$), to manual stimulation, food calls and control vocalizations. Responses measured as: (a) duration of gaping (s) or (b) number of calls given per second spent gaping. Means + SE are shown.

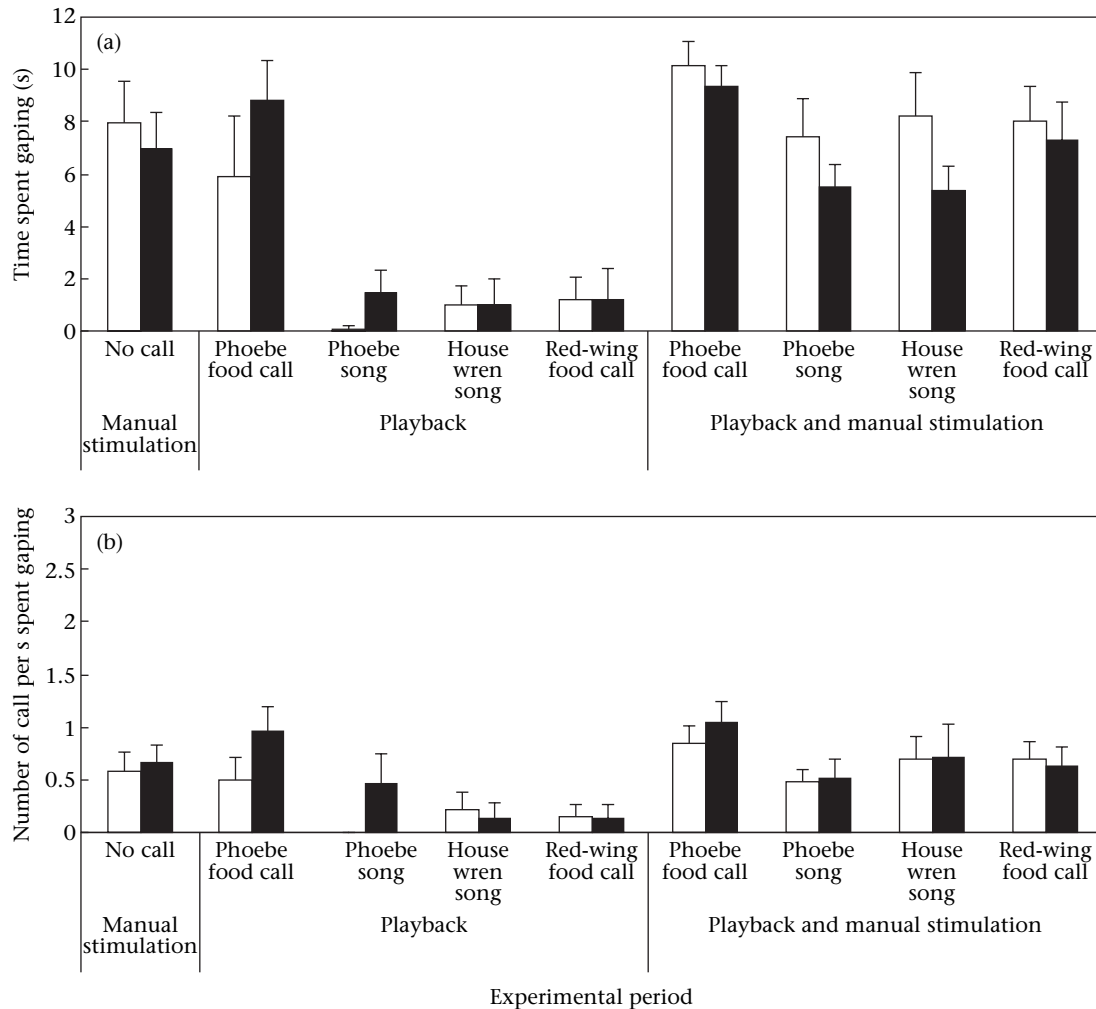


Figure 4. Food call experiment responses of 20 red-winged blackbird nestlings, reared either with siblings by conspecifics (□; $N = 12$) or alone by eastern phoebes (■; $N = 8$), to manual stimulation, food calls and control vocalizations. Responses measured as: (a) duration of gaping (s) or (b) number of calls given per second spent gaping. Means + SE are shown.

(Playback \times Species: gape: $F_{1,12} = 4.37$, $P = 0.057$; calling: $F_{1,12} = 8.07$, $P = 0.015$), and responded differently to particular cues, begging much more to playback of phoebe food calls (Call \times Species: gape: $F_{3,36} = 20.65$, $P < 0.001$; calling: $F_{3,36} = 7.01$, $P = 0.001$).

DISCUSSION

Switching On Begging

Cowbird nestlings did not appear to eavesdrop on the parent-offspring communication system used by a common host, the eastern phoebe. The phoebe operates a 'switch-on' begging system, where host nestlings are reluctant to beg unless they hear a species-specific food call or see the adults approaching the nest carrying food (Madden et al. 2005). However, cowbirds reared by phoebes did not start to beg in response to this call, but instead begged vigorously to any form of manual stimulation. Their response to a vibrational rather than a vocal

cue occurred irrespective of whether they had been reared alone or with phoebe young and so had experienced the strong food call response of host nestmates.

Our results differ from those of Hauber (2003b) who showed that cowbird chick begging could be induced with vocal stimuli alone. His nestlings were more responsive to a variety of cowbird and heterospecific calls than to a suite of sympatric passerine species. Indeed, cowbirds in his study responded more vigorously to any vocal cue than did nestlings belonging to various host species. None of the calls used by Hauber were described as food calls, but rather included flight calls, alarms and songs. We presented different stimuli, including manual stimulation, as well as a measure of gaping with no playback of calls. Hauber's cowbirds were younger than those used in our experiment, initially tested aged 5–6 days old when their eyes were still closed or just opened, and, of these, gaping was recorded in only about one-third of cases. Repeating his tests a few days later, he found that the older cowbirds were less likely to respond to any acoustic stimuli (Hauber et al. 2001). Hauber accounted for age-related changes in

begging behaviour by suggesting that the begging response is learnt after repeated exposure to parental stimuli, accompanied by reinforcement with food rewards. However, our results do not support this idea. Phoebe adults consistently gave food calls in the days before we tested nestlings (Madden et al. 2005), yet cowbirds unanimously failed to respond to playback of this call type during our experiments. Even when cowbirds were reared alongside phoebe chicks, which did beg to phoebe food calls, we found no evidence of learning, as the parasite still failed to produce a correct begging response to host food calls.

At first sight, it seems that a learning mechanism may apply to the related, but nonparasitic, icterid, the red-winged blackbird, because those red-winged blackbirds reared by phoebes begged dramatically to phoebe food calls. However, red-winged blackbirds reared by conspecifics also showed the same strength of response to phoebe food calls. This result is remarkable, especially because red-winged blackbirds responded more strongly to phoebe food calls than to red-winged blackbird food calls. One possibility is that the phoebe chatter food calls act as super-normal red-winged blackbird chits food calls, being structurally more complex with more variation in syllable structure and order, as well as containing more numerous overtones (see figure 2 of Madden et al. 2005).

Why do cowbirds fail to respond to their foster parent's food calls? Adult cowbirds certainly have the capacity to learn about vocal cues (e.g. West & King 1985). One explanation may be simply a mechanistic limitation. With many potential host species available to a single female cowbird (Woolfenden et al. 2003), it is hard to imagine that a cowbird chick could possess an innate template to guide its learning of all the possible food calls. Any begging response to food calls would therefore have to be entirely learnt. However, we failed to find any evidence of this, either from reinforcement from parental feeds, or social learning from the food call response of host nestmates. Alternatively, there may be no selective advantage to be gained from responding to food calls. If vibrational cues are frequently encountered, it may be simpler for a generalist brood parasite to react to nest movement. However, cowbirds were no more responsive to vibrational cues than were the nonparasitic red-winged blackbirds reared by phoebes. Therefore, the vibrational trigger that evokes cowbird begging is not a special adaptation for its parasitic lifestyle.

Switching Off Begging

Cowbirds varied in their response to different alarm calls depending on whether or not they were reared alongside host young. Those reared alone by phoebes did not differ in their response from red-winged blackbirds that were also reared alone by phoebes. They reduced both gaping and calling much more in response to the alarm of the related red-winged blackbird than to the other playbacks. In almost a fifth of cases, cowbirds crouched to the alarm, just as red-winged blackbirds do (Madden et al. 2005). This is suggestive of an innate, family level alarm response in the Icteridae. Further support for this contention

is provided by our finding that red-winged blackbirds retained their strong response to conspecific alarms, even when reared by phoebes. It is possible that our cowbirds and red-winged blackbirds reared by phoebes could have heard red-winged blackbird alarms. However, we think this is highly unlikely because the phoebe nests on the sides of buildings were usually several hundred metres from the ponds and marshes in which the nearest red-winged blackbirds nested and, as far as we are aware, the red-winged blackbird sees alarm is given only at the nest.

In contrast, cowbirds reared alongside phoebe chicks lost their specific, marked reduction in gaping in response to red-winged blackbird alarms, although they still reduced their calling rate most strongly during red-winged blackbird alarm playback. One explanation could be that because cowbirds reared with two phoebe chicks grew at a faster rate than those reared alone (Kilner et al. 2004), they were less hungry and so less motivated to beg, making it harder to detect differences in their responses to the vocalizations we broadcast. However, this possibility seems unlikely, because we found no significant effect of rearing treatment on overall begging intensity. A second possibility is that the cowbird's change in behaviour was an adaptive response. Their ancestral response to red-winged blackbird alarms would be adaptive in the nests of red-winged blackbirds, a frequently used cowbird host (Ortega 1998). However, in the nests of other host species, it might compromise the cowbird chick's ability to compete for food, so it would pay to learn to ignore inappropriate alarms by copying the responses of the host chicks. However, such adaptive flexibility would surely have enabled the cowbirds to learn to respond to the phoebe food calls, which clearly they did not do. We cannot otherwise account for these differing cowbird responses.

We conclude that brood-parasitic cowbird nestlings do not tune in to the communication system of their phoebe hosts. Instead, they beg simply in response to vibrational (and perhaps visual) cues. Dearborn (1998) also noted that cowbirds begged in response to vibrations of the nest or nearby vegetation and suggested this crude response would be adaptive given the wide range of host species' nests in which the cowbird chick could be reared. Furthermore, a cowbird nestling's response to alarm calls appears to reflect its icterid ancestry. Our results support Friedmann's (1929, pp. 272–273) qualitative observations reported nearly 80 years ago: 'In normal nesting birds, a danger call from the parent immediately causes the young to crouch down and remain quiet', but the cowbird chick does not 'respond to, or understand the alarm calls and danger signals of its foster parents.... On many occasions I have gone up to the nests containing young cowbirds, and the foster parents hopped about greatly excited and repeatedly uttered their danger calls, while the young parasites kept begging for food, not paying the least attention to them'.

Such a simple set of responses may be appropriate for a generalist parasite which targets over 100 regular host species, and whose offspring are reared sometimes alone and sometimes alongside host young (Ortega 1998). Nevertheless, given the increased readiness of cowbird

chicks to beg, compared to host chicks, wasteful begging when the host parents are not present is likely to result. Tuning into host parent vocalizations would, therefore, surely be of benefit. Perhaps the difficulty of evolving a mechanism to tune in to such a variety of host alarm and food calls is a cost associated with a generalist brood-parasitic lifestyle. Our studies of other hosts of brood parasites suggest that host nestlings have innate neural templates that enable them to recognize features of their own species' alarm calls from a background of irrelevant sounds, but learning then fine-tunes the response to reduce recognition errors (Davies et al. 2004). The cowbird's problem, therefore, is not only to tune into such a variety of host calls, but also to avoid the costs of mistaking alarms for food calls and vice versa. This may be unfeasible, given the variety of calls of its many host species. Specialist parasites such as common cuckoos, *Cuculus canorus*, that target a narrower range of hosts, may be better able to tune into the specific communication systems of their hosts.

Acknowledgments

We thank M. E. Hauber for showing us round his study site in Tomkins County and for providing details of phoebe nest sites he had found previously. In particular, we are most grateful to the many residents of Tomkins County who generously allowed us access to nest sites on their properties and made us very welcome. C. Wilson and C. & E. Kramer were especially hospitable. D. W. Winkler kindly hosted us at Cornell University and arranged relevant permits. We thank the Natural Environment Research Council for funding this work (J.R.M. & N.B.D.). R.M.K. was supported by a Royal Society University Research Fellowship. We thank S. Quader for statistical advice. M. Hall provided a car for our work. H. Simpson offered us invaluable advice in the field. B. Kempenaers, D. Dearborn and an anonymous referee provided helpful comments on the manuscript.

References

- Briskie, J. V., Naugler, C. T. & Leech, S. M. 1994. Begging intensity of nestling birds varies with sibling relatedness. *Proceedings of the Royal Society of London, Series B*, **258**, 73–78.
- Chappell, M. A. & Bachman, G. C. 2002. Energetic costs of begging behaviour. In: *The Evolution of Begging: Competition, Cooperation and Communication* (Ed. by J. Wright & M. L. Leonard), pp. 143–162. Dordrecht: Kluwer.
- Davies, N. B. 2000. *Cuckoos, Cowbirds and Other Cheats*. London: T & A.D. Poyser.
- Davies, N. B., Kilner, R. M. & Noble, D. G. 1998. Nestling cuckoos, *Cuculus canorus*, exploit hosts with begging calls that mimic a brood. *Proceedings of the Royal Society of London, Series B*, **265**, 673–678.
- Davies, N. B., Madden, J. R. & Butchart, S. H. M. 2004. Learning fine-tunes a specific response of nestlings to the parental alarms of their own species. *Proceedings of the Royal Society of London, Series B*, **271**, 2297–2304.
- Dearborn, D. C. 1998. Begging behaviour and food acquisition by brown-headed cowbird nestlings. *Behavioral Ecology and Sociobiology*, **43**, 259–270.
- Dearborn, D. C. 1999. Brown-headed cowbird nestling vocalizations and risk of nest predation. *Auk*, **116**, 448–457.
- Friedmann, H. 1929. *The Cowbirds: A Study in the Biology of Social Parasitism*. Springfield, Illinois: Charles C. Thomas.
- Griffiths, R., Double, M. C., Orr, K. & Dawson, R. J. G. 1998. A DNA test to sex most birds. *Molecular Ecology*, **7**, 1071–1075.
- Haskell, D. 1994. Experimental evidence that nestling begging behaviour incurs a cost due to nest predation. *Proceedings of the Royal Society of London, Series B*, **257**, 161–164.
- Hauber, M. E. 2003a. Hatching asynchrony, nestling competition and the cost of interspecific brood parasitism. *Behavioral Ecology*, **14**, 227–235.
- Hauber, M. E. 2003b. Lower begging responsiveness of host versus parasitic brown-headed cowbird (*Molothrus ater*) nestlings is related to species identity but not to early social experience. *Journal of Comparative Psychology*, **117**, 24–30.
- Hauber, M. E., Russo, S. A. & Sherman, P. W. 2001. A password for species recognition in a brood-parasitic bird. *Proceedings of the Royal Society of London, Series B*, **268**, 1041–1048.
- Hosoi, S. A. & Rothstein, S. I. 2000. The enigma of nest desertion: is it really a defence against cowbird parasitism? *Animal Behaviour*, **59**, 823–840.
- Johnson, K. P. & Lanyon, S. M. 1999. Molecular systematics of the grackles and allies, and the effect of additional sequence (cyt b and ND2). *Auk*, **116**, 759–768.
- Kilner, R. M. 2001. A growth cost of begging in captive canary chicks. *Proceedings of the National Academy of Sciences, U.S.A.*, **98**, 11394–11398.
- Kilner, R. M. 2003. How selfish is a cowbird nestling? *Animal Behaviour*, **66**, 569–576.
- Kilner, R. M. & Davies, N. B. 1998. Nestling mouth colour: ecological correlates of a begging signal. *Animal Behaviour*, **56**, 705–712.
- Kilner, R. M., Noble, D. G. & Davies, N. B. 1999. Signals of need in parent-offspring communication and their exploitation by the common cuckoo. *Nature*, **397**, 667–672.
- Kilner, R. M., Madden, J. R. & Hauber, M. E. 2004. Brood parasitic cowbird nestlings use host young to procure parental resources. *Science*, **305**, 877–879.
- Leech, S. M. & Leonard, M. L. 1997. Begging and the risk of predation in nestling birds. *Behavioral Ecology*, **8**, 644–646.
- Lichtenstein, G. 2001. Selfish begging by screaming cowbirds, a mimetic brood parasite of the bay-winged cowbird. *Animal Behaviour*, **61**, 1151–1158.
- Lichtenstein, G. & Sealy, S. G. 1998. Nestling competition, rather than supernormal stimulus, explains the success of parasitic brown-headed cowbird chicks in yellow warbler nests. *Proceedings of the Royal Society of London, Series B*, **265**, 249–254.
- Lorenzana, J. C. & Sealy, S. G. 1999. A meta-analysis of the impact of parasitism by the brown-headed cowbird on its hosts. *Studies in Avian Biology*, **18**, 241–253.
- Madden, J. R., Kilner, R. M. & Davies, N. B. 2005. Nestling responses to adult food and alarm calls: 1. Species-specific responses in two cowbird hosts. *Animal Behaviour*.
- Martin, T. E., Scott, J. & Menge, C. 2000. Nest predation increases with parental activity: separating nest site and parental activity effects. *Proceedings of the Royal Society of London, Series B*, **267**, 2287–2293.
- Ortega, C. P. 1998. *Cowbirds and Other Brood Parasites*. Tucson: University of Arizona Press.

- R Development Core Team.** 2003. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.
- Redondo, T.** 1993. Exploitation of host mechanisms for parental care by avian brood parasites. *Etologia*, **3**, 235–297.
- Redondo, T. & Zuniga, J. M.** 2002. Dishonest begging and host manipulation by *Clamator* cuckoos. In: *The Evolution of Begging: Competition, Cooperation and Communication* (Ed. by J. Wright & M. L. Leonard), pp. 389–412. Dordrecht: Kluwer.
- Rothstein, S. I.** 1990. A model system for coevolution: avian brood parasitism. *Annual Review of Ecology and Systematics*, **21**, 481–508.
- Soler, M., Martinez, J. G., Soler, J. J. & Møller, A. P.** 1995. Preferential allocation of food by magpies *Pica pica* to great spotted cuckoos *Clamator glandarius* chicks. *Behavioral Ecology and Sociobiology*, **37**, 243–248.
- West, M. J. & King, A. P.** 1985. Studying the dialects in songbirds: finding the common ground. *Behavioral and Brain Sciences*, **8**, 117–118.
- Woolfenden, B. E., Gibbs, H. L., Sealy, S. G. & McMaster, D. G.** 2003. Host use and fecundity of individual female brown-headed cowbirds. *Animal Behaviour*, **66**, 95–106.