Learning fine-tunes a specific response of nestlings to the parental alarm calls of their own species

N. B. Davies*, J. R. Madden and S. H. M. Butchart

Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK

Parent birds often give alarm calls when a predator approaches their nest. However, it is not clear whether these alarms function to warn nestlings, nor is it known whether nestling responses are species-specific. The parental alarms of reed warblers, *Acrocephalus scirpaceus* ('churr'), dunnocks, *Prunella modularis* ('tseep'), and robins, *Erithacus rubecula* ('see') are very different. Playback experiments revealed that nestlings of all three species ceased begging only in response to conspecific alarm calls. These differences between species in response are not simply a product of differences in raising environment, because when newly hatched dunnocks and robins were cross-fostered to nests of the other two species, they did not develop a response to their foster species' alarms. Instead, they still responded specifically to their own species' alarms. However, their response was less strong than that of nestlings raised normally by their own species. We suggest that, as in song development, a neural template enables nestlings to recognize features of their own species' signals from a background of irrelevant sounds, but learning then fine-tunes the response to reduce recognition errors.

Keywords: alarm calls; vocal communication; learning; nestling vocalizations; parental behaviour; signal detection

1. INTRODUCTION

Nestling birds often have remarkably conspicuous begging displays, with brightly coloured gapes and loud calls, which not only command the attention of parents but also attract predators to the nest (Haskell 1994; Leech & Leonard 1997; Dearborn 1999). Parents can reduce this predation cost by giving alarm calls, which cause their nestlings to cease begging and crouch (Greig-Smith 1980; Knight & Temple 1986; Platzen & Magrath 2004; Madden *et al.* 2004; but see Maurer *et al.* 2003). However, it is not yet known whether nestling responses are specific to their own species' alarms. Furthermore, parent alarms may sometimes have other functions, such as alerting mates, who might otherwise visit the nest and so reveal its location (East 1981), or distracting predators away from the nest (Greig-Smith 1980; Knight & Temple 1986).

We test nestling responses to parental alarm calls in three species with open cup nests vulnerable to predation, namely reed warbler, *Acrocephalus scirpaceus*, dunnock, *Prunella modularis*, and robin, *Erithacus rubecula*. First, we show that parents of all three species give distinctive, species-specific alarm calls when a predator approaches the nest, and particularly at the nestling stage, suggesting that the alarms might function to warn nestlings. Second, we demonstrate through playback experiments that nestlings of each species cease begging only in response to conspecific alarm calls. This result raises an interesting developmental question: how do nestlings distinguish these alarms from other parental calls and from the variety of other sounds near the nest, such as the calls of other species or noises made by vegetation or inanimate objects?

This is a problem common to all discrimination tasks, namely how to optimize the balance between acceptance errors (in this case treating a non-threatening signal as an alarm) and rejection errors (ignoring a true alarm). The optimal response will depend both on the overlap in the distributions of the acoustic features of false and true alarms, and on the fitness consequences of responding to or ignoring false and true alarms (Reeve 1989; Sherman *et al.* 1997). A nestling that sets its discrimination threshold too low will crouch in response to false alarms and so miss the chance of competing for food, whereas one that sets its discrimination threshold too high will continue to beg during a true alarm and so attract the predator to the nest.

We suggest that two factors would make this discrimination task easier. The first concerns signal production; parents could reduce the chance of false alarms by giving alarm calls distinctive from other sounds in their environment. The second concerns signal perception. It is now well established that neural systems are not blank slates but are pre-tuned to stimuli relevant for the animal's survival and reproduction. For example, human infants (Streeter 1976) and young songbirds (Marler 1997; Whaling *et al.* 1997; Soha & Marler 2000) have neural templates that focus their attention on sound features of their own species' language or song. These cues are then used to guide learning of their own species' signals in an environment full of other irrelevant sounds. In the same way, it would benefit a young bird to be pre-tuned to features of its own species' alarm calls so it could respond appropriately the first time a predator approached. Nevertheless, we might also expect learning to be involved, because repeated exposure to parent alarms could fine-tune an auditory template and so reduce recognition errors. This would be advantageous if there was local variation in the sounds of false alarms, or variation in the alarm calls between adults within a species,

* Author for correspondence (n.b.davies@zoo.cam.ac.uk).

which is likely because individuals may learn the details of their calls from their parents (Zann 1990; Slagsvold & Hansen 2001).

Our final aim, therefore, is to investigate the role of innate predispositions and learning by comparing alarm responses of nestlings raised by their own species with those cross-fostered and raised in the nest of another species.

2. MATERIAL AND METHODS

(a) *Study sites and parent alarm calls*

The study took place over three breeding seasons, April–July, 2001–2003. We studied reed warblers on Wicken Fen and the surrounding fenland along the Burwell and Reach Lodes, Cambridgeshire, and dunnocks and robins in the University Botanic Garden, Cambridge, and in the woodlands and hedgerows on the edge of the city.

We recorded alarm calls given in response to a human observer standing 2 m from the nest. Adults usually returned within a few minutes and perched 5–15 m away. We counted the number of calls given during the first minute by the first adult to return to the nest vicinity. Reed warblers ('churr') and dunnocks ('tseep') each gave one distinctive alarm call. Robins usually gave a high pitched 'see', which observations suggest cause fledglings to become silent (East 1981), but they occasionally also gave 'tic' calls. 'Tics' are given in other contexts too, as contact calls, and in this case may serve to distract a predator or warn a mate (East 1981). We therefore scored only 'see' alarms. The calls were analysed using AVISOFT-SASLABPRO v. 4.15. Calls were digitized at a sample rate of 22 kHz and spectrograms produced using the filter settings in AVISOFT (FFT = 512, Frame = 50%, Window = Flattop, Overlap = 50%). Call structure was quantified using automatic parameter measurements, recording syllable duration (seconds); peak, maximum and minimum frequency (kilohertz); and bandwidth (kilohertz).

(b) *Playback experiment to test nestling responses*

We made field recordings of alarm calls onto metal audio-cassette tapes, using a Sennheiser MKH 416T directional gun microphone and a Sony WM-D6C cassette recorder. For a control call, we recorded the advertisement calls of the chaffinch, *Fringilla coelebs*. This call ('hreet') is given by males during the breeding season, usually as a long series of notes from a tree top, and is structurally quite different from the high pitched 'see' alarm that chaffinches give when predators approach their nest (Cramp & Perrins 1994). Calls were downloaded onto a computer and edited to give 6 s playback cuts, each with five calls. This is within the natural range of alarm calling rate for both reed warbler and dunnock, and although it is greater than the natural range for robin alarms we thought it important to standardize call rate in the playbacks. We made no more than two cuts from the recordings of each adult, and each nestling was given a different playback cut in all tests to avoid pseudoreplication.

Nestlings were tested at 6 days of age, with no more than two tested from any one nest (broods varied between two and five nestlings). They were removed from their nest temporarily, and taken to a laboratory nearby. We ensured that at least two nestlings remained in the nest so that the parents would not desert, introducing chicks from part of a nearby brood if necessary. At the end of the experiment all chicks, including test chicks, were returned to their original nests and were readily accepted back by their parents.

In the laboratory, nestlings were first weighed and measured and then placed singly into an old nest housed in a plastic canary nest-pan that was heated from below using an insulated jug of warm water, to maintain the nest temperature at 25–30 °C, and this was placed in a wooden test-box (Kilner & Davies 1998). Nestlings were then stimulated to beg, by gently tapping the sides of their bills with plastic forceps, and fed with small balls of Nectarblend rearing mix (from Haith's, Cleethorpes, UK) until they stopped begging. They were then covered with cotton wool to simulate brooding by a parent. After 80 min we removed the cotton wool and stimulated the nestling to beg, as before. We chose this period because our previous work has shown that broods stimulated to beg in the laboratory 80 min after feeding to satiation beg at the same intensity as natural, unmanipulated broods in the field (Kilner & Davies 1998).

In the test-box, nestling behaviour was recorded simultaneously on videotape, using a Sony CCD-TR 840E Hi-8 video recorder, and on audiotape, using a Sony ECM-T6 tie-clip microphone connected to a Sony WM-D6C tape recorder (2001–2002), or with a Canon MV 500i digital video and audio camcorder plus tie-clip microphone (2003). Calls were broadcast with a Sony SRS-57 loudspeaker placed next to the test-box, at a standard sound intensity of ca. 60 dB at 3 m from the speaker.

Each nestling received three treatments in a random order: own species alarm, another species alarm, and chaffinch control call, with 2.5 min between successive treatments. For each treatment, the nestling was stimulated to beg, and then it experienced three periods: (i) first, 18 s playback (three repeats of a 6 s cut) during which it was manually stimulated to beg every 3 s by gentle taps with forceps on the bill; followed immediately by (ii), 18 s playback (three more repeats of the same 6 s cut) with no manual stimulation; followed immediately by (iii), 12 s manual stimulation only. This protocol allowed us to test the response of begging nestlings to alarm calls, and their willingness to beg after they had recently heard alarm calls.

Our sample sizes were sometimes constrained by availability of suitable nests or recordings. For heterospecific alarms, all reed warblers ($n = 20$) and robins ($n = 14$) were played dunnock alarm calls, whereas dunnocks were played either reed warbler alarms ($n = 11$) or robin alarms ($n = 4$). A further sample of dunnocks ($n = 8$) were cross-fostered to other dunnock nests (see § 2c) and were also played robin alarms as their heterospecific alarm call. There were no significant effects of this conspecific cross-fostering on dunnock responses to alarm calls (see § 3c), and when we compared dunnock responses from this combined sample with robin alarms ($n = 12$) versus reed warbler alarms ($n = 11$), we found no significant differences. Therefore, we have combined the dunnock responses to these two heterospecific alarms in the presentation of the results of this experiment.

(c) *Cross-fostering experiment*

To test whether experience of alarms influenced nestling responses, we cross-fostered newly-hatched chicks, within 24 h of hatching, into the nests of another species. We were unable to cross-foster by swapping eggs because robins and reed warblers reject eggs different from their own (though dunnocks accept; Davies & Brooke 1989), whereas all three species readily accept foreign chicks. To avoid the possibility that cross-fostered chicks might learn responses from the foster parents' own chicks we arranged for foster parents to raise broods composed entirely of foster chicks.

Robins and dunnocks are similar in adult mass (ca. 20 g), so we swapped whole broods between pairs of nests where the chicks

Figure 1. Typical sonograms of a reed warbler alarm ('churr'), a dunnoack alarm ('tseep'), a robin alarm ('see'), and a chaffinch advertisement control ('hreet').

hatched on the same day. Nests were surrounded by green PVC coated wire mesh (50 mm × 50 mm), which prevented predation by corvids and squirrels. The newly hatched chicks of reed warblers (adults *ca.* 11 g) were so much smaller that we decided not to cross-foster them. However, reed warblers often raise cuckoo, *Cuculus canorus*, chicks whose hatchlings are larger than those of dunnoacks and robins, so we cross-fostered dunnoack and robin chicks into reed warbler nests. In these cases we transferred just two robin or dunnoack chicks into each warbler nest, which was too small to accommodate more, leaving the remainder of the brood in their home nest. The reed warblers' own chicks were transferred to synchronous, nearby conspecific nests where brood sizes were smaller than average. As a control for the cross-fostering procedure, we transferred some dunnoack chicks to conspecific nests, by swapping whole broods between pairs of nests where chicks hatched on the same day.

Nestlings were tested at 6 days of age (maximum of two tested per brood) using the same playback procedure described above. For all statistical analyses we used SPSS v. 11.

(d) Ethical considerations

Playback and cross-fostering experiments were performed under licence from English Nature. Cross-fostered chicks did not differ in growth or mass from chicks raised by their own species (see § 3). None of our experiments led to desertions and after testing at day 6 all chicks were returned to their original nests and were readily accepted back by their parents.

3. RESULTS

(a) Parent alarm calls

There were striking differences between the alarm calls of the three species (figure 1). Reed warblers gave a low-pitched, broad frequency 'churr', dunnoacks gave a narrow bandwidth and higher pitched 'tseep', while robins gave a still higher pitched and more drawn out 'see'. The control call, the advertisement call of the chaffinch, 'hreet', sounded somewhat intermediate between the alarms of the dunnoack and reed warbler.

A discriminant function analysis based on minimum frequency of a single call sampled from recordings of 16 reed warblers, 17 dunnoacks, 13 robins and 17 chaffinches assigned all the robin and dunnoack calls to the correct species, and also 12 of the reed warblers (75%) and 13 of the chaffinches (76%). Three reed warblers were assigned to the chaffinch grouping and one to the dunnoack grouping, while four chaffinch calls were assigned to the reed warbler grouping. Using five parameters in the discriminant

function (minimum, maximum and peak frequency, bandwidth and duration) led to correct assignment of all robin, dunnoack and chaffinch calls, but 31% of the reed warbler alarms were grouped with other species (four with chaffinch and one with dunnoack).

We measured rate of alarm calls at 131 reed warbler nests, 28 dunnoack nests and 35 robin nests (figure 2), and analysed the results using ANOVA, with nest entered as a random factor (to control for repeated measures from the same nest). In all three species, parents were more likely to call at the chick stage than at the egg stage, when the clutch was complete and incubation had begun (reed warbler, $F_{1,98} = 15.1$, $p < 0.001$; dunnoack, $F_{1,78} = 8.79$, $p = 0.004$; robin $F_{1,19} = 26.8$, $p < 0.001$). In fact, reed warblers never gave alarm calls at the egg stage ($n = 53$ nests), while dunnoacks (2 out of 19 nests) and robins (2 out of 27 nests) rarely did so. In all three species, rate of alarm calling increased with nestling age (reed warbler, $F_{12,105} = 17.69$, $p < 0.001$; dunnoack, $F_{10,44} = 14.23$, $p < 0.001$; robin $F_{12,29} = 2.71$, $p = 0.014$). However, there were no differences for any species in alarm rates at nests containing own young versus foster species young (reed warbler, $F_{1,105} = 1.47$, $p = 0.23$; dunnoack, $F_{1,44} = 0.22$, $p = 0.64$; robin, $F_{1,29} = 1.77$, $p = 0.19$). Therefore, our cross-fostered nestlings experienced the normal rate of alarm calls from their foster parents.

Reed warblers began to give alarm calls when their nestlings were 3 days old (figure 2a), which is the age at which their chicks start to call regularly while begging (Kilner & Davies 1999). Dunnoack and robin nestlings often give begging calls at an earlier age (by 1 day old, personal observation), so it is interesting to note that some dunnoack and robin parents gave alarm calls on the day their chicks hatched and at 1 day (figure 2b,c). These results suggest that parents may give alarm calls in response to the onset of calling by their begging chicks. Nevertheless, it is relevant to note for our cross-fostering experiment that on the day the chicks hatched, dunnoacks gave alarm calls at only three out of 17 nests and robins did so at only three out of 11 nests, so exposure to their own species alarms before nestlings were cross-fostered is unlikely to be extensive.

(b) Playback experiment to test nestling responses

We tested 20 reed warbler, 15 dunnoack and 14 robin nestlings at 6 days old, which had all been raised by their own parents. We measured two responses: time (seconds) spent gaping, and number of calls per second, during each

Figure 2. Alarm calling rate of one parent in response to a human observer near the nest at the egg stage (incubating a complete clutch) and chick stage (hatching, day 0, to fledging, day 10–12), for (a) reed warblers, (b) dunnocks and (c) robins. Open circles refer to broods of own young whereas filled circles refer to foster broods of one of the other species. The smallest symbol refers to one observation. The area of the larger symbols is directly proportional to the sample size.

of the three successive periods of a treatment, namely playback with stimulation to beg (PBS), playback alone (PB) and stimulation alone (S). Responses were analysed with a repeated-measures ANOVA with two factors (playback call type, period of treatment) and we tested for significant effects within subjects.

In all three species, nestlings begged only during periods of stimulation to beg (PBS and S) and they did not gape and rarely called during the period of playback alone (figure 3; significant effects of period for both gaping and calling in all three species, $p < 0.0001$ in every case). There were marked effects of playback call type on both gaping and calling in all three species (reed warbler: gaping, $F_{2,38} = 46.20$, $p < 0.0001$; calling, $F_{2,38} = 7.75$, $p = 0.0015$; dunnock: gaping, $F_{2,28} = 31.71$, $p < 0.0001$; calling, $F_{2,28} = 21.79$, $p < 0.0001$; robin: gaping $F_{2,26} =$

66.39, $p < 0.0001$; calling, $F_{2,26} = 7.31$, $p = 0.003$). Nestlings of all three species responded most strongly to the alarm calls of their own species, gaping and calling significantly less both during and after playback of conspecific alarms than during and after heterospecific alarms or control calls (figure 3; *post hoc* LSD tests, $p < 0.01$ in all comparisons). However, there were no significant differences for any species in nestling response to heterospecific alarms versus control calls ($p = 0.19$ – 0.76).

(c) *Effects of cross-fostering on nestling responses*

i) *Controls: dunnocks cross-fostered to other dunnock nests*

We tested eight dunnock nestlings that had been cross-fostered to other dunnock nests. They behaved just like the dunnocks raised by their own parents, with markedly different responses to the three playbacks (gaping, $F_{2,14} = 36.1$, $p < 0.001$; calling, $F_{2,14} = 24.1$, $p < 0.001$), reducing begging much more strongly to dunnock alarms than to robin alarms or chaffinch control calls ($p < 0.001$ for both gaping and calling in each case), but with no difference in response to robin versus chaffinch calls (gaping, $p = 0.70$; calling, $p = 0.59$). We conclude that the act of moving nestlings to another nest does not fundamentally alter their alarm response. Therefore, in the following analyses we have combined these eight nestlings with the 15 raised by their own parents to provide a larger sample of 23 dunnocks raised by their own species.

ii) *Dunnocks cross-fostered to nests of another species*

We tested 10 dunnocks raised by reed warblers and seven raised by robins, and analysed their responses to dunnock alarms, the foster species alarms and chaffinch control calls. Dunnocks raised by reed warblers and robins did not differ in their responses to these three playbacks, so we combined the two cross-fostered groups in the analysis (no significant interaction between playback call type and foster species for either gaping, $p = 0.82$, or for calling, $p = 0.78$).

First, we used ANOVA to compare the responses of these 17 cross-fostered dunnocks with those of the 23 dunnocks raised by their own species. There was a significant effect of raising environment: dunnocks raised by a foster species gaped more ($F_{1,38} = 22.58$, $p < 0.001$) and called more ($F_{1,38} = 6.17$, $p = 0.017$) than those raised by their own species. There was also a significant interaction between raising environment and playback response, for both gaping ($F_{2,76} = 18.67$, $p < 0.001$) and calling ($F_{2,76} = 3.61$, $p = 0.032$). Therefore, we conclude that responses to calls differed between dunnocks raised by their own species and those raised by a foster species (see figure 4a).

Dunnocks raised by a foster species showed a marginally significant difference in gaping response to the three playback calls (figure 4a: $F_{2,32} = 2.86$, $p = 0.072$), with slightly less gaping during dunnock alarms compared with both foster species alarms (*post hoc* LSD tests, $p = 0.024$) and chaffinch control calls ($p = 0.071$), but no difference between foster species alarms and chaffinch control calls ($p = 0.93$). Their calling response to playbacks differed more strongly (figure 4a: $F_{2,32} = 8.11$, $p = 0.0014$), with less calling during dunnock playbacks than during foster species alarms ($p < 0.001$) and chaffinch control calls

Figure 3. Nestling responses to playbacks of alarm calls of their own species (filled circles), another species' alarm (open circles) and the chaffinch control call (filled triangles), measured as means (± 1 s.e.m.) time (seconds) spent gaping per second (i) and number of calls per second (ii), for (a) reed warblers $n = 20$, (b) dunnocks $n = 15$ and (c) robins $n = 14$. The three successive periods of the experiment are: PBS (playback during stimulation to beg), PB (playback alone) and S (stimulation alone).

($p = 0.028$), but no difference between foster species and chaffinch calls ($p = 0.17$).

We conclude that dunnocks raised by a foster species did not tune into their foster species' alarm calls (no difference in response compared with control calls), but did retain a significant response to dunnock alarm calls. Nevertheless, figure 4a shows that this response was less marked than that of dunnocks raised by dunnocks. Compared with dunnocks raised by their own species, they gaped much more ($p < 0.001$) and called much more ($p < 0.001$) during dunnock playbacks. They also gaped slightly more during foster species ($p = 0.015$) and chaffinch playbacks ($p = 0.017$), though they did not call more during foster species ($p = 0.11$) or chaffinch ($p = 0.36$) playbacks.

There were no significant differences between dunnocks raised by a foster species and by their own species in 6-day-old nestling mass, or bill length (from outer corner of base of gape flange to bill tip), or gape width (across base of gape flange on either side of the mouth), nor did the two groups differ in mass of food eaten at the end of the playback experiment (two-tailed t -tests, $p = 0.28$ – 0.66). Therefore

the differences in responses to playbacks were not caused by differences in growth or hunger.

iii) Robins cross-fostered to nests of another species

We tested six robins raised by reed warblers and six raised by dunnocks, and analysed their responses to robin alarms, the foster species alarms and chaffinch control calls. Robins raised by reed warblers and dunnocks did not differ in their responses to these three playbacks, so we combined the two cross-fostered groups in the analysis (no significant interaction between playback call type and foster species for either gaping, $p = 0.45$, or for calling, $p = 0.72$).

Again, we first used ANOVA to compare the responses of these 12 cross-fostered robins with those of the 14 robins raised by their own species. There were no significant differences between these two treatment groups in the amount of gaping ($F_{1,24} = 0.021$, $p = 0.89$) or calling ($F_{1,24} = 0.36$, $p = 0.55$). However, there was a significant interaction between raising environment and playback response for both gaping ($F_{2,48} = 5.26$, $p = 0.0086$) and for calling ($F_{2,48} = 3.73$, $p = 0.031$). Therefore, once again

Figure 4. Responses to stimulation during and after playback (estimated marginal means $\pm$ 1 s.e.m.), comparing nestlings raised by their own species (open bars) and by a foster species (black bars), for (a) dunnocks ($n = 23$ raised by own species, $n = 17$ raised by foster species), and (b) robins ($n = 14$ raised by own species, $n = 12$ raised by foster species). (i) Time (seconds) spent gaping per second, and (ii) number of calls per second.

responses to calls differed between nestlings raised by their own species and by a foster species (see figure 4b).

Robins raised by a foster species showed a significant difference in gaping response to the three playback calls (figure 4b: $F_{2,22} = 8.64$, $p = 0.0017$), with less gaping during robin alarms than during foster species alarms ($p = 0.006$), or during chaffinch control calls ($p = 0.015$), but no difference in response to foster species alarms or chaffinch calls ($p = 0.18$). As with the dunnocks, figure 4b suggests that the significant effect of raising environment on gaping arises because foster-species-raised robins had a less specific response to robin alarms. However, we were unable to pinpoint the cause of the difference because none of the pairwise comparisons of gaping responses with own-species-raised robins was significant (for robin alarms, $p = 0.14$; foster species alarms, $p = 0.97$; chaffinch control calls, $p = 0.30$).

In marked contrast to robins raised by their own species, foster-species-raised robins showed no significant variation in calling response across the three playback call types (figure 4b: $F_{2,22} = 1.80$, $p = 0.19$). However, again we were unable to pinpoint the cause of the significant effect of raising environment because none of the pairwise comparisons with own-species-raised robins was significant (for robin alarms, $p = 0.38$; foster species alarms, $p = 0.64$; chaffinch control calls, $p = 0.15$).

We conclude that, in common with the cross-fostered dunnocks, robins raised by a foster species did not tune into their foster species' alarms (no differences in response compared with control calls), but retained a response to their own species alarms, though less marked than that shown by robins raised by their own species. There were no significant differences between robins raised by a foster species and by their own species in 6-day-old nestling mass, bill length or gape width, nor in mass of food eaten at the

end of the playback experiment (two-tailed t -tests, $p = 0.35$ – 0.79). Once again, therefore, their different responses to playbacks were not caused by differences in growth or hunger.

4. DISCUSSION

(a) *Different alarm calls*

The differences in the chick-warning alarm calls (figure 1) are remarkable, given that the 'hawk alarm' calls of many passerines, produced in response to an aerial predator, have a similar structure, namely a high pitched 'seet' (Marler 1955). It has been suggested that the similarity between species here reflects convergent evolution on a call with acoustic characteristics that are difficult for a predator to locate (Marler 1955; Brown 1982; Klump & Shalter 1984) or detect (Shalter 1978; Klump *et al.* 1986). The similarity might have been enhanced by the advantage gained from responding to the alarms of other species, because most passerines are vulnerable to hawk predation (Klump & Shalter 1984). Why, then, are the chick-warning alarms so different?

We suggest two hypotheses that require testing. First, different alarms may be best suited to different nesting habitats, because signal degradation varies with habitat structure (Morton 1975; Wiley & Richards 1982), or because there are different background noises (sources of false alarms) in different habitats. Second, the nests of different species may differ in their vulnerability to particular predators, so there is less benefit from responding to other species' alarms, and hence less selection for similarity, than with hawk alarms.

(b) Innate species differences in nestling response

Nestlings of all three species responded specifically to their own species' alarm calls (figure 3). If these species differences in response were entirely due to experience, then cross-fostered nestlings should have developed a response to their foster species' alarm calls. However, neither cross-fostered dunnocks nor robins responded to their foster species alarms, even though they would have been exposed to these at the normal rate (figure 2). Instead, these cross-fostered nestlings responded most strongly to their own species' alarms, though their response was less than that of nestlings raised normally by their own species (figure 4).

In field experiments it is, of course, impossible to have precise control over exposure to alarms. Cross-fostered nestlings may have had some exposure to their own species alarms before transfer, either in the egg or on the day they hatched. However, our data on alarm calling at these stages suggest that exposure would not have been extensive (figure 2). They may have also heard their own species' alarms after cross-fostering, from the calls of conspecifics in nearby territories. This would have been more likely for robins raised by dunnocks, or dunnocks raised by robins, because these two species nest in the same habitat, sometimes with 20–50 m between neighbouring nests in our study sites, and so probably within earshot of each others' alarms. However, these dunnocks and robins cross-fostered to each others' nests did not respond more strongly to their own species' alarms than those cross-fostered to reed warbler nests, whose nesting habitat in the fens was usually at least 100 m, and often 500 m or more, from the nearest dunnock or robin territory, and so unlikely to be in auditory contact. We suggest, therefore, that post-transfer exposure was unlikely to have affected the results.

Despite the possibility of some limited exposure to their own species' alarms, in addition to the foster species' normal alarm rate, the fact that cross-fostered nestlings responded only to the alarms of their own species suggests that they have neural circuitry pre-tuned only to features of their own species' alarm calls.

(c) Role of learning in tuning nestling response

Why was the response of the cross-fostered nestlings less strong than that of those raised by their own species? Our measurements suggest that this was not due to any differences in growth or hunger. One possibility is that the cross-fostered nestlings had the same potential to respond, but because they had rarely (if ever) heard their own species' alarms during their first 6 days they assessed predation to be a low risk, and so made a strategic decision to respond less to the playback. However, such behaviour would surely be maladaptive because threats of nest predation may be rare events and it might be vital for a 6-day-old nestling, with conspicuous begging signals, to respond strongly to a parental alarm.

We favour a second possibility, namely that experience of parental alarms is necessary for development of the specific response. We suggest that although a pre-tuned neural template is required to recognize own species' alarm calls from a background of irrelevant sounds, an entirely innate response would be susceptible to recognition errors, either because of variation in adult alarm calls within a species, or local variation in the acoustic features of sounds that are

false alarms. Our results suggest that by 6 days, some fine-tuning through exposure has occurred which enables nestlings raised normally by their own species to respond more selectively. Nestlings do not start to produce loud begging calls until they are several days old, so fine-tuning through exposure early in life is unlikely to be too costly to their survival. Young vervet monkeys, *Cercopithecus aethiops*, also need experience before they respond appropriately to their own species' alarm calls, and are likely to learn by observing adult responses (Cheney & Seyfarth 1990). However, nestling birds will not always have an appropriate model present to learn from, because both parents are often away foraging. It is more likely that their response develops simply through repeatedly hearing the alarm calls.

It would presumably benefit nestlings to also respond to the chick-warning alarms of other species, because open-nesting passerines are vulnerable to many of the same predators (e.g. members of the crow and weasel family). However, innate recognition of a range of such diverse alarms, against a barrage of various background sounds, may be unfeasible. Nevertheless, adults do sometimes eavesdrop on other species' alarm calls (Vieth *et al.* 1980; Seyfarth & Cheney 1990; Rainey *et al.* 2004). They probably learn to associate these alarms with predator presence or conspecific anti-predator behaviour (Curio *et al.* 1978; Hauser 1988). Perhaps experienced adults could translate the message of other species' alarms for their nestlings by giving their own alarm calls in response.

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