



## False alarms and begging in nestling birds

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(Received 11 October 2003; initial acceptance 23 January 2004;  
final acceptance 21 May 2004; published online 25 January 2005; MS. number: A9730R)

In theory, for any communication system, receivers cannot increase their responsiveness to signals without simultaneously increasing their risk of responding to inappropriate stimuli. This inevitable trade-off may be an important selective pressure on signalling systems, but has rarely been studied. Nestling tree swallows, *Tachycineta bicolor*, produce a begging display when their parents arrive at the nest with food, but they also beg to apparently inappropriate stimuli in the absence of parents, such as movements of the nest or broodmates. To explore the implications of these errors for begging, we experimentally determined how begging errors vary with nestling hunger and age, two factors that affect begging rate and intensity in response to parents. Specifically, we examined how begging rate and intensity varied in response to recordings of (1) a tree swallow adult landing on a nestbox and calling and (2) a common grackle, *Quiscalus quiscula*, a nest predator, landing on a nestbox, during a 1-h period of food deprivation and also across two ages (5–6 and 7–9 days posthatch). Nestlings increased the rate and intensity of their begging responses to both swallow and grackle stimulus sounds as time without food increased, although responses to the grackle sounds were always less than to the swallow sounds. Begging rate, but not intensity, increased with age for both swallow and grackle sounds; both measures of response were lower for the grackle sound at both ages. Thus, as nestlings become more responsive to parents, they also risk committing more errors. This trade-off supports theoretical predictions and may be an important selective force shaping parent–offspring signalling.

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Errors, or ‘evolutionarily inappropriate responses’ (Wiley 1994), are expected to occur in all communication systems, because receivers cannot detect and assess signals with complete certainty. Signals inevitably overlap with background noise, making them less detectable, or with other signals, making them less discriminable. This overlap can result in two types of receiver error: false alarms, which occur when receivers respond to incorrect or inappropriate signals, and missed detections, which occur when receivers fail to respond to correct signals (Wiley 1994; Wollerman & Wiley 2002). Note that, from the receiver’s point of view, false alarms are ‘correct’ in that they may be responses to the same perceptual cues that yield correct detections; only the outside observer recognizes that the responses are being given in an inappropriate situation.

Given their perceptual limitations, receivers cannot simultaneously reduce both types of error. If they attempt to decrease false alarms by being less responsive to signals, they will increase their risk of missed detections. Alternatively, if they attempt to lower the risk of missed

detections by being more responsive, they will increase their risk of false alarms. Thus, unless a receiver’s perceptual abilities improve, its level of responsiveness must be a balance between the two types of error (Wiley 1994; Bradbury & Vehrencamp 1998).

This trade-off may be an important selective pressure shaping signalling interactions between animals (e.g. Wiley 1994; Getty 1997; Bradbury & Vehrencamp 1998). For example, if the cost of false alarms is low, then receivers may respond eagerly, tolerating occasional false alarms in order to avoid missing correct signals. Their readiness to respond could, in turn, make them more susceptible to manipulation by signallers. Conversely, if the cost of false alarms is high, then receivers may respond cautiously, accepting the occasional missed signal in order to avoid costly false alarms. This hesitancy to respond could then select for more extreme displays, as signallers attempt to stimulate reluctant receivers (Wiley 1994; Dawkins & Guilford 1997; Rodríguez-Gironés & Lotem 1999; Godfray & Johnstone 2000). Thus, the risk of error may have fundamental effects on the behaviour of both signallers and receivers.

Despite the potential for error to influence the evolution of signalling behaviour, it has gained relatively little empirical attention in studies of animal communication

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(Wiley 1994; Dawkins & Guilford 1997; but see Wollerman & Wiley 2002). This may be because, in most communication systems, receiver error is difficult to observe and characterize. A potentially tractable system for the study of error, however, may be signalling between nestling passerine birds and their parents. Nestlings respond to the arrival of their parents at the nest with food by producing a vigorous begging display that involves calling, posturing and gaping. Parents respond to variation in the display by feeding the most intensively begging of their offspring (Budden & Wright 2001a). This interaction can occur hundreds of times per day (M. L. Leonard & A. G. Horn, unpublished data) and, in many species, is readily observable. Thus, this communication system may provide an excellent opportunity to examine the frequency and nature of error.

Most begging occurs when parents arrive at the nest to feed (Leonard & Horn 2001a). However, it also occurs between parental visits, in response to movement of the nest or broodmates (Clemmons 1995; Price et al. 1996; Budden & Wright 2001b; Leonard & Horn 2001b). Begging in the absence of parents appears to provide no obvious benefit (Leonard & Horn 2001b; but see Roulin et al. 2000; Roulin 2001) and potentially increases the energetic (Kilner 2001) and predation costs (Haskell 2002) of begging for some species. Thus, such responses might reasonably be considered errors and, more specifically, false alarms. The risk of false alarms may be an important selective pressure on begging behaviour because nestlings, like any receivers, may be unable to increase their correct detections (i.e. begging to parents) without also increasing their risk of false alarms. If so, then costly false alarms may affect when and how nestlings beg.

Only two descriptive studies have examined potential begging errors in nestling birds (Budden & Wright 2001b; Leonard & Horn 2001b). In southern grey shrikes, *Lanius meridionalis*, begging in the absence of parents decreased with nestling age and with increasing prey size at the last feeding (Budden & Wright 2001b), while in tree swallows, *Tachycineta bicolor*, it increased with age and time since the last feeding (Leonard & Horn 2001b). Neither study, however, examined the relationship between these responses and correct responses. In addition, because the studies were descriptive, the effects of age and hunger on the frequency of begging errors may have been confounded by other uncontrolled variables.

Here, we determine whether nestling tree swallows commit false alarms by begging to the sound made when a common grackle, *Quiscalis quiscula*, a potential nest predator of tree swallows (Robertson et al. 1992), lands at the nest. We also investigate how the rate and intensity of begging to this stimulus varies in relation to hunger and age, both of which are known to affect the frequency of correct detections (i.e. begging to parents) in many species (Budden & Wright 2001a).

If an increase in correct detections is accompanied by an increase in false alarms, as predicted by theory, we would expect responses to the grackle stimulus to increase with nestling hunger and age, as do responses to parents (Leonard & Horn 1996, 2001a). The exact form of the increase in false alarms relative to correct detections as

hunger increases may depend on changes both in motivation to respond and in attention, and thus is hard to predict a priori (Alsop 1998). The overall increase in the perceptual abilities of nestlings with age (Khayutin 1985; Clemmons 1995), however, may result in fewer false alarms per correct detections at older ages than at younger ages.

## METHODS

We conducted this study at two sites in the Gaspereau Valley, Nova Scotia, Canada using methods that conformed to both federal and institutional requirements for the use of animals in research (Dalhousie University Animal Utilization Proposal 99-041 and 02-059). We designed two experiments. Experiment 1 examined the relationship between false alarms and hunger and was conducted between 1 May and 31 July 2000. Experiment 2 focused on how false alarms varied with age and was conducted between 1 May and 31 July 2002. The study sites are described in detail in Leonard & Horn (1996). Tree swallows at these sites nested in wooden boxes and the first egg dates and hatching dates were determined by checking nestboxes every second day until 2 days before the predicted hatching date, after which they were checked daily.

### Stimulus Tapes

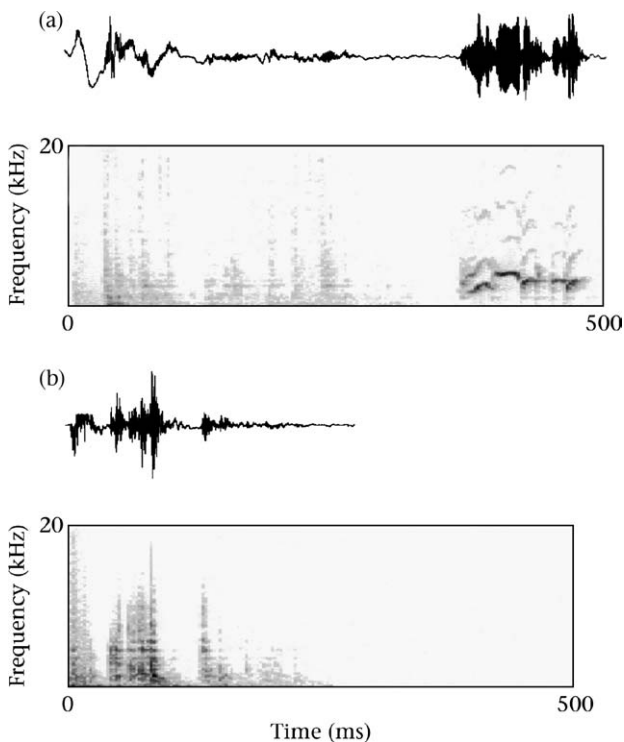
Throughout this paper, we use the term 'signal' to refer to a trait that is specialized for its function in communication, such as a tree swallow's call. We use the word 'stimulus' or 'sound' to refer more broadly to anything that might cause a nestling to beg, whether or not it is specialized for this function.

In both experiments, we presented nestlings with two types of stimulus sounds over a 1-h period of food deprivation: (1) the sound of a tree swallow landing at the nest entrance, accompanied by the call that parent swallows give to stimulate begging (Leonard et al. 1997) and (2) the sound of a common grackle, a nest predator of tree swallows (Robertson et al. 1992), landing on a tree swallow nestbox. We presented nestlings with the swallow stimulus to confirm the relationship between correct detections and hunger documented in previous experiments (Leonard & Horn 1996, 1998, 2001a). We presented nestlings with the sound of a predator, rather than another nonparental sound, to ensure that a response to this stimulus could be unambiguously categorized as a false alarm (i.e. begging to a predator is reasonably considered an inappropriate response). Thus, we considered a response to the swallow stimulus to be a correct detection and a response to the grackle stimulus to be a false alarm.

We obtained the swallow stimuli by placing a Genexxa 33-3003 lapel microphone attached to a Sony DM-100 digital tape recorder inside nestboxes and recording sounds made when parents came to the nest to feed. We recorded grackle stimuli using the same microphone placement and recording levels, when grackles landed

on the top or opening of unused tree swallow nestboxes to retrieve peanuts that we placed on the box. We selected five tree swallow stimuli and five grackle stimuli that were free of background noise and recorded from different birds on different days (Fig. 1). Using more than one recording, and playing each to more than one subject, enabled us to test whether treatment effects varied depending on the playback tapes used (see below).

The taped sounds were digitized at 44 kHz and 16 bits using Canary 1.2 software (Charif et al. 1995), then re-recorded with a Sony WM D6 Professional cassette recorder on Sony metal SR cassette tapes for playback. For each playback tape, we took five repetitions of a swallow sound and five of a grackle sound, placed them in random order, and separated them from each other by 30 s of silence. This sequence of 10 sounds was then repeated six times, with each sequence separated from the next by 5 min of silence. Thus, each playback tape was approximately 1 h long, with six test sequences, each composed of five swallows and five grackle sounds. Because nestlings were without food during the 1-h period (see below), later test sequences presumably correspond to greater hunger levels. This design might cause nestlings to habituate to the playback, which, in turn, might lead to an underestimation of the effects of deprivation for either stimulus sound. However, we have found no apparent habituation by nestlings in previous experiments that used the presentation rates used here (e.g. Leonard & Horn 2001a).



**Figure 1.** Waveforms (top panels) and spectrograms (bottom panels) of (a) a swallow stimulus sound (i.e. a tree swallow contact call with landing sound) and (b) a grackle stimulus sound (i.e. a grackle landing sound) used in playbacks to nestlings.

## Experiment 1: False Alarms and Hunger

When broods were 10 or 11 days old (mean: 10.1 days) we weighed nestlings in each of 27 broods and removed the nestling closest to the middle of the weight hierarchy. We stimulated it to beg and then fed it moistened Hartz's Egg Biscuit for birds until begging stopped. The nestling was then placed in a nest cup in an empty nestbox located at each study site. We placed a Plexiglas plate in the hinged opening of the box, pointed a Panasonic PV-900-K VHS video camera at the open side and covered it with a plastic bag. To the left and 10 cm from the nestbox entry hole, we placed a Realistic 40-1259B speaker amplifier that was attached to a Sony TC3 D5M tape recorder.

Twenty minutes after the nestling was fed, we began the playback tape. We alternated playback tapes across trials. Nestlings were fed and returned to their home nestbox following the completion of each trial, having been removed from the box for a maximum of 2 h.

## Experiment 2: False Alarms and Age

To examine the effects of nestling age on response to the two stimuli, we repeated experiment 1 on 21 broods with the following changes: (1) we tested nestlings at days 5–6 posthatch (mean:  $5.56 \pm 0.121$ ,  $N = 18$ , hereafter 'younger' nestlings) and days 7–9 (mean:  $8.33 \pm 0.767$ ,  $N = 18$ , hereafter 'older' nestlings); (2) at each age, we placed two nestlings from each brood in separate nestboxes and tested them simultaneously to safeguard against failed trials; (3) we conducted experiments indoors because an extended period of inclement weather prevented outdoor trials and (4) we used five replicates of the playback tape, which we balanced across trials. Nestlings were not marked at younger ages, so tests on younger and older nestlings from a given brood were not necessarily done on the same individual nestlings.

## Video Analyses

We examined two aspects of nestling begging response: (1) the rate of response to swallow and grackle sounds in each test sequence (i.e. the total number of responses to each stimulus in each sequence divided by five) and (2) the intensity of those begging responses. We scored begging intensity by assigning each begging response a value based on the following scale: (1) head down, gaping, sitting on tarsi; (2) head up, gaping, sitting; (3) same as 2, plus neck stretched upward; (4) same as 3, but body lifted off tarsi; and (5) same as 4, plus wings waving. We averaged the begging scores for each stimulus in a given test sequence.

## Statistical Analyses

In all analyses, we consider differences between the swallow and grackle stimuli to be fixed effects (i.e. differences that are not formally generalizable beyond the playback tapes used here). We could not formally test

whether our results held for swallow and grackle sounds in general, because we could not consider our tapes to be randomly selected replicates of those sounds (Bennington & Thayne 1994). Using more than one playback tape did, however, allow us to check whether the particular tapes we used yielded similar results. Specifically, we tested for variation in results across playback tapes by including tape as a blocking factor, in analyses similar to those reported below, and found that the different tapes yielded similar results ( $F < 1.4$ ,  $P > 0.30$  for all treatment\**tape* interactions).

### Experiment 1: false alarms and hunger

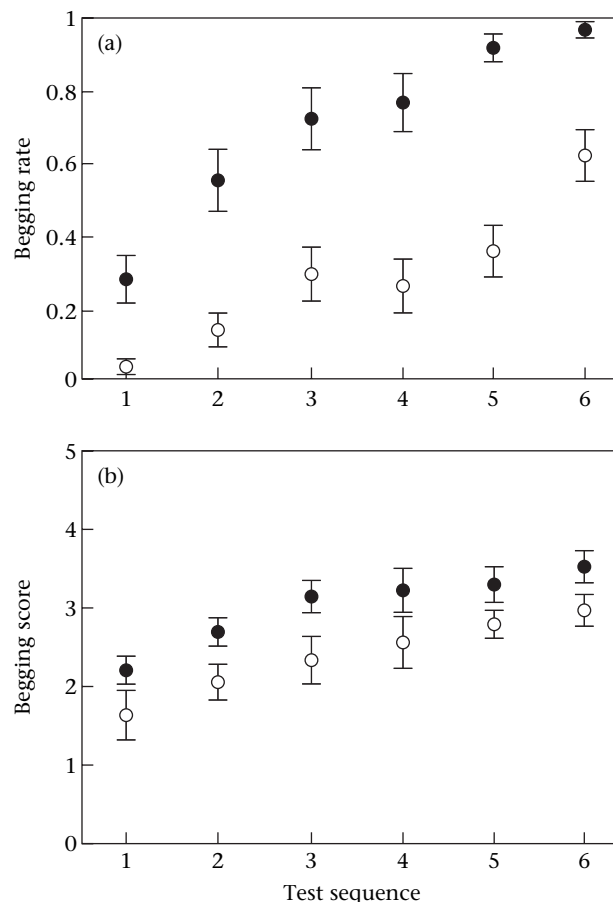
To quantify changes in begging rate and mean begging score with hunger, we regressed each of these variables against the six test sequences (i.e. time without food) for individual nestlings. To be included in the analysis, a nestling had to respond to each stimulus in at least two test sequences. We used Kendall's robust line-fit method for nonparametric regression (Sokal & Rohlf 1995) and, for each nestling, calculated a slope and intercept for the relationship between begging rate and test sequence and between begging score and test sequence. This method measured the linear component of changes in begging across test sequences. In exploratory analyses, we tested for curvilinearity by performing parametric regressions using quadratic models (as in Leonard & Horn 2001a). Curvilinearity was only present in begging rates to swallow stimuli, because nestlings reached the maximum possible begging rate (1.0) by about the fifth test sequence (Fig. 2a). Analyses using only the data preceding this levelling off gave similar results to analyses that included all the data, so only the latter analyses are presented here.

Once we calculated slopes and intercepts for each variable, we used a one-sample *t* test to examine whether the slopes of the regression lines, averaged across all nestlings, differed significantly from zero. We also used paired *t* tests, using nests as blocks, to test whether slopes and intercepts differed between regression lines for swallow and grackle stimuli.

### Experiment 2: false alarms and age

In this experiment, we focus on the relationship between overall levels of false alarms and age, so we first calculated the mean begging rate and begging score for each nestling across all six test sequences, at each age. For trials in which both nestlings responded, we averaged their responses, so that each brood would contribute only one datum to any given analysis. For trials in which nestlings did not respond, we could not calculate a begging score, but we could at least assume that their response was lower than the response of nestlings that begged. Therefore, we ranked all begging scores, assigning the lowest rank to nestlings that did not beg.

To test how begging rates and begging scores varied with stimulus and age, we used repeated measures ANOVA, in which trials were 'blocks' and stimulus (swallow or grackle), age (younger or older), and their



**Figure 2.** Mean  $\pm$  SE (a) begging rate and (b) begging score during each test sequence for tree swallow nestlings in response to the swallow stimulus (●) and the grackle stimulus (○).

interaction were 'within-block' effects. Analyses of rank transformed data, such as the begging scores analysed here, can obscure interaction effects and yield invalid results when interactions are present. However, analysis of the aligned ranks, which corrects for this problem (Richter & Payton 1999), showed no significant interactions and yielded similar results to the analyses of the original ranks that are reported here.

Although the raw data were proportions and ranks, the data entered into the analyses (slopes and intercepts for experiment 1, mean proportions and ranks for experiment 2) produced normally distributed errors and homogeneous variances (Shapiro-Wilk *W* tests and Brown-Forsythe tests:  $P > 0.10$ ). The data therefore met the assumptions of the parametric tests that we used, although because the ANOVA on begging scores in experiment 2 was performed on ranked data, it was equivalent to a nonparametric rank test (Conover & Iman 1981). Analyses were performed using JMP Version 3.1 (SAS Institute 1994). Means are presented  $\pm$  SEM, and significance levels set at  $P = 0.05$ . As a guide for judging whether marginal results are robust (Colegrave & Ruxton 2003), we provide confidence intervals for effects where  $0.05 < P < 0.10$ .



## RESULTS

### Experiment 1: False Alarms and Hunger

Begging rate increased with food deprivation for both swallow and grackle stimuli, although the swallow stimulus elicited higher rates than the grackle stimulus (Fig. 2a). The slope of the regression line between begging rate and test sequence was positive and significantly different from zero for both swallow and grackle stimuli (mean slope: swallow:  $0.10 \pm 0.016$ ; one-sample  $t$  test:  $t_{24} = 5.78$ ,  $P < 0.0005$ ; grackle:  $0.11 \pm 0.016$ ;  $t_{17} = 6.51$ ,  $P < 0.0005$ ; Fig. 2a), and did not differ significantly between the two stimuli (comparison of slopes: paired  $t$  test:  $t_{17} = 0.84$ ,  $P = 0.41$ ; Fig. 2a). The intercept for the line describing responses to the swallow stimulus was, however, significantly higher than that of the line describing responses to the grackle stimulus (intercepts: swallow:  $0.33 \pm 0.103$ ; grackle:  $-0.02 \pm 0.060$ ;  $t_{17} = 4.58$ ,  $P = 0.0003$ ; Fig. 2a).

Begging score also increased significantly with food deprivation for both swallow and grackle stimuli (mean slope: swallow:  $0.35 \pm 0.038$ , one-sample  $t$  test:  $t_{24} = 9.27$ ,  $P < 0.0005$ ; grackle:  $0.34 \pm 0.080$ ; one-sample  $t$  test:  $t_{17} = 4.19$ ,  $P = 0.001$ ; Fig. 2b), and again, showed no significant difference in the slopes of the lines for the two stimuli (comparison of slopes: paired  $t$  test:  $t_{17} = 0.02$ ,  $P = 0.82$ ). The intercepts did not differ significantly (swallow:  $1.91 \pm 0.231$ ; grackle:  $1.18 \pm 0.329$ ;  $t_{17} = 1.80$ ,  $P = 0.09$ ), although the average response to the swallow stimulus was higher than to the grackle stimulus in each test period (Fig. 2b; the 95% confidence interval for the difference in intercepts was  $-0.13$ – $1.59$ ).

### Experiment 2: False Alarms and Age

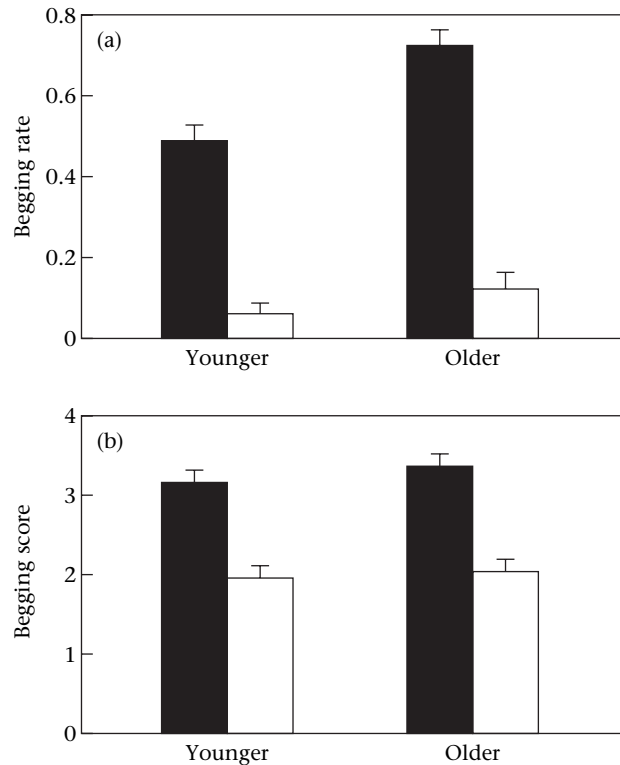
As in experiment 1, nestlings begged at significantly higher rates to the swallow stimulus than to the grackle stimulus ( $F_{1,15} = 151.72$ ,  $P < 0.0005$ ; Fig. 3a). Mean begging rates also increased with age ( $F_{1,15} = 5.14$ ,  $P = 0.039$ ) to both stimuli (age\*stimulus interaction:  $F_{1,15} = 2.29$ ,  $P = 0.15$ ; Fig. 3a).

Begging scores for the swallow stimulus were significantly higher than for the grackle stimulus ( $F_{1,15} = 28.96$ ,  $P = 0.0001$ ; Fig. 3b). Mean begging scores did not increase with age ( $F_{1,15} = 0.53$ ,  $P = 0.48$ ) for either stimulus (age\*stimulus interaction:  $F_{1,15} = 2.34$ ,  $P = 0.15$ ; Fig. 3b).

## DISCUSSION

### False Alarms and Hunger

The rate and intensity at which nestlings begged to the grackle stimulus increased as the time without food increased, following the same pattern as responses to the swallow stimulus, albeit at lower levels. These results are consistent with the prediction that, as the cost of missing correct stimuli increases, receivers will become more responsive overall, which, in turn, will increase the likelihood of both correct detections and false alarms



**Figure 3.** Mean  $\pm$  SE (a) begging rate and (b) begging score for tree swallow nestlings at days 5–6 posthatch (younger) and days 7–9 (older) in response to the swallow stimulus (■) and the grackle stimulus (□).

(Johnstone 1998). Specifically in this case, as nestlings grow hungrier, they presumably lower their threshold for response to stimuli that might signal an adult swallow's arrival. In so doing, they increase the likelihood that they will respond to parents, but concomitantly increase the likelihood that they will respond to other events, such as the arrival of a predator. Both possibilities increased at similar rates over the deprivation times we tested, although, over longer deprivation times, false alarms might increase disproportionately as the frequency of correct detections reaches its maximum.

Thus, as nestlings grow hungrier and beg more readily, they must weigh an increase in the likelihood of being fed against an increased risk of begging unnecessarily, or worse, begging to a predator at the nest. The potential costs of false alarms have been ignored in most studies of begging (but see Budden & Wright 2001b; Leonard & Horn 2001b). False alarms may be frequent, however; up to 30% of begging responses by 8-day-old tree swallows are to stimuli in the absence of parents (Leonard & Horn 2001b). If false alarms also covary with nestling hunger, as suggested by the present study, they may be an important influence on how often and how intensively nestlings beg. For example, if false alarms were particularly costly (e.g. because acoustically orienting nest predators were locally common), then nestlings might beg less readily or intensively for any given level of need than they otherwise would.

Further experiments are needed to clarify these potential costs, especially experiments that present a broader range of predator and nonpredator stimuli. For example, pilot experiments with tree swallows showed that nestling responses to a parent landing on a nestbox without calling were less frequent and intense than responses to a parent landing with a call, but were greater than responses to a grackle landing (M. L. Leonard & A. G. Horn, unpublished data). Thus, the costs of false alarms might be lowered if nestlings can distinguish the sounds made by predators from those made by adult swallows or by the other harmless songbird species that frequently land on nestboxes. The main cost of false alarms might then be the energetic cost of unnecessary begging, rather than the risk of responding to a predator.

### False Alarms and Age

Begging rates to both swallow and grackle stimuli increased significantly with nestling age. Older nestlings might beg more readily because they need more resources or because they are more likely to exaggerate their needs (Kilner 2002). Our results suggest, however, that whatever benefits older nestlings gain from their greater responsiveness could be counteracted, at least partly, by a higher risk of committing false alarms. In nature, the risk of false alarms may be increased still further than our experiment suggests, because, as nestlings age, parents are less likely to call when they arrive at the nest (Leonard et al. 1997), so their arrival may be harder to distinguish from other sounds.

One factor that may reduce the increased risk of false alarms, however, is an improvement in perceptual abilities with age (Khayutin 1985; Clemmons 1995). This improvement should result in older nestlings performing fewer false alarms for a given level of correct detections. In the present study, such a pattern would have appeared as a significant age\*stimulus interaction. We did not detect such an effect, although the mean begging rates were in the predicted direction (Fig. 3a) and the 95% confidence interval for the interaction (i.e. how much the difference between the swallow and grackle response rates changed with age) was narrow ( $-0.03$ – $0.23$ ; Colegrave & Ruxton 2003).

Observations from the two earlier descriptive studies of how apparent false alarms vary with age yielded conflicting results (Budden & Wright 2001b; Leonard & Horn 2001b). In tree swallows, the proportion of total begging responses that were to stimuli other than parents with food increased as nestlings aged (Leonard & Horn 2001b), but in southern grey shrikes, it decreased (Budden & Wright 2001b; see also Clemmons 1995). These differences may reflect fundamental interspecific differences in the begging response (Budden & Wright 2001b). Alternatively, they may result from differences in factors that were controlled for statistically, but not experimentally, in the two studies, such as nestling hunger, the stimuli that elicited begging, and the responses of nestmates (Budden & Wright 2001b; Leonard & Horn 2001b). Experimental controls like those employed in the present study are needed to distinguish interspecific

differences in the begging response from interspecific differences in the stimuli to which nestlings are exposed.

### Responses to Swallow versus Grackle Stimuli

Our results showed that, for the same time without food, nestlings begged more frequently (in both experiments) and more intensively (at least in experiment 2) to the swallow stimulus than to the grackle stimulus. In the wild, nestlings also beg less intensively to stimuli such as the movement of nestmates or the nest than they do to stimuli associated with the arrival of the parent (M. L. Leonard & A. G. Horn, unpublished data). Thus, in both laboratory and field, begging appears to be affected not only by nestling need, but also by the stimulus that elicits the response. Few studies have examined this source of variation in the intensity of begging signals (but see Kedar et al. 2000; Hauber 2003).

The stimuli that elicit begging deserve more study for at least two reasons. First, a variety of stimuli, tapping or the human voice, for example, have been used to elicit begging and to measure variation in its frequency and intensity in relation to need. Our results, however, suggest that some of the variation in the begging signal is dependent on how that signal was elicited, and this source of variation should be considered in the design of experiments on begging.

Second, parent birds might be able to better assess the need of nestlings by signalling their arrival either unambiguously with a call, or ambiguously without a call. More ambiguous arrivals should stimulate only the hungriest nestlings, thus ensuring that parents feed the neediest of their brood. Such behaviour might add a new dimension to current theories of parent–offspring communication, in which parents act mainly through adjusting their provisioning, rather than through directly manipulating their offsprings' signals (Johnstone & Godfray 2002).

### Signal Detection Theory and Begging

Ideally, the stimuli that elicit begging should be studied with techniques based on signal detection theory (SDT, Macmillan 1993), because these techniques can separate a nestling's readiness to respond from its ability to perceive the stimuli. In the present experiment, for example, a nestling may respond more strongly to a swallow stimulus because it is more eager to respond or because it more readily recognizes the sound as an adult swallow. According to SDT, responses to the grackle can be used to separate the two explanations. Greater eagerness (i.e. 'bias' in SDT terminology) would increase responses to both stimuli, while better discrimination (i.e. 'sensitivity') would preferentially increase responses to the swallow stimulus. Appropriate transformations of response data can separate these components as two uncorrelated variables.

Exploratory analyses of our data using a variety of transformations (including those based on matching law

and choice theory, Irwin & Davison 1998), however, failed to separate bias and sensitivity. This difficulty is frequently encountered in studies on nonhuman subjects, because how they perceive stimuli is often more tightly linked to their readiness to respond than simpler versions of SDT would suggest (Alsop 1998). While, in theory, SDT is a promising way to think about animal communication (Wiley 1994), in practice, it may require a fuller knowledge of the relationship between stimulus and response than we currently have for begging nestling birds.

### Acknowledgments

We thank Don Dearborn, Elsie Krebs, Rob Magrath, Doug Nelson and Emily Parks for reading earlier drafts of this manuscript and making many helpful comments, and Rob Magrath and Pete McGregor for helpful discussion. We also thank Anne Duncan, Emily Parks and Jackie Porter for their excellent assistance in the field and the Coldwell and Minor families for access to their land. This work is supported by a Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery Grant to M.L.L. and an NSERC Undergraduate Scholarship to A.M.

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