# Nest predation and the evolution of nestling begging calls

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Begging by nestling birds can be conspicuous and loud. Such displays are thought to function in signalling nestling condition and securing parental care, but they also may inadvertently attract the attention of predators. We compared the structure of nestling begging calls to the risk of predation among 24 species of birds breeding in a forest community in central Arizona. After controlling for body size and phylogeny, we found that species subject to greater nest predation had calls with higher frequency (pitch) and lower amplitude (loudness) than species subject to lower rates of nest predation. As these acoustic features make it difficult for potential predators to pinpoint the source of a sound, our results suggest that an increased risk of predation has led to the evolution of begging calls that minimize locatability. The relationship between call structure and the risk of predation also supports the hypothesis that attracting predators is a direct cost of begging and that such costs can constrain any evolutionary escalation in the intensity of nestling begging.

**Keywords:** begging behaviour; nestling vocalizations; nest predation; nestling birds

## 1. INTRODUCTION

Anyone who has watched a parent bird feed its brood of nestlings will have been struck by the conspicuous and noisy begging that accompanies the process. Nestlings are assumed to benefit from begging because it results in a net increase in the allocation of resources to the signaller over a non-begging strategy (e.g. Macnair & Parker 1979; Harper 1986). As the benefits of begging increase with the intensity and frequency of the displays (e.g. Smith & Montgomerie 1991; McRae *et al.* 1993), begging intensity might be expected to escalate indefinitely or become unreliable unless constrained by ever-increasing costs (Macnair & Parker 1979; Harper 1986; Grafen 1990; Godfray 1991, 1995*a,b*).

The vigorous gaping, stretching and jostling that accompanies begging has been suggested to lead to an energetic cost, but recent measurements of oxygen consumption by begging nestlings have produced equivocal results (Leech & Leonard 1996; McCarty 1996; Verhulst & Wiersma 1997; Weathers *et al.* 1997). However, even if begging incurs a low energetic cost, it may not be the only cost. Nestling vocalizations may inadvertently attract the attention of predators and increase the cost of begging (Harper 1986; Redondo & Castro 1992). Playbacks of recorded begging calls increased the rate of predation on both artificial open-cup nests and artificial cavity nests (Haskell 1994; Leech & Leonard 1997). As artificial nests do not provide parental activity cues which potential predators could use to locate the nest, the

increase in predation seems to have resulted solely from the cues provided by begging vocalizations. Predation risk could thus lead to the evolution of begging vocalizations that minimize their locatability and such responses might be expected to be most strongly manifested in species at greatest risk.

If potential predators use begging calls to find the signaller, then it would be advantageous for nestlings to use calls that reduce the effectiveness with which their source can be pinpointed. Not all types of sound are transmitted through the environment with the same efficiency and so the locatability of a sound can be reduced by changing the structure of the call (Wiley & Richards 1982). One of the most obvious ways to reduce locatability is by reducing the amplitude (loudness) of the signal. Because sound waves spread in an approximately spherical pattern from a point source, the intensity of sound (i.e. decibel level) attenuates in proportion to the inverse square of the radius (Wiley & Richards 1982). For example, the distance at which a call could be detected by a predator decreases fourfold by reducing the amplitude of a begging call by half. Thus, species particularly prone to predation should evolve begging vocalizations with low amplitude.

The attenuation of sound waves also varies with the frequency (pitch) of the call: higher frequency sounds tend to show greater attenuation because they are more prone to absorption by the atmosphere and to scattering by objects in their path (Wiley & Richards 1982). In contrast, low-frequency sounds are more likely to bend around objects and are less affected by atmospheric conditions. Such sounds are easy to locate and might serve as location cues for both parents and predators. At the simplest level, this suggests that species subject to a

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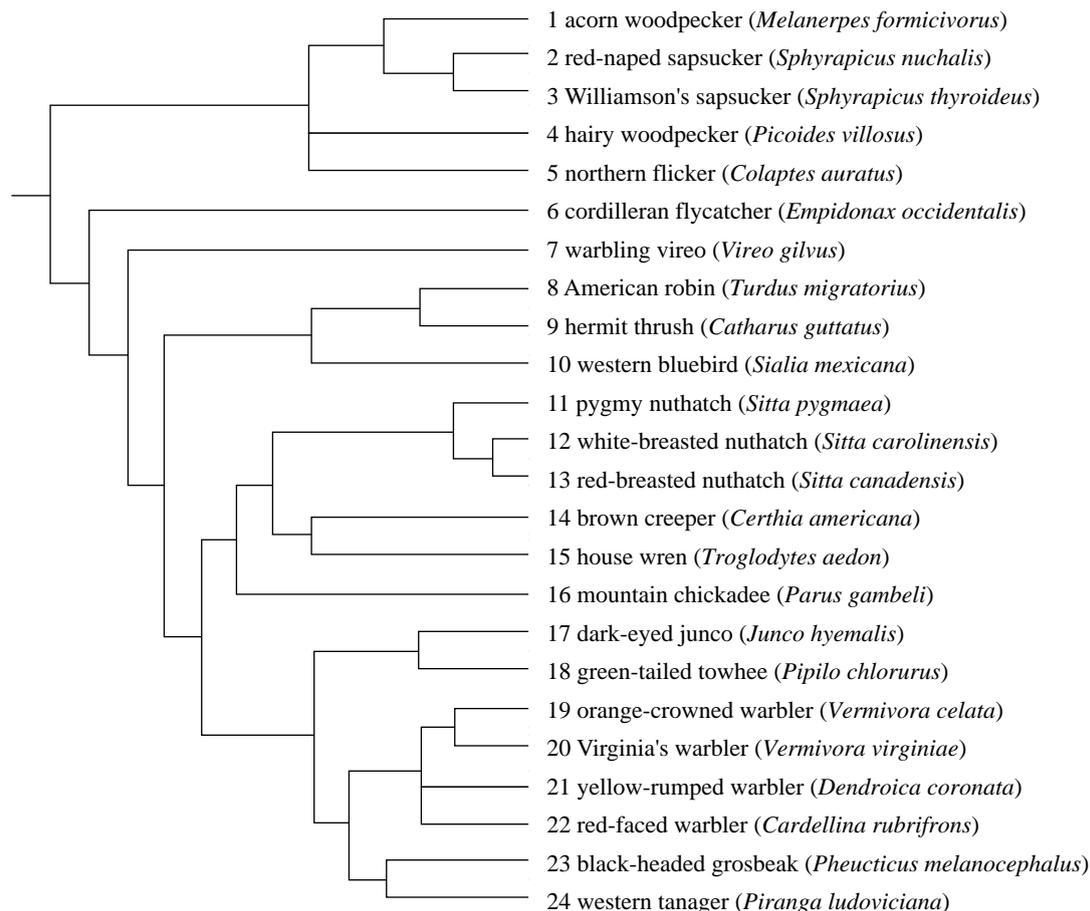
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Figure 1. Phylogeny derived from Sibley & Ahlquist (1990) for the 24 species of birds used in this study.

high risk of predation should produce calls with higher frequencies than species less at risk. However, begging vocalizations are seldom restricted to a single frequency and instead cover a range of frequencies. Such wide-spectrum sounds are generally easier to locate by avian and mammalian ears through phase-difference detection (at low frequencies) and amplitude differences (at higher frequencies) and so would be more likely to attract the attention of predators. Species subject to increased risk of predation should therefore evolve begging calls not only with a high frequency but also with a narrow frequency range.

In this study, we examined the structure of nestling begging calls among a community of birds subject to varying levels of predation risk. Our objective was to determine whether those species subject to higher rates of predation have evolved begging calls that minimize their locatability. We predicted that calls with decreased amplitude, increased frequency and decreased frequency range should evolve in species with the greatest rate of nest predation.

## 2. METHODS

Begging calls of nestling birds were recorded from 24 species of birds (listed in figure 1) nesting in the Coconino and Apache Sitgreaves National Forests, near Flagstaff, Arizona, USA. The study site consisted of a series of snow drainages situated along the southern edge of the Mogollon Rim (elevation 2300 m; see

Martin 1998). Most of the area is covered by a forest of ponderosa pine (*Pinus ponderosa*), white fir (*Abies concolor*), Douglas fir (*Pseudotsuga menziesii*), Gambel oak (*Quercus gambellii*), big-toothed maple (*Acer grandidentatum*) and quaking aspen (*Populus tremuloides*). As part of a long-term study of community dynamics and life-history evolution, nests of all species were monitored yearly from 1987 to 1997 (Martin & Li 1992; Martin 1993a,b, 1998).

Nests were located by following adults during daily searches from early May to mid-July. To estimate the predation risk, we checked the nests at two to four day intervals until their outcome could be determined. The nests were checked at a distance using binoculars to reduce the predation risk due to disturbance by the observer. Several hundred nests were monitored each year and our estimates of nest predation rates are based on a total of 5050 nests over the ten year period. The number of nests monitored per species ranged from 38 in the acorn woodpecker to 544 in the house wren (mean = 210 nests per species). We did not record the begging calls of any species for which we had less than 35 nests to estimate the predation rate. The daily predation rate was calculated as the inverse of daily survival based on the Mayfield (1961, 1975) method and as modified by Hensler & Nichols (1981). Nests from all years were pooled. Because of the large sample sizes and long-term nature of the data, we are confident that our measures of predation are fairly robust and reflect real differences in the risk of predation to which the different species are exposed.

Begging calls themselves may influence the rate of predation, so we only used predation rates during the incubation stage as

an index of predation risk. Although the rate of predation on eggs is likely to differ somewhat from that of nestlings, this measure is independent of the behaviour of the nestlings and represents the 'background' predation rate into which nestlings hatch. The rate of predation on nestlings is strongly correlated with that on eggs ($F_{1,22} = 45.4$, $r = 0.83$ and $p < 0.001$) and our results did not change if we used nestlings to calculate the daily predation rate. The primary predators in our study site were red squirrels (*Tamiasciurus hudsonicus*), grey-neck chipmunks (*Eutamias cinereicollis*), long-tailed weasels (*Mustela frenata*) and Steller's jays (*Cyanocitta stelleri*; Martin 1988, 1993b). All of these predators are active diurnally and have the potential ability to use auditory cues in locating prey.

Recordings were made in May–July during the 1995–1997 breeding seasons. The sample of species includes almost the entire community of birds present in this area, except for the rarest species and those which could not be safely accessed. To ensure recordings were comparable among our group of 24 species, our recording protocol was standardized to recording level, microphone distance and chick development. Special care was taken to ensure that the same procedure was used for all nests. Calls were recorded by using a Sony Professional Walkman (model WM-D3) and a Sony PC-62 microphone. Two different tape recorders were used but each was set at an identical recording level (setting 6) and calibrated with a series of five to eight tones before each session. We had previously determined that these tones were highly invariant in amplitude and frequency. The microphone was set 15 cm above the centre of the nestlings and connected to a recorder by a 25 m long cable. For cavity nests, the inner cavity depth was first measured and then the microphone placed 15 cm above the level of the nestlings. In most cases, this put the microphone at the opening of the cavity, although in six particularly deep nests (out of 87) it was placed 1–3 cm within the cavity. It is possible that placing the microphone within the cavity may have altered some measurements. However, this was necessary to keep recordings comparable among species and there were no obvious differences in the recordings between nests that could be related to microphone location.

Once the microphone was secure, we retreated out of sight and continued recording for a series of three to five feeding bouts. Parent birds usually returned within a few minutes of setting up the microphone and soon continued feeding deliveries. Only begging calls in response to a parental visit were used. We controlled for nestling developmental stage by recording birds on the day their primaries emerged from the sheaths (feathers *ca.* 1–3 mm long). The developmental stage of cavity-nesting birds was determined by either pulling out one or more chicks for examination or by inspecting the nest with an optical endoscope. At least one nestling was weighed to obtain an estimate of chick mass. A total of 87 nests were recorded among the 24 species. The number of nests recorded per species ranged from one to seven (mean = 3.6). All recordings were made on Sony Type II (CrO$_2$) recording tape.

The recordings were analysed by using the Canary software package from Cornell University. For each begging bout, we selected the first 1 s sequence of begging after the parent arrived back at a nest and then calculated the following variables: minimum and maximum frequency (kHz), frequency range (maximum minus minimum frequency), frequency at maximum amplitude, and maximum amplitude (dB). Note that all these measurements refer to the average combined measures for all begging calls within the 1 s period and not to a single begging

call. We chose to analyse the data in this manner as it was sometimes difficult to discern individual calls from single nestlings (particularly in the woodpeckers) and because we felt it was also more representative of the sound that a predator might detect. Amplitude or 'loudness' was measured digitally and was defined as the maximum amplitude from the average power spectrum. This measure of amplitude could be inflated in species with larger brood sizes as a result of the additive effect of the greater number of calling nestlings and so we controlled for brood size in our analyses. Frequency (minimum, maximum and range) was also measured directly off the power spectrum graph. We report amplitude on a decibel scale with the amplitude of the calibration tone set at zero. This allowed us to calibrate for slight differences between the two machines and from one recording session to the next. The mean of the three to five bouts was calculated to give an overall measure for that nest. These values were then averaged to obtain a species estimate. To minimize background interference, recordings were not made during windy or inclement weather.

Comparisons between species were made using the methods outlined by Harvey & Pagel (1991) to control for phylogeny. Such controls are required because the structure of begging calls may be similar in closely related species simply through inheritance from a common ancestor, rather than as independent adaptations to similar predation rates. We first constructed a phylogeny of the species studied by using the DNA-based classification of Sibley & Ahlquist (1990; figure 1). We then calculated a series of unique linear contrasts for each node in our phylogeny for which there was variation in the independent variable using the Comparative Analysis by Independent Contrast (CAIC) program of Purvis & Rambaut (1994). To test for relationships between taxa, the linear contrasts for one variable are correlated with those of another. Thus, the sample sizes in these analyses are the number of independent contrasts and not the original number of species. All correlations were forced through the origin as recommended by Harvey & Pagel (1991). A significant correlation between two variables suggests that the evolution of one character is associated with that of the second.

The frequency range and nestling body mass were normalized by $\log_{10}$ transformation. The daily mortality rate was normalized by an angular transformation, while the frequency at maximum amplitude was normalized by a square-root transformation. Amplitude was measured on a log scale and was normally distributed.

## 3. RESULTS

The maximum amplitude (ANOVA, $F_{23,86} = 22.8$ and $p < 0.0001$), frequency at maximum amplitude ($F = 23.3$ and $p < 0.0001$) and frequency range ($F = 12.6$ and $p < 0.0001$) varied significantly among the species we sampled (table 1). Some differences between species were dramatic and readily discernible by the human ear. For example, the amplitude (decibels) of begging calls by nestling acorn woodpeckers was five orders of magnitude greater than the amplitude of red-faced warbler calls. The frequency at maximum amplitude similarly varied across species, ranging from a low of 1.16 kHz in the northern flicker to a high of 7.63 kHz in the red-breasted nuthatch, while the frequency range of acorn woodpecker calls was more than seven times the range of red-faced warbler begging calls. The body masses of nestlings were also quite variable, ranging from 7.1 g in the Virginia's warbler

Table 1. *Predation rates, mean nestling masses and begging call features for the 24 species of birds used in this study*

(All values were measured directly by the authors. The taxonomy follows Sibley & Ahlquist (1990).)

| species | mean nestling mass (g) | daily predation rate | call feature amplitude (dB) | frequency at maximum amplitude (kHz) | frequency range (kHz) |
|---|---|---|---|---|---|
| family Picidae | | | | | |
| *Melanerpes formicivorus* | 42.0 | 0.0078 | 8.82 | 5.101 | 8.271 |
| *Sphyrapicus nuchalis* | 41.3 | 0.0029 | 4.35 | 2.198 | 8.114 |
| *Sphyrapicus thyroideus* | 37.1 | 0.0035 | 4.87 | 2.536 | 8.129 |
| *Picoides villosus* | 40.5 | 0.0000 | 8.61 | 4.791 | 7.723 |
| *Colaptes auratus* | 76.5 | 0.0049 | 5.34 | 1.155 | 8.241 |
| family Tyrannidae | | | | | |
| *Empidonax occidentalis* | 11.0 | 0.0412 | −21.93 | 6.274 | 1.510 |
| family Vireonidae | | | | | |
| *Vireo gilvus* | 10.8 | 0.0186 | −22.14 | 4.407 | 5.008 |
| family Muscicapidae | | | | | |
| *Turdus migratorius* | 41.5 | 0.0365 | −13.46 | 4.077 | 5.549 |
| *Catharus guttatus* | 23.3 | 0.0952 | −19.74 | 5.949 | 2.678 |
| *Sialia mexicana* | 23.9 | 0.0075 | −1.24 | 5.642 | 5.501 |
| family Sittidae | | | | | |
| *Sitta pygmaea* | 8.1 | 0.0074 | −6.23 | 6.429 | 5.773 |
| *Sitta carolinensis* | 18.6 | 0.0168 | 3.29 | 6.896 | 2.385 |
| *Sitta canadensis* | 7.5 | 0.0106 | −8.91 | 7.631 | 1.585 |
| family Certhiidae | | | | | |
| *Certhia americana* | 7.2 | 0.0128 | −22.50 | 6.572 | 1.938 |
| *Troglodytes aedon* | 9.7 | 0.0035 | −7.77 | 6.309 | 6.502 |
| family Paridae | | | | | |
| *Parus gambeli* | 9.5 | 0.0101 | −2.16 | 6.983 | 4.965 |
| family Fringillidae | | | | | |
| *Junco hyemalis* | 14.3 | 0.0428 | −24.58 | 7.320 | 1.822 |
| *Pipilo chlorurus* | 21.3 | 0.0671 | −24.72 | 7.142 | 2.631 |
| *Vermivora celata* | 7.5 | 0.0316 | −29.69 | 6.945 | 1.321 |
| *Vermivora virginiae* | 7.1 | 0.0257 | −25.80 | 6.297 | 1.872 |
| *Dendroica coronata* | 10.5 | 0.0234 | −21.27 | 6.825 | 2.697 |
| *Cardellina rubrifrons* | 8.4 | 0.0333 | −32.36 | 6.933 | 1.147 |
| *Pheucticus melanocephalus* | 18.3 | 0.0128 | −23.02 | 3.245 | 1.216 |
| *Piranga ludoviciana* | 16.3 | 0.0200 | −9.89 | 2.976 | 6.214 |

to 76.5 g in the northern flicker. Because several measures of begging calls were significantly correlated with body size (e.g. the maximum amplitude increased with body size), we controlled for body mass in all subsequent analyses.

The maximum amplitude was negatively correlated with the daily predation rate (figure 2*a*). Independent contrasts also showed a negative relationship between amplitude and predation, suggesting that an increase in predation risk is associated with a decrease in the loudness of nestling begging calls (figure 2*b*). In a multiple regression analysis of the contrasts (controlled for phylogeny and body mass), the maximum amplitude was significantly and negatively correlated with the daily predation rate (partial $F_{1,16} = 9.9$, $r = -0.51$ and $p = 0.006$). As the maximum amplitude was not significantly related to the average brood size (partial $F_{1,16} = 0.5$, $r = 0.17$ and $p = 0.49$), the negative relationship between amplitude and predation was not due to smaller brood sizes in species with high rates of predation.

The frequency at maximum amplitude of begging calls increased with the daily predation rate (figure 3*a*): those

species at greatest risk of predation generally produced calls with a higher pitch than species less likely to be predated. In a multiple regression analysis of contrasts (controlled for body mass and phylogeny), the frequency at maximum amplitude was significantly and positively correlated with the daily predation rate (figure 3*b*; partial $F_{1,16} = 5.4$, $r = 0.40$ and $p = 0.034$).

The frequency range of a call and the risk of predation were not correlated. The frequency range was expected to decrease with increased risk of predation but, after controlling for body mass and phylogeny, there was no significant relationship between the frequency range and daily predation rate (partial $F_{1,16} = 0.3$, $r = 0.10$ and $p = 0.57$).

We reanalysed our data for open- and cavity-nestling species separately to test the possibility that our results may be confounded by differences in the acoustic environment between the two types of nest site. In a multiple regression (controlling for body mass and phylogeny), both the maximum amplitude (partial $F_{1,9} = 12.6$, $r = -0.71$ and $p = 0.006$) and frequency at maximum amplitude (partial $F = 5.7$, $r = 0.41$ and $p = 0.041$) were
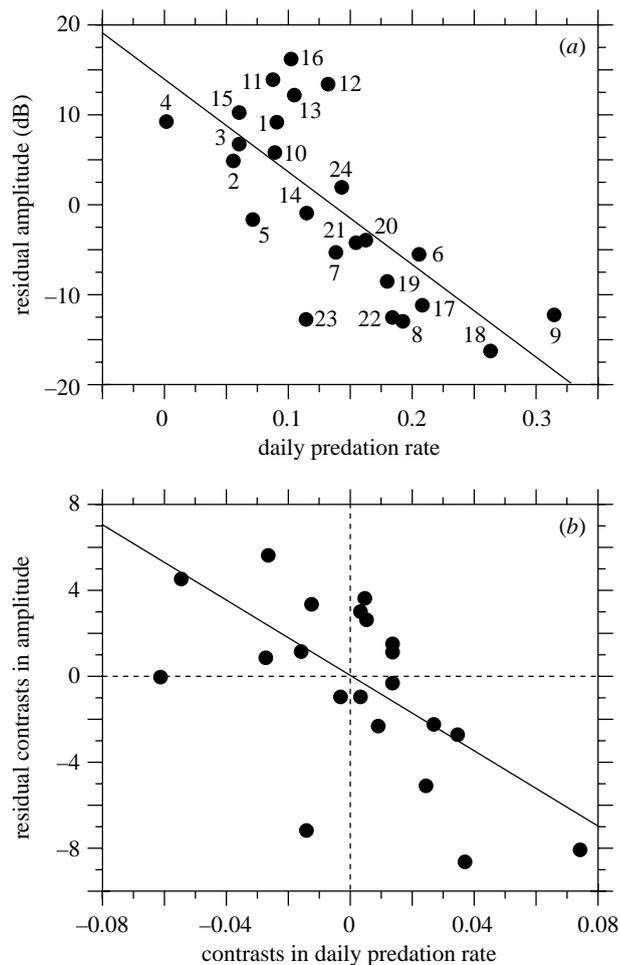
Figure 2. (*a*) Relationship between the risk of predation (as measured by arcsine-transformed daily predation rates) and amplitude of nestling begging calls across the 24 species of birds used in this study. (*b*) Independent contrasts for these variables controlling for phylogeny. Residuals (controlling for body mass) are plotted for illustration only; in all analyses body mass was controlled for by using multiple regression. The numbers refer to the species listed in figure 1.

Figure 3. (*a*) Relationship between the risk of predation (as measured by the daily predation rate) and frequency of begging calls at maximum amplitude across the 24 species of birds used in this study. (*b*) Independent contrasts for these variables controlling for phylogeny. Residuals (controlling for body mass) are plotted for illustration only; in all analyses body mass was controlled for by using multiple regression. The numbers refer to the species listed in figure 1.

significantly correlated with the daily predation rate in cavity-nesting species ($n = 14$ species). However, this pattern did not hold among our sample of open-nesting species: neither the maximum amplitude (partial $F_{1,6} = 0.03$, $r = 0.05$ and $p = 0.88$) nor frequency at maximum amplitude ($F = 4.6$, $r = 0.61$ and $p = 0.076$) were significantly correlated with the daily predation rate (although the latter approached significance). The black-headed grosbeak (point 23 on figure 2) appears to be an outlier but our results did not change if this species was excluded. Part of the difference between open- and cavity-nesting species probably stems from the smaller number of open-nesting species in our sample ($n = 10$) but it may also reflect a difference between the two groups.

A further potentially confounding problem is the inclusion of both passerine and non-passerine species in our sample. The structure of the syrinx in passerine birds differs from that of non-passserine birds and it is possible that the differences between the two groups may constrain the evolution of particular types of begging
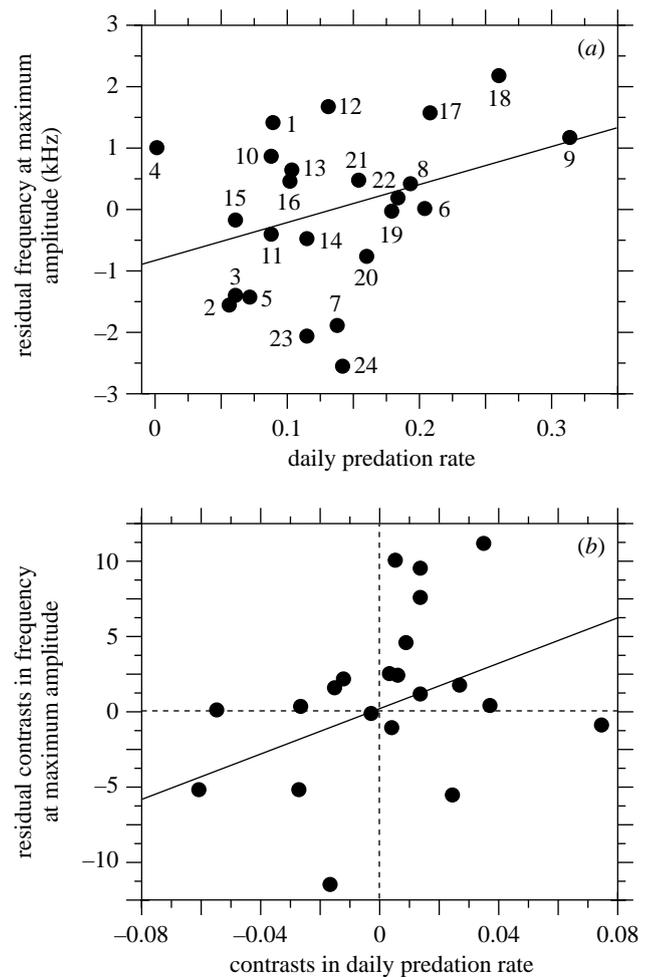
calls. The number of non-passerine species in our study was too small to analyse separately ($n = 5$), but among passerine species ($n = 19$) we found the same results as with the combined sample: the daily predation rate was correlated with the maximum amplitude (partial $F_{1,13} = 6.4$, $r = -0.52$ and $p = 0.025$) and frequency at maximum amplitude ($F = 4.7$, $r = 0.45$ and $p = 0.049$), but not with the frequency range ($F = 0.6$, $r = 0.15$ and $p = 0.46$).

## 4. DISCUSSION

The variation in the structure of nestling begging calls from one species to the next is striking. Although begging plays an important role in parent–offspring communication, it is not clear why an acorn woodpecker nestling should produce begging calls that are five orders of magnitude louder than those of a red-faced warbler nestling. Interspecific variation in the structure of begging calls has been recognized by other authors (e.g. Redondo & Arias de Reyna 1988; Popp & Ficken 1991) but to date

there are few convincing explanations for this diversity. In this study, we found that the risk of nest predation plays an important role in explaining some variation in the structure of nestling begging calls. Our comparison across a community of 24 species in an Arizona forest suggested that those species most at risk of nest predation have evolved begging calls with a higher frequency and lower amplitude than species with higher survival rates. Both of these features reduce the locatability of a sound source and so would reduce the risk of attracting the attention of predators. In contrast, species with relatively low levels of nest predation had begging calls characterized by a low frequency and high amplitude, features which increase the ease with which mammalian and avian ears can pinpoint the source of a sound.

Despite the prediction that calls with narrower frequency ranges will be less easy for predators to locate (Wiley & Richards 1982), we did not find a significant relationship between predation risk and the frequency range of begging calls. In a comparative study of begging vocalizations, Redondo & Arias de Reyna (1988) reported that the frequency range of begging calls of cavity-nesting species tended to be wider than that of open-nesting species (but see Popp & Ficken 1991). As they assumed that cavity-nesting species experienced reduced predation risk relative to open-nesting species, Redondo & Arias de Reyna (1988) suggested the difference between these two groups was an adaptation to their differing levels of predation. However, neither body mass nor phylogeny was controlled for in their study. When we controlled for such confounding variables (and used direct measures of the predation rate), the frequency range was not significantly related to predation risk. This suggests that at least some features of begging vocalizations are shaped by selective pressures other than predation risk.

Apart from amplitude and frequency, begging calls also vary across species in the duration of each call, the complexity of calls, the shape of each call element and the rate at which calls are delivered. We did not analyse these structural features of calls as it was not always clear how the predation risk is predicted to influence their evolution. Nonetheless, these features were highly variable among the species in our study (e.g. the duration of calls varied from 30.5 ms in orange-crowned warblers to 610 ms in the green-tailed towhee). Some of the variation is clearly related to phylogeny and body size (J. V. Briskie, unpublished data; see also Popp & Ficken 1991), but even congeneric species may differ in the basic shape and complexity of each call element. At present we have no explanation for this diversity, although it is possible that predation risk may play some role in the evolution of these call features.

If begging increases the risk of attracting a predator (Harper 1986; Redondo & Castro 1992; Haskell 1994; Leech & Leonard 1997), then why do not all species have calls that minimize locatability? The answer may lie in the fact that begging also functions to advertise the location of the chick to its parent. Even when in a fixed location (e.g. its nest), a chick may still benefit by advertising its presence and position within the nest. This would be particularly advantageous in those species in which nestlings must compete against siblings for a limited amount of food. However, advertising location to a parent

may inadvertently provide the same information to predators. Nestlings are thus faced with a trade-off between the benefits of advertising their location to their parents and the cost of doing the same to predators. As the rate of predation was not equal across the species in our study (e.g. the daily mortality rate of hermit thrushes was > 25 times that of Williamson's sapsuckers), the cost of begging will also not be equal. Such strong differences in predation risk could rapidly favour a reduction in the locatability of calls in those species bearing the greatest predation costs.

In a comparative study of call amplitude, Briskie et al. (1994) found that the loudness of nestling begging calls increased as the relatedness amongst the members of a brood declined. Those species with high levels of mixed paternity (and, therefore, where the young were more likely to be half-sibs) begged at a higher amplitude than species with little cuckoldry (and where the young were full-sibs). As more intense begging is known to increase the allocation of parental feeding (e.g. Mondloch 1995), these results suggested that sibling relatedness could play an important role in the evolution of call structure (Briskie et al. 1994). The results of the present study do not preclude such a role for kin selection, but instead suggest that predation risk may prevent a rampant escalation of begging intensity when sibling relatedness is low. In other words, even though a low level of relatedness is expected to lead to more intense begging calls, increased escalation could be curtailed under conditions of high predation risk. The relative roles of sibling relatedness and predation risk could not be assessed in our sample as paternity is currently known for only a few species, but we predict that increased intensity of begging as a consequence of reduced relatedness is only likely to be exhibited in those species with a relatively low cost of predation.

The negative correlation between the locatability of begging calls and the rate of nest predation supports the assumption of several recent models that predation risk is an important cost of begging (Macnair & Parker 1979; Harper 1986; Grafen 1990; Godfray 1991, 1995a,b). The fact that calls were most intense (loudest) and locatable (low frequency) in species least at risk further supports the assumption that the cost of predation is an increasing function of begging intensity. As begging calls appear to be structured in ways predicted to reduce the risk of attracting predators, the cost of predation may thus dampen any run-away escalation in begging intensity as a result of parent–offspring conflict or sibling competition. This suggests that variation in the relative costs of begging may provide part of the explanation for the wide diversity of begging behaviour seen among different species of birds.

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