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A predation risk-and-avoidance model of nestling responses to parental vocalizations

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ABSTRACT

Question: How does the nest type of a bird species – cup versus cavity – affect the evolution of its nestlings' responses to parental vocalizations?

Background: Nestling birds show distinct behavioural responses either to parental begging-solicitation calls (switch-on begging, lower-frequency sounds) or to parental alarm calls (switch-off begging, high-frequency sounds), but rarely to both. Previous theory suggested that differences in the vibrational conductance of cup versus cavity nests drive the evolution of divergent nestling responses to the different types of parental vocalizations. Many predators eavesdrop on begging displays of nestling birds, then locate the nest and prey on the brood. The risk of predation on broods in cup nests is consistently greater than on broods in cavity nests.

New theory: Whether nestlings respond to parental begging-solicitation calls (switch-on) or to parental alarm calls (switch-off) is dependent on a trade-off influenced by predation risks. Although switch-on calls are more efficient at protecting the nestlings that perceive them, they are less efficient at delivering their signal to younger nestlings with poorer sensory and discriminatory abilities (compared with switch-off calls). Thus, where predation risk is high, 'off' calls are favoured; where predation risk is lower, 'on' calls are favoured.

Hypotheses: Cup-nesting species, which have higher rates of predation, use 'off' signals, which their young are able to sense early in life before they can sense 'on' signals. Cavity-nesting species are the opposite in all particulars. In addition, cavity nestlings develop the ability to sense low-frequency 'on' sounds later than cup nestlings develop the ability to sense high-frequency 'off' signals.

Method: We examined existing comparative data on predation rates at different nesting locations. Using auditory brainstem response studies, we also examined data on the development (ontogeny) of acoustic sensitivity in altricial avian species.

Results: Nestlings of cup-nesting species suffer relatively higher predation rates than nestlings of cavity-nesting species. At first, nestlings can hear only a narrow range of sound frequencies. Nestlings gradually develop sensitivity to the full spectrum of vocalizations only after several weeks. The sparse data available on avian auditory ontogeny indicate that cup-nesting species develop early sensitivity to high-frequency sounds, and cavity nesters do so to lower-frequency sounds.

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Conclusion: The higher predation rates of cup nesters compared with cavity nesters, coupled with the post-hatching delay of all nestlings in achieving full sensitivity to the different types and frequency ranges of parental calls, provide a reasonable explanation for the evolutionary advantage of alarm calls to cup nesters and begging-solicitation calls to cavity nesters.

Keywords: nestling begging, parental vocalizations, predation, predator avoidance.

INTRODUCTION

Displays by nestlings to motivate and monopolize parental provisioning can be costly if these behaviours attract predators to the brood (Haskell, 1994; McCarty, 1996; Dearborn, 1999). Parent–nestling communication is a mechanism through which parents and chicks may lower nest predation rates (for reviews, see Searcy and Nowicki, 2005; Magrath *et al.*, 2010), while also reducing the energetic costs of inappropriately timed nestling begging displays (McCarty, 1996). For example, nestlings of the reed warbler *Acrocephalus scirpaceus*, dunnock *Prunella modularis*, and European robin *Erithacus rubecula* respond with silence and crouching behaviour to parental alarm calls (Davies *et al.*, 2004), thus reducing the conspicuousness of the brood to nearby predators (Haskell, 1994, 1999; Hauber *et al.*, 2001). In contrast, black-capped chickadee *Poecile atricapillus* (Clemmons, 1995) and tree swallow *Tachycineta bicolor* (Leonard *et al.*, 1997) nestlings beg in response to playbacks of conspecific parental begging-solicitation calls, presumably reducing energy expenditure for inappropriately timed begging displays (Moreno-Rueda and Redondo, 2011). The evolutionary drivers of these parent–nestling communication strategies are a critical area of research that requires both adequate theory and strong experimentation (Johnstone and Kilner, 2011).

Madden *et al.* (2005a) propose a verbal theory regarding the evolution of nestling responses to parental vocalizations. They base their theory on the vibrational conductance of the nest structure. They suggest that chicks of species that nest in grasses, reeds, and fine tree branches (henceforth, ‘cup nests’) often experience weather-generated (i.e. wind and rain) vibrations that stimulate nestlings to beg at inappropriate times. The theory proposes that cup-nesting species are likely to evolve switch-off parental signals that silence (Davies *et al.*, 2004) or reduce the intensity of (Anderson *et al.*, 2010) inappropriately timed nestling begging displays. In contrast, species that nest in rocky recesses, burrows, and tree holes (henceforth, ‘cavity nests’) are unlikely to experience the weather-generated stimuli that inappropriately induce nestlings to beg. Thus, cavity nesters have little need for a mechanism to silence inappropriate begging, and Madden *et al.* (2005a) suggest that cavity nesters use switch-on (i.e. begging-solicitation) calls to signal parental arrival at the nest and to trigger nestling begging displays (Fig. 1). We term this ‘vibration theory.’

Many studies of nestling behaviour match the predictions made by vibration theory. For instance, many cup-nesting species indeed use a switch-off vocalization (i.e. parental alarm call) to stop or reduce the intensity of nestling begging (Clemmons, 1995; Davies *et al.*, 2004; Magrath *et al.*, 2009). Cavity nesters, on the other hand, often use a switch-on parental vocalization to stimulate nestling begging displays (Madden *et al.*, 2005a, 2005b).

Although the vibration theory proposed by Madden and colleagues may help explain the evolution of parental vocalizations and nestling responses, we believe that it is unlikely to be a full explanation. Rather, or in addition, the relative difference in predation rates experienced by cup- and cavity-nesting species (Bosque and Bosque, 1995) may be a better predictor

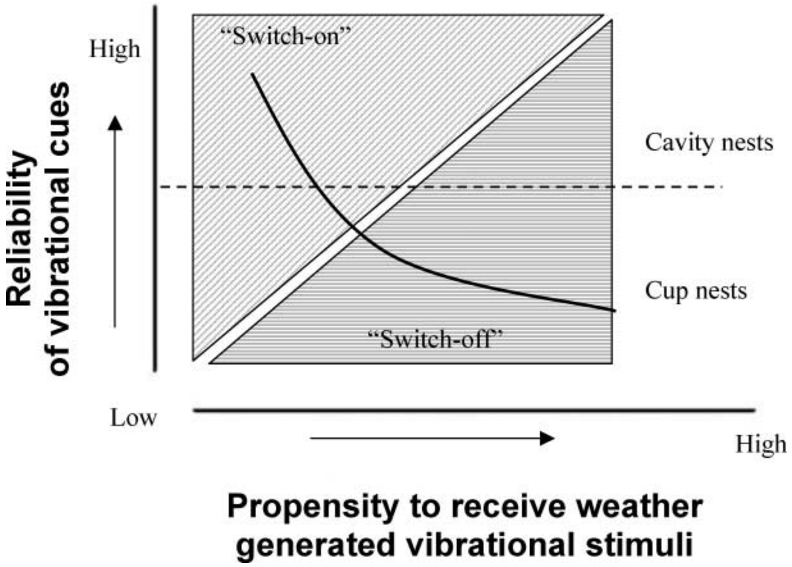

Fig. 1. The 'vibration theory' model, as developed by Madden *et al.* (2005a), predicts that avian nestlings differentially respond to parental 'switch-off' and 'switch-on' vocalizations. Nestlings in cup nests are prone to respond to weather-generated stimuli that would trigger inappropriately timed begging displays instead of begging upon the arrival of a provisioning parent to the nest. Parental 'switch-off' vocalizations silence these displays. Nestlings in cavity nests receive few weather-generated vibrational stimuli due to the rigid structure in which the nest is built. Nestlings in cavity nests can detect arriving parents and start begging by responding to parental 'switch-on' vocalizations produced by the nearby provisioning parents.

of the evolution of parental vocal stimuli and nestling responses. Here we develop a new theory of these phenomena based on the relative difference in predation rates between nest types. This new theory does account for the evolution of the different nestling responses to parental alarm calls and to parental begging-solicitation calls. It also accounts for differences in the timing of the development of certain sensory capacities, which we will describe below.

STRUCTURE OF THE THEORY

Setting

Nestling birds beg for food using loud and repeated sounds along with conspicuous visual displays that include raised body postures, open beaks, and fluttering wings. As they beg, predators eavesdrop, locate them, and prey on them (Haskell, 1994). The risk of predation on cup nestlings is substantially greater than that on cavity nestlings (Bosque and Bosque, 1995). To reduce the predation losses, parents use vocalizations of two sorts. One – parental alarm calls – stops the nestlings from begging (switch-off). The second solicits begging behaviour from quiet nestlings (switch-on). Parents of a given species use either one or the other call type, rarely both (Magrath *et al.*, 2007). Nestlings take time to develop auditory sensitivity, perceptual processing, and motor responses to all parental calls (Richter *et al.*, 1996), including the ability to discriminate between different classes of sounds (Brittan-Powell and Dooling, 2004; Brittan-Powell *et al.*, 2005).

Consequences of switch-on signals

Advantages: Broods beg only in response to their parents' signals and not in response to irrelevant environmental stimuli (e.g. weather or predator-generated signals). Broods that frequently beg in response to false environmental stimuli and are quieted by parental alarm (switch-off) signals should be more conspicuous to acoustically and visually oriented predators than broods that remain quiet until a parent arrives at the nest and emits a begging-solicitation call (East, 1981; Haskell, 1994, 1999; Dor *et al.*, 2007; Haff and Magrath, 2010). Thus, switch-on signals provide considerable protection from predation. In addition, they reduce the energetic waste (growth loss) associated with parent-absent begging displays (Kilner, 2001).

Disadvantages: Nestlings will sometimes respond to irrelevant environmental stimuli (i.e. nest movement or the sounds of broken branches) and reveal themselves to nearby predators. In addition, very young chicks may not be mature enough to sense, perceive or respond to switch-on signals (Fig. 3) and, as a result, fail to get enough to eat.

Consequences of switch-off signals

Advantage: Very young nestlings hear switch-off signals with high probability because switch-off signals are alarm calls, and alarm calls are given repeatedly and loudly over a short time interval, which gives very young nestlings a better chance to recognize danger when signalled by parents (East, 1981; Anderson *et al.*, 2010).

Disadvantage: Broods sometimes do beg in response to irrelevant environmental stimuli, revealing themselves to predators. When they do, their parents may be too far away to protect them with a switch-off signal.

The trade-off

If predation pressure is very high, the advantage of a more certain warning (i.e. an alarm call), as early in life as possible, outweighs the cost of responding to irrelevant environmental stimuli. If predation pressure is lower, the cost of responding to irrelevant environmental stimuli is less than the cost of not hearing the parental signal to commence begging.

The prediction

At high predation pressure, species should evolve to use switch-off signalling, whereas at low predation pressure, they should evolve to use switch-on signalling. Thus cup nesters, which suffer higher predation pressure, should use switch-off signalling, and cavity nesters, which suffer lower predation pressure, should use switch-on signalling.

During this period of auditory development (Richter *et al.*, 1996), nestlings are more likely to recognize acoustic signals that are emitted multiple times than signals that are emitted just once (Reeve, 1989). Nestlings may be able to perceive and then respond opportunistically to parental switch-off signals at an earlier stage of development than to other adult vocalizations (Fig. 2).

We now explicitly assume that, in order for nestlings to perceive parental begging-solicitation calls, nestlings need a more discriminating and better developed auditory system than they need to perceive switch-off signals. So nestlings would have to undergo a longer period of development to detect switch-on cues than to detect switch-off signals. Hence, presuming that the youngest nestlings cannot discriminate switch-on and switch-off vocalizations (Leonard *et al.*, 1997; Lotem, 1998; Madden *et al.*, 2005a, 2005b; Magrath *et al.*, 2010), it may be

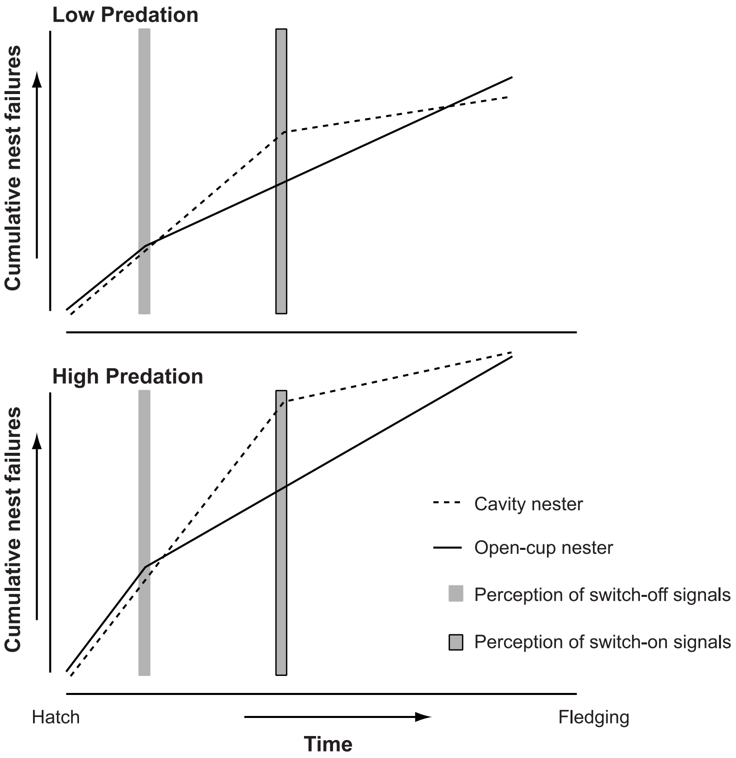

Fig. 2. The theoretical cumulative count of nesting attempts that do not fledge chicks owing to predation. The young of cavity nesters (dashed lines) respond only to parental 'switch-on' vocalizations and endure high rates of predation for a greater proportion of the nesting stage than do open-cup nesters (solid lines). The young of open-cup nesters respond to parental 'switch-off' vocalizations and reduce predation rates at an earlier stage of the nesting period compared with cavity-nesting species. However, the extent of this reduction in predation rate associated with nestling perception of 'switch-off' vocalizations is smaller than the reduction associated with nestling perception of 'switch-on' vocalizations. Compared with lower predation rates overall (upper panel), when predation pressure is high (lower panel), the evolution of nestling response to 'switch-on' signals may be unfavourable because the longer developmental period required for the perception of these vocalizations would be too costly. Thus, species in which nestlings are exposed to higher rates of predation are likely to adopt the strategy of earlier responses to 'switch-off' signals due to higher predation cost of the longer developmental period (i.e. in systems with higher predation rates, species that respond to 'switch-off' signals will fledge more young than species that respond only to 'switch-on' signals).

advantageous for nestlings to delay the development of the perception of parental alarm calls long enough to allow sufficient development of auditory sensory mechanisms to enable the detection and recognition of parental begging-solicitation calls (Magrath *et al.*, 2009; Anderson *et al.*, 2010).

In contrast, for species that experience high rates of nest predation, offspring perception of parental alarm calls may reduce predation rates early in the nesting period, counteracting the cost of adopting this less effective anti-predator strategy (i.e. response only to parental begging-solicitation calls) (Fig. 2). The longer developmental period needed for nestlings to perceive begging-solicitation calls may therefore reduce nestling survival greatly and offset the advantages of adopting the superior anti-predator strategy (i.e. response to switch-on signals only).

THE RELATIONSHIP BETWEEN PREDATION AND DEVELOPMENT

Developmental rate and ontogenetic sequence, like other variable life-history traits, should be under the influence of natural selection so that high offspring mortality will select for shortening of the developmental period (Reznick and Endler, 1982), favouring those offspring that develop quickly through the relatively helpless nestling life stage. Developing rapidly requires considerable amounts of energy input per unit time (Mountford, 1968); thus, parents may be unable to rear large, rapidly developing broods due to limitations on food availability, time, and parental energy reserves (Ricklefs, 2002). Compared with precocial birds and other vertebrate lineages, altricial birds have the highest rate of development and growth (Case, 1978), suggesting that selection has strongly favoured the shortening of the developmental period, despite the trade-off of smaller clutch sizes (Hanssen *et al.*, 2005).

In a group of bird species that share developmental modalities (e.g. altricial birds), those that experience low levels of predation pressure should evolve slower development rates and bigger brood sizes (Bosque and Bosque, 1995) relative to species under more intense predation. Indeed, Bosque and Bosque (1995) collected data on development rates for species in a range of settings and their findings agree with this prediction. They assumed that the setting is a suitable proxy for the intensity of nest predation pressure. Bosque and Bosque compared egg and nestling life stage length of continental and oceanic bird species that nested in cup and cavity nests. Three conclusions drawn from their study are relevant to our considerations. First, species that live on island systems with little or no predator abundance take significantly longer to develop compared with sister taxa on continents where predator abundance is high. Second, both cup- and cavity-nesting species recently introduced to islands from continents have significantly shorter developmental durations than do related cup- or cavity-nesting species with a longer island-based evolutionary history. Last, and most relevant, cavity-nesting species in both island and continental areas have significantly longer developmental durations than cup-nesting species in those areas (Fig. 3). Bosque and Bosque argue that this difference in developmental duration is due to more intense predation rates experienced by cup-nesting relative to cavity-nesting altricial birds.

WHEN AND WHAT DO ALTRICIAL BIRDS HEAR?

According to our theory, cup-nesting species are expected to develop auditory sensitivity to parental alarm calls at an early stage of development, whereas cavity nesters should develop sensitivity to parental begging-solicitation calls before sensitivity to other parental

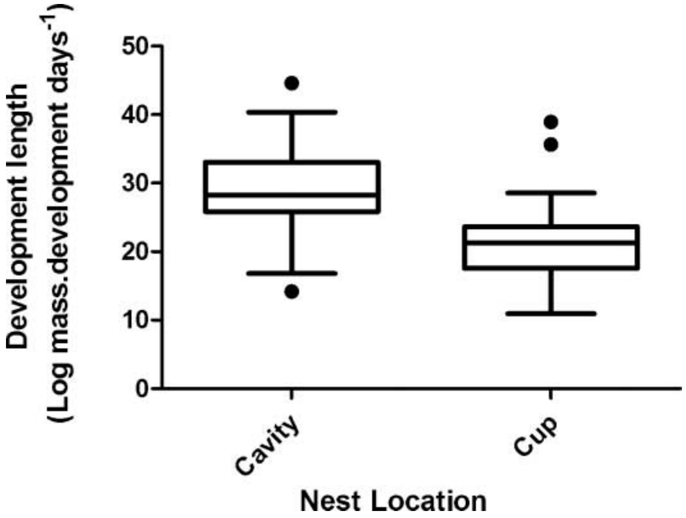

Fig. 3. The duration of the egg and nestling life stages of altricial bird species that nest in cup versus cavity nests (the data have been summed across islands and continents, and normalized to account for differences in development length associated with variation in body size). Cavity-nesting species have significantly longer developmental periods (Student's *t*-test: $t_{181} = 3.33$, $P < 0.01$) than cup-nesting species, implying that cup nesters also experience higher rates of predation than cavity nesters.

vocalizations. Auditory brainstem response (ABR) studies – the detection of neural impulses travelling between the ear and the brain via the brainstem indicating the perception of an auditory signal – are a useful tool in understanding changes in animal behaviour in response to postnatal development of auditory physiology, neurology, and the anatomical structures associated with hearing (Platzer *et al.*, 2000).

Few studies of auditory development have been conducted on diverse lineages of altricial birds, despite a rich literature on hearing development in precocial birds and mammals (Dmitrieva and Gottlieb, 1992). Brittan-Powell and Dooling (2004) reported on the age of stimulus-evoked ABR signals of postnatal hearing development in the nestlings of an altricial bird species, the budgerigar *Melopsittacus undulates*. In addition to studies on budgerigars, auditory development in the rock pigeon *Columba livia* (Richter *et al.*, 1996), pied flycatcher *Ficedula hypoleuca* (Brittan-Powell and Dooling, 2004), and barn owl *Tyto alba* (Köppl and Nickel, 2007) has also been examined using ABR techniques.

Three general conclusions are consistently drawn from auditory brainstem response studies:

- First, at hatching, nestling auditory brainstem responses are induced for a limited range of frequencies, typically from 1 to 5 kHz.
- Second, the range of frequencies that induces auditory brainstem responses increases with age to adult-like values at around the time of fledging and independence: at two weeks post-hatching in the budgerigar and pied flycatcher, and at three months in the barn owl.
- Third, cup- and cavity-nesting species develop acoustic sensitivity to different frequency ranges at different stages during development. Pigeons, which construct flimsy cup nests,

develop acoustic sensitivity to high frequencies early in their development, with lower-frequency sensitivity developing later (Richter *et al.*, 1996). In contrast, the budgerigar and pied flycatcher, which both nest in cavities, show low levels of sensitivity to high frequencies until two weeks post-hatching and instead respond to low-frequency stimuli early in development (Brittan-Powell and Dooling, 2004). To demonstrate the generality of this trend – cup-nesting species develop early sensitivity to high-frequency sounds, while cavity nesters develop early sensitivity to lower-frequency sounds – we need considerably more data on auditory development from many different species. Nonetheless, from the limited data available, we tentatively suggest that cup- and cavity-nesting species develop sensitivity to acoustic stimuli differently, potentially affecting the type of parental vocalizations that nestlings of these two groups of birds are able to perceive.

ACOUSTIC STRUCTURE OF PARENTAL VOCALIZATIONS

Next, we provide a preliminary examination of the acoustic structure of parental alarm and begging-solicitation calls to explain further the relationship between the frequency ranges to which a bird species first develops acute hearing, and the location of the nest. Irrespective of the causes and benefits of the specific trajectory of parent–offspring communication, it is likely that selection favours the early development of auditory sensitivity that corresponds with the frequency of the parental vocalization to which a nestling needs to respond.

Based on a limited set of published data, we compiled median, maximum, and minimum frequencies of parental alarm and begging-solicitation calls for eight species: the black-capped chickadee *Poecile atricapillus*, reed warbler *Acrocephalus scirpaceus*, European robin *Erithacus rubecula*, dunnock *Prunella modularis*, eastern phoebe *Sayornis phoebe*, red-winged blackbird *Agelaius phoeniceus*, red-faced crombec *Sylvietta whytii*, and grey-capped warbler *Eminia lepida*. Across the species examined, parental alarm calls had a significantly greater median frequency (mean = 5 kHz, range 4–6 kHz) than did begging-solicitation calls (mean = 3 kHz, range 2–5 kHz) ($t_{10} = 2.82$, $P = 0.02$). There were no statistically significant differences between peak and minimum frequencies in parental alarm (peak: mean = 7 kHz, range 6–15 kHz; minimum: mean = 4 kHz, range 2–5 kHz) and begging-solicitation calls (peak: mean = 8.5 kHz, range 5–15 kHz; minimum: mean = 2 kHz, range 1–3 kHz) (peak frequency: $t_{10} = 1.11$, $P = 0.79$; minimum frequency: $t_{10} = 2.28$, $P = 0.054$). Thus, these patterns imply that the significantly higher median frequency of parental switch-off vocalizations corresponds to the earlier development of high-frequency sensitivity in cup-nesting species. In turn, low-frequency sensitivity develops first in cavity nesters, corresponding with the significantly lower median frequency of parental switch-on vocalizations.

DISCUSSION AND CONCLUSIONS

Nestlings of cup-nesting species stop begging when their parents call, whereas nestlings of cavity-nesting species begin begging when theirs do. The cup-nesting call is often similar to a high-frequency alarm call of short duration. The cavity-nesting call is quite different – often of lower pitch and with fewer notes given at a more leisurely tempo. We suggest that unequal rates of nest predation between cup nesters and cavity nesters may cause the divergence between cup-nesting and cavity-nesting signals and the offsprings' responses to them.

Bosque and Bosque (1995) analysed developmental rates in altricial birds and inferred that predation pressure is significantly greater in cup-nesting species than in cavity nesters. To reduce predation as early as possible, cup-nesting species should evolve behavioural responses to parental alarm calls even though doing so may subject them to some losses to acoustically or visually oriented predators. Due to less intense predation pressure, cavity nesters can delay nestling response to parental vocalizations until they are able to recognize begging-solicitation signals, which more efficiently avoid predation than do alarm calls (Fig. 2).

Madden *et al.* (2005a) describe a different theory to account for the divergence between cup-nesting and cavity-nesting signals. They suggest that compared with cavity nests, cup nests are much more likely to vibrate in response to wind and rain, thus initiating inappropriate, conspicuous, and dangerous begging behaviour. That in turn would account for the divergent nestling responses to parental vocalizations between cup and cavity nestlings. Their theory does agree with some observations. However, if all nestlings begged only in response to parental begging-solicitation calls, nestlings would never respond to inappropriate signals such as wind-generated noise and so would not need to recognize any parental signal that switches begging off. Hence, it is difficult to use the vibration idea to explain the evolution of nestling responses to parental vocalizations that silence inappropriately timed nestling begging displays. That is why, in this paper, we explored an alternative theory that builds differences in predation pressure and considers auditory developmental rates to explain the divergent parent–offspring communication behaviours between cup and cavity nesters.

Our theory does not fully explain why each species should be restricted to one or the other type of signal. We did note that nestlings responding only to parental begging-solicitation calls would have little need to evolve a behavioural response to parental alarm calls simply because inappropriate nestling begging would be minimal or altogether absent. But why shouldn't a species whose nestlings respond to the early switch-off alarm-style calls not subsequently develop an additional behaviour, i.e. reliance on the less risky begging-solicitation calls? In fact, why don't all species adopt such a sequential developmental strategy?

As more acoustic, behavioural, and auditory physiological data become available, especially for different species where nest architecture is shared but predation pressure is variable (e.g. island versus continental cup-nesting species), we hope that our theory will be subjected to more extensive tests. For example, comparisons can be made between cup-, cavity-, and pendulum-nesting birds on the historically mammalian predator-free biogeographical province of New Zealand compared with the related taxa of Australia where birds and their mammalian predators have co-evolved (Briskie, 2006). New data on parent–offspring communication and its evolution in altricial birds will provide novel hypotheses of the forces driving similar strategies in altricial mammals and amphibians, stimulating new and exciting research into how ecology shapes the evolution of communication strategies (Johnstone and Kilner, 2011).

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REFERENCES

Anderson, M.G., Brunton, D.H. and Hauber, M.E. 2010. Species-specificity of grey warbler begging solicitation and alarm calls revealed by nestling responses to playbacks. *Anim. Behav.*, **79**: 401–409.

Bosque, C. and Bosque, M.T. 1995. Nest predation as a selective factor in the evolution of developmental rates in altricial birds. *Am. Nat.*, **145**: 234–260.

Briskie, J.V. 2006. Introduced birds as model systems for the conservation of endangered native birds. *Auk*, **123**: 949–957.

Brittan-Powell, E.F. and Dooling, R.J. 2004. Development of auditory sensitivity in budgerigars (*Melopsittacus undulatus*). *J. Acoustic. Soc. Am.*, **115**: 3092–3102.

Brittan-Powell, E.F., Lohr, B., Hahn, D.C. and Dooling, R.J. 2005. Auditory brainstem responses in the eastern screech owl: an estimate of auditory thresholds. *J. Acoustic. Soc. Am.*, **118**: 314–321.

Case, T.J. 1978. Evolution and adaptive significance of postnatal-growth rates in terrestrial vertebrates. *Q. Rev. Biol.*, **53**: 243–282.

Clemmons, J.R. 1995. Vocalizations and other stimuli that elicit gaping in nestling black-capped chickadees (*Parus atricapillus*). *Auk*, **112**: 603–612.

Davies, N.B., Madden, J.R. and Butchart, S.H.M. 2004. Learning fine-tunes a specific response of nestlings to the parental alarm calls of their own species. *Proc. R. Soc. Lond. B*, **271**: 2297–2304.

Dearborn, D.C. 1999. Brown-headed cowbird nestling vocalizations and risk of nest predation. *Auk*, **116**: 448–457.

Dmitrieva, L.P. and Gottlieb, G. 1992. Development of brain-stem auditory pathway in mallard duck embryos and hatchlings. *J. Comp. Physiol. A*, **171**: 665–671.

Dor, R., Kedar, H., Winkler, D.W. and Lotem, A. 2007. Begging in the absence of parents: a ‘quick on the trigger’ strategy to minimize costly misses. *Behav. Ecol.*, **18**: 97–102.

East, M. 1981. Alarm calling and parental investment in the robin *Erithacus rubecula. Ibis*, **123**: 223–230.

Haff, T.M. and Magrath, R.D. (2010). Vulnerable but not helpless: nestlings are fine-tuned to cues of approaching danger. *Anim. Behav.*, **79**: 487–496.

Hanssen, S.A., Hasselquist, D., Folstad, I. and Erikstad, K.E. 2005. Cost of reproduction in a long-lived bird: incubation effort reduces immune function and future reproduction. *Proc. R. Soc. Lond. B*, **272**: 1039–1046.

Haskell, D.G. 1994. Experimental evidence that nestling begging behaviour incurs a cost due to nest predation. *Proc. R. Soc. Lond. B*, **257**: 161–164.

Haskell, D.G. 1999. The effect of predation on begging-call evolution in nestling wood warblers. *Anim. Behav.*, **57**: 893–901.

Hauber, M.E., Russo, S.A. and Sherman, P.W. 2001. A password for species recognition in a brood-parasitic bird. *Proc. R. Soc. Lond. B*, **268**: 1041–1048.

Johnstone, R.A. and Kilner, R.M. (2011). New labels for old whines. *Behav. Ecol.*, **22**: 918–919.

Kilner, R.M. 2001. A growth cost of begging in captive canary chicks. *Proc. Natl. Acad. Sci. USA*, **98**: 11394–11398.

Köppl, C. and Nickel, R. 2007. Prolonged maturation of cochlear function in the barn owl after hatching. *J. Comp. Physiol. A*, **193**: 613–624.

Leonard, M.L., Fernandez, N. and Brown, G. 1997. Parental calls and nestling behavior in tree swallows. *Auk*, **114**: 668–672.

Lotem, A. 1998. Differences in begging behaviour between barn swallow, *Hirundo rustica*, nestlings. *Anim. Behav.*, **55**: 809–818.

Madden, J.R., Kilner, R.M. and Davies, N.B. 2005a. Nestling responses to adult food and alarm calls: 1. Species-specific responses in two cowbird hosts. *Anim. Behav.*, **70**: 619–627.

Madden, J.R., Kilner, R.M. and Davies, N.B. 2005b. Nestling responses to adult food and alarm calls: 2. Cowbirds and red-winged blackbirds reared by eastern phoebe hosts. *Anim. Behav.*, **70**: 629–637.

Magrath, R.D., Pitcher, B.J. and Dalziell, A.H. 2007. How to be fed but not eaten: nestling responses to parental food calls and the sound of a predator's footsteps. *Anim. Behav.*, **74**: 1117–1129.

Magrath, R.D., Pitcher, B.J. and Gardner, J.L. 2009. Recognition of other species' aerial alarm calls: speaking the same language or learning another? *Proc. R. Soc. Lond. B*, **276**: 769–774.

Magrath, R.D., Halt, T.M., Horn, A.G. and Leonard, M.L. 2010. Calling in the face of danger: predation risk and acoustic communication by parent birds and their offspring. *Adv. Study Behav.*, **41**: 187–253.

McCarty, J.P. 1996. The energetic cost of begging in nestling passerines. *Auk*, **113**: 178–188.

Moreno-Rueda, G. and Redondo, T. 2011. Begging at high level simultaneously impairs growth and immune response in southern shrike (*Lanius meridionalis*) nestlings. *J. Evol. Biol.*, **24**: 1091–1098.

Mountford, M.D. 1968. Significance of litter size. *J. Anim. Ecol.*, **37**: 363–376.

Platzer, J., Engel, J., Schrott-Fischer, A., Stephan, K., Bova, S., Chen, H. *et al.* 2000. Congenital deafness and sinoatrial node dysfunction in mice lacking class D L-type Ca2 + channels. *Cell*, **102**: 89–97.

Reeve, H.K. 1989. The evolution of conspecific acceptance thresholds. *Am. Nat.*, **133**: 407–435.

Reznick, D. and Endler, J.A. 1982. The impact of predation on life-history evolution in Trinidadian guppies (*Poecilia reticulata*). *Evolution*, **36**: 160–177.

Richter, C.P., Sauer, G., Hoidis, S. and Klinke, R. 1996. Development of activity patterns in auditory nerve fibres of pigeons. *Hearing Res.*, **95**: 77–86.

Ricklefs, R.E. 2002. Sibling competition and the evolution of brood size and development rate in birds. In *The Evolution of Begging* (J. Wright and M.L. Leonard, eds.), pp. 283–301. Dordrecht: Kluwer.

Searcy, W.A. and Nowicki, S. 2005. *The Evolution of Communication: Reliability and Deception in Signaling Systems.* Princeton, NJ: Princeton University Press.