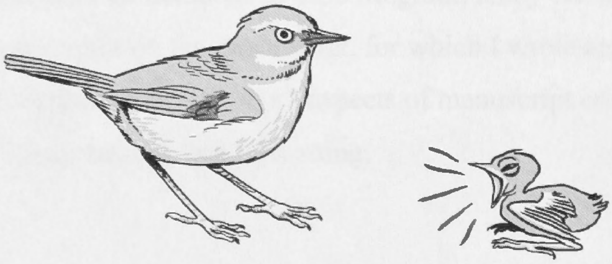
Parent-offspring communication under the risk of predation in the white-browed scrubwren



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A thesis submitted for the degree of Doctor of Philosophy to the
Australian National University

February 2012

Declaration

This thesis is my own original work, and has not been submitted for any other degree. Robert Magrath contributed discussion of ideas, comments on all manuscript drafts, financial support, and provision of equipment for all data chapters. Alex Dorland, Adam Searcy, and Alexis Billings all helped with fieldwork; A. Dorland and A. Searcy also assisted with sound recordings. I conducted all experiments, sound and statistical analyses, and I am the principal contributor to all aspects of this thesis. Appendix A is a published manuscript co-authored by Rob Magrath, Andy Horn, Marty Leonard, and me. I am second author on the manuscript, for which I wrote approximately one third of the text, and contributed heavily to all aspects of manuscript creation, including discussion of ideas, editing, and formatting.

Signed:

Tonya M. Haff
February 2012

Acknowledgments

I am deeply indebted to Rob Magrath, whose patient supervision, guidance, and tireless manuscript feedback has made this thesis possible. I thought that his work sounded interesting and his picture on the school website looked friendly, and I am happy that my intuition proved right. His attention to detail, strong work ethic, and generally laid-back attitude allowed me both the freedom and the guidance that I needed to stay inspired and work hard. Thank you, Rob.

This thesis would not have been possible without a lot of help in the field, and I am particularly grateful to Alex Dorland, Adam Searcy and Alexis Billings. All three were either inspired or foolish enough to come all the way from North America help me in my work by standing outside for days on end in the freezing cold and blistering heat, through wind and leaf blowers, trying to get into the minds of alternatingly secretive, uncooperative, angry and endearing scrubwrens. That they all came to be good nest searchers and even to think that scrubwrens are 'cooler than lyrebirds' (Alex) is a testament to their patience and fantastic attitudes that made long days in the field fun. Thanks especially to Adam, who dragged himself around the gardens in search of scrubbers with sarcastic humour to spare, even when his dreaded unknown tick-borne disease got him down.

Thank you also to my other committee members, Naomi Langmore and Andrew Cockburn, to the ANU Bioacoustics Group, and to visiting academics Marty Leonard, Andy Horn, Elsie Krebs and David Green for experiment and manuscript advice, and for support and friendship in general. Thanks especially to fellow PhD student Brani Igic, whose feedback, advice and compatriotism in the field I really appreciated. I also deeply appreciate all the undergraduates and fellow grad students who volunteered to help me in the field, particularly with banding: Laura Johnson, Chloe Raderschall, Sam Vertucci, Will Feeney, and Trevor Murray, to name a few.

I don't think I would have got through this time as quickly and as happily if it hadn't been for the support and friendship of my friend, then boyfriend, now husband Rob Lanfear, ridiculous boarding school experiences not withstanding. I also deeply appreciate the support of my delightful housemates Jacki Sculthorp and Ainsley Seago, who were both lucky enough to escape the English boarding school system. Thanks to

Rob especially for caring for Bimi, our first baby (below). Ainsley, who is not only an outstanding biologist but also one of the finest illustrators I have ever met, generously created all the artwork in this thesis.

I am also grateful to the support of my parents and brother, and to my dear friends in Santa Cruz, California, who all encouraged me to take the leap and go to Australia to study. Their guidance, love, and friendship has been never-ending, and I cannot thank them enough for helping me to be here.

This work was supported by the ANU, the Gould League of NSW Cayley Memorial Fund, the Canberra Ornithologists Group Canberra Bird Conservation Fund (grants to me), and an Australian Research Council grant to RDM. My fieldwork was kindly hosted by the Australian National Botanic Gardens, whose friendly gardeners never complained about us tramping around off-trail and building ridiculous wire cages around their plants. Thanks in particular to Rosella for her cheery waves and occasional cups of tea and snacks. And of course I cannot forget to mention AC Hughes, whose extremely tardy, poor quality colour bands not only made banding an interesting experience, but also allowed me to have enough unusable bands to make colour band earrings to share with friends. That's quality.

Finally, I would like to think the Right Honourable Captain Sir Doctor Bimbimbi Runnyford the First Junior, and all the other scrubwrens that suffered my well-meaning attention over the past four years. Bimi helped me to realize how smart and charismatic fledglings are, and to think more deeply about the potential for learning in young birds. In fact, Bimi provided me with great insight into the lives and minds of scrubwrens in general. Thanks, Bimi.

Abstract

Acoustic signaling is in important way that animals communicate, but the features that enhance the detectability of signals by receivers may also enhance detectability by eavesdropping predators. Parent-offspring communication in birds offers a superb window into how animals communicate under the risk of predation, as most species rely heavily upon vocal signaling and are particularly vulnerable to predation during the reproductive period. This thesis describes a series of experiments on nesting white-browed scrubwrens, *Sericornis frontalis*, focusing on three main questions:

1) Do nestling calls attract predators?

Chapter 2 presents the first realistic test of the cost of nestling begging on predation risk at active nests attended by parents. Nestling vocalizations attracted predators, and this risk was highest for the hungriest and therefore noisiest broods (Haff & Magrath 2011, *Biology Letters*).

2) How do parents manage the trade-off between warning young of danger and betraying nest location to predators?

Chapter 3 shows that parents were more likely to warn noisier compared to quieter nestlings when an eavesdropping predator was near the nest, demonstrating that parents take nestling conspicuousness into account in a decision rule likely to reduce the risk of nest predation. This work is in preparation for publication.

3) How do young reduce predation risk independently of parents?

Chapter 4 shows that nestlings respond with silence to very specific features of the sound made by a predator walking near the nest. They are therefore able to reduce risk independently of parents, while not suppressing calling unnecessarily (Haff & Magrath 2010, *Animal Behaviour*).

Chapter 5 shows that young nestlings respond to heterospecific mobbing alarm calls that are structurally similar to parental mobbing alarm calls, while older nestlings can respond appropriately to heterospecific alarm calls that are not similar to those of conspecifics. Nestlings therefore gain information about danger from the signals of other species, potentially through both innate recognition and learning. This work has been submitted for publication.

Chapter 6 focuses on the development of fledgling responses to heterospecific aerial alarm calls, which are given to flying predators and are relevant to fledglings but not nestlings. Fledglings just out of the nest did not suppress calling after playback of heterospecific aerial alarm calls, but most did so only two weeks later and all responded by the time they were five-weeks old. Furthermore, young responded at an earlier age on territories on which the heterospecific was more common, suggesting that learning was important in the recognition of heterospecific aerial alarm calls.

Overall, this thesis illustrates that the behaviour of both parents and young can strongly affect the risk posed by nest predators, and helps to advance an understanding of parent-offspring communication under the risk of predation. An appendix to the thesis includes a broad review of this topic, co-authored by myself, R. D. Magrath, A. G. Horn & M. L. Leonard (Magrath et al. 2010, *Advances in the Study of Behavior*).

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CHAPTER 1

Introduction

Overview of thesis

Acoustic signaling is an important way that many offspring communicate with their parents (Barber et al. 2010; Bradbury & Vehrencamp 2011). The vocal signals produced by young are designed to aid parents in locating specific young, and thus help offspring both communicate hunger and compete with siblings for their parents' attention (Godfray 1995b; Price et al. 1996; Rodríguez-Gironés et al. 1996; Kilner & Johnstone 1997; Johnstone 1999; Johnstone 2004). Unfortunately, the same features that enhance the detectability of acoustic signals by receivers also enhance detectability by eavesdropping predators (Ryan et al. 1982; Redondo & Arias de Reyna 1988; Peake 2005; Searcy & Nowicki 2005; Bradbury & Vehrencamp 2011). This problem is further compounded when there is more intense selection on signalers to induce a response in receivers than there is for receivers to respond (Maynard Smith & Harper 2003; Searcy & Nowicki 2005), such as in signaling about hunger by young animals to their parents (Searcy & Nowicki 2005; Kilner & Hinde 2008). How, then, do offspring effectively communicate about the need for food without becoming a meal themselves?

This thesis focuses on how young birds and their parents communicate with one another while minimizing the risk from eavesdropping predators. Parent-offspring communication in birds offers a superb window into how animals successfully communicate while avoiding predation (Magrath et al. 2010), as most species rely heavily upon vocal communication, and are particularly vulnerable to predation during the reproductive period (Ricklefs 1969; Martin 1995). I used a wild population of white-browed scrubwren, *Sericornis frontalis*, to study parent-offspring communication under the risk of predation. Scrubwrens are ideal for such studies, as their nests are protected from predators by crypsis alone (Higgins & Peter 2002), and both parents and young have a rich vocal repertoire that can attract the attention of eavesdropping predators (Platzen & Magrath 2004; Haff & Magrath 2011).

Each data chapter in this thesis reports the results of playback experiments I carried out in the Australian National Botanic Gardens in Canberra between 2008 and 2011. Chapter Two presents the results of an experiment testing the predation costs of nestling begging, and was published in *Biology Letters* (Haff & Magrath 2011). Chapter Three reports the results of an experiment examining how parents balance the risk between communicating information about danger to their offspring and attracting eavesdropping predators through such communication, and is in preparation for publication. Chapters Four and Five focus on the ways that offspring can minimize risk from eavesdropping predators even when parents are away from the nest. Chapter Four was published in *Animal Behaviour* (Haff & Magrath 2010), and Chapter Five is in preparation for publication. Chapter Six explores the timing of acquisition of response by fledglings to the aerial or 'hawk' alarm calls of sympatric species vulnerable to similar predators. This chapter is in preparation for publication. Appendix A consists of an extensive review on parent-offspring communication under the risk of predation coauthored with Robert Magrath, Andrew Horn and Marty Leonard, published in *Advances in the Study of Behavior* (Magrath et al. 2010), for which I wrote approximately one third of the final manuscript.

Background and experiments

Many theoretical models predict that parents and their offspring often have divergent interests in the amount of care that each offspring receives, such that young should escalate calling in order to receive more food than is the parents' optimum to provide (Trivers 1974; Godfray 1995a; Godfray & Johnstone 2000; Kilner & Hinde 2008). Most models therefore also predict that vocalizations by young must also be costly, in order to remain an evolutionarily stable strategy (Parker et al. 2002; Royle et al. 2002; but see Maynard Smith 1994). One common assumption of these models is that predation is a major cost of nestling calls, as nestlings that beg more intensely should also be more likely to be detected by eavesdropping bystanders (Zahavi 1977; Godfray 1991, 1995a). Empirical tests of this prediction have generally found increased predation rates with increased begging. Unfortunately, problems with methodology such as use of artificial nests and artificially high begging-call playback rates have hampered the interpretation of past experiments (Møller 1990; Cresswell 1997; Haskell 2002; Zanette 2002). These problems are addressed directly in Chapter Two, which presents the first empirical test of the cost of nestling begging on predation risk using realistic levels of call playback at active nests. In support of theoretical predictions and past empirical studies, I found that nestling vocalizations did indeed increase predation risk to young, and that this risk was highest for the hungriest and therefore noisiest broods.

Calling may be risky, but young birds must still vocalize in order to be fed. Indeed, young may even call when parents are not directly at the nest (reviewed in

Magrath et al. 2010), which may also attract predators. In many species, adults can reduce the risk of predators eavesdropping upon these vocalizations by using alarm calls to silence noisy young (Rydén 1978; Khayutin 1985; Knight & Temple 1986; Kleindorfer et al. 1996; Halupka 1998; Davies et al. 2004; Platzen & Magrath 2004; Madden et al. 2005a). Calling to silence young when predators are nearby is a double-edged sword, however, because alarm calling can also inform predators about the presence of nests, and thus actually increase the risk of nest predation (Krama & Krams 2005; Krams et al. 2007).

One way that parents might be able to effectively wield the double-edged sword of alarm calls is by moderating their response based on how vocally conspicuous young are when a predator is nearby (Harvey & Greenwood 1978). This type of dynamic risk assessment and extreme sensitivity to both intended and eavesdropping audiences has been documented in primates (Wich & de Vries 2006; Papworth et al. 2008), but has not yet been demonstrated in other taxa (Zuberbühler 2008). This topic is explored in Chapter Three, which presents the results of an experiment that manipulated how parent scrubwrens perceived both nestling conspicuousness (vocal activity) and predation risk, in order to test whether adult birds are able to evaluate relative risk to young when making decisions about how to respond to predators. I found that parents were more likely to warn more conspicuous young when an eavesdropping predator was near the nest than to warn nestlings that were already quiet.

Although parents can use alarm calls to silence noisy young, nestlings also vocalize when parents are absent (Roulin et al. 2000; Budden & Wright 2001; Leonard & Horn 2001; Maurer et al. 2003; Dor et al. 2007; Bulmer et al. 2008; Zuberbühler 2008; Rivers 2009). Nestlings may not be completely helpless in these situations, however, if they are able to assess and respond to cues of danger independently. Indeed, hearing itself may have evolved in order to allow animals to better monitor their surroundings (Barber et al. 2010). Whether young birds can independently assess cues of danger remains largely untested thus far, but at least in nestling scrubwrens, young go silent after hearing playback of the sound of a common predator walking in leaf litter (Magrath et al. 2007a). However, it is unknown whether this response is specific to a predator's sound, or to a component of the sound such as being broadband and atonal, having a walking tempo, or is simply due to novelty.

Chapter Four presents the results of an experiment specifically testing which components of the sound of a predator walking nestling scrubwrens use as a cue of danger. Another experiment presented in Chapter Four tested whether or not nestlings are able to moderate their response to cues of danger when also presented with the conflicting information of sounds of a parent arriving at the nest. Together, these experiments investigated the decision rules that nestlings make in order to minimize risk of detection from eavesdropping predators while still being fed by their parents. I found that nestlings did not treat novel sounds alone as cues of danger, but that they did respond moderately to both broadband sounds in general and to broadband sounds in a walking tempo. Nestling response was strongest to the actual sounds of a predator walking, however, demonstrating that they use very specific aspects of broadband sounds as the most reliable cues of danger. Further, young interpreted ambiguous sounds pessimistically, and did not modify their response to an independently assessed cue of danger even when potential interpretation of that sound was modified by the conflicting sound of a parent approaching the nest.

In addition to independent assessment of acoustic cues of danger produced by predators, young might reduce risk posed by eavesdropping predators when parents are absent by responding to the alarm calls of other species vulnerable to similar threats. Indeed, adult animals across a wide range of taxa respond to the alarm calls of heterospecifics (Hurd 1996; Zuberbühler 2000; Forsman & Monkkonen 2001; Rainey et al. 2004; Goodale & Kotagama 2005; Magrath et al. 2007b; Vitousek et al. 2007; Ito & Mori 2010; Flower 2011). Surprisingly, however, we know little about when or how young animals develop responses to heterospecific alarm calls. Nestlings might respond innately, for example, if the alarm calls of another species are structurally similar to conspecific alarms (Johnson et al. 2003; Russ et al. 2004; Fallow et al. 2011). Alternatively, young might learn to respond to heterospecific alarms (Lima 1998; Griffin 2004; Hollén & Radford 2009; Magrath & Bennett 2012; but see Davies et al. 2004; Madden et al. 2005b).

Chapter Five presents the results of an experiment testing the responses of nestlings at two ages to the mobbing alarm calls of three sympatric songbird species that nest in similar habitats and that are vulnerable to similar predators. This experiment did not specifically test how the responses of nestlings were acquired, but instead set the framework for understanding whether or not young birds raised in their own nests can respond to heterospecific calls, and if so, when such a response develops. I found that young nestlings respond to parental alarm calls and to the alarms of one heterospecific that that are structurally similar to scrubwren alarms. However, young nestlings ignored or increased vocalizing to the other species' alarm calls. In contrast to young nestlings, older nestlings reduced calling to all three heterospecific alarm calls, suggesting that learning may have been important in the development of an appropriate response by young.

Even once fledged, young are still extremely vulnerable to predators. Fledglings continue to vocalize in order to be fed by their parents, and so remain vulnerable to eavesdropping predators. Furthermore, fledglings are naïve and their flight uncoordinated, making them particularly at risk from aerial predators (Naef-Daenzer et al. 2001; Thompson & Burhans 2004; Verspoor et al. 2007). Fledglings should therefore benefit greatly from responding early on to aerial or 'hawk' alarm calls, which indicate a predator approaching in flight, of both conspecifics and heterospecifics. No study that I am aware of, however, of has investigated how fledgling birds respond to other species' aerial alarm calls, and to my knowledge there has been only one such study in young mammals (Hauser 1988). Chapter Six presents the results of an experiment testing whether or not fledgling scrubwrens respond to the aerial alarm calls of two common songbird species to which adult scrubwrens respond, and if so, when those responses develop. This experiment thus provides base information for further investigation of how these responses are acquired. I found that fledglings just out of the nest listened to but did not suppress calling after hearing heterospecific aerial alarm calls, but that most responded appropriately to these same playbacks only two weeks later. The only fledglings that did not respond to heterospecific alarms when they were two-weeks out of the nest were those on territories on which heterospecifics did not regularly occur, providing strong evidence that exposure facilitates learning about other species' alarm calls. All fledglings responded appropriately to heterospecific alarm calls by the time they were five-weeks out of the nest.

Parent-offspring communication offers opportunities to understand how signaling systems evolve under pressure from eavesdropping predators, and provides insight into how family members work both independently and together to reduce predation risk (Magrath et al. 2010). For example, investigating the breadth and flexibility of the rules parents use about alarm calling near young provides insight not only into the ways that parents can mitigate risk near the nest, but also into the cognitive abilities of non-primates in general (Zuberbühler 2008). Further, understanding when and how nestlings and fledgling birds respond to environmental and heterospecific cues of danger provides opportunities to explore learning and cognition in young animals, which in turn may strongly affect offspring survivorship and other early life history patterns (Naef-Daenzer et al. 2001; Griffin 2004; Hollén & Radford 2009). The experiments I conducted as part of this thesis have illustrated that the behaviour of both parents and young can strongly affect the risk posed by eavesdropping predators. Further, young scrubwrens can respond not only to parental alarm calls and independently to environmental cues of danger, but to the alarm calls of other species' as well. This work thus helps to answer some of the questions raised in our 2010 review, and helps to advance an understanding of parent-offspring communication under the risk of predation (Magrath et al. 2010). Future work investigating the mechanisms that enable response by young to heterospecific alarm calls will be crucial to understanding how learning contributes to the changing response of offspring as they age, and will help illuminate the full range of cognition and flexibility available to young animals as they attempt to survive to adulthood.

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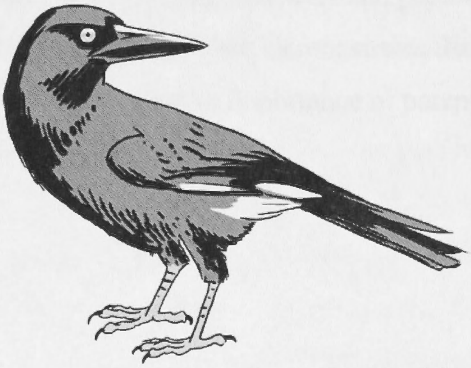
CHAPTER 2

Calling at a cost: elevated nestling calling attracts predators to active nests



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SUMMARY

Begging by nestling birds has been used to test evolutionary models of signaling but theory has outstripped evidence. Eavesdropping predators potentially impose a cost on begging that ensures signal honesty, yet little experimental evidence exists for such a cost at active nests because the use of artificial nests, long playback bouts, and absence of parents may have exaggerated costs. We broadcast short periods (1hr) of either nestling vocalizations or background noise at active white-browed scrubwren, *Sericornis frontalis*, nests. Nestlings called naturally during both treatments, allowing us to test whether elevated calling increases risk, a key but rarely tested assumption of evolutionary models. Predators visited nests exclusively during periods of elevated calling. Furthermore, playbacks affected neither adult visits nor nestling activity, suggesting that calling alone attracted predators. Adults gave alarm calls and nestlings usually called less when predators approached nests. Predation risk to broods is therefore likely to fluctuate substantially over short periods of time, depending on nestling hunger and whether adults or young have detected predators. This study confirms a present-day cost of nestling begging, demonstrates that this cost can be incurred over short periods, and supports the importance of parent-offspring antipredator strategies in reducing predation risk.

INTRODUCTION

Predation is the major cause of breeding failure in many bird species (Ricklefs 1969), and the risk posed by eavesdropping predators is an important component of evolutionarily stable models of nestling begging (Godfray 1995), but to date there is limited experimental evidence that nestling vocalizations at active nests attract predators (Haskell 2002). Here, we report the predation risks of nestling vocalizations using realistic playbacks of nestlings at active songbird nests.

Previous studies have been valuable in showing that predators can be attracted to begging calls, but their ability to assess begging costs at active nests has been limited (Haskell 2002). First, playback methods have probably exaggerated predation risk. Most studies have played back loops of nestling begging at high rates for long periods (Haskell 1994; Dearborn 1999; Haskell 1999), and several have played back the begging calls of cavity or tree nesting species at ground nests (Haskell 1994; Leech & Leonard 1997; Haskell 1999), even though ground-nesting species tend to have more cryptic begging calls (Briskie et al. 1999). Additionally, most studies have compared the costs of begging at high rates to silence, even though nestlings are not silent for extended periods of time (but see Haskell 1994; Dearborn 1999; McDonald et al. 2009). Second, the use of artificial nests can be misleading. Most studies have used artificial nests, yet even when carefully placed they frequently have higher predation rates, and are depredated by different predators, than real nests at sites chosen by parents (Weidinger 2001; Thompson & Burhans 2004; Fontaine et al. 2007). The use of dummy eggs can also bias our understanding of what predators visit nests, because damage to eggs may not reflect risk to nestlings, which can be vulnerable to different predators (Thompson & Burhans 2004). Finally, the use of artificial nests discounts adult and nestling behaviour, which could either increase or decrease predation risk (reviewed in Lima 2009; Magrath et al. 2010). Adult activity can attract predators (Martin et al. 2000), and nestling jostling could increase conspicuousness, regardless of vocal behaviour (Redondo & Castro 1992). Alternatively, adults can mitigate risk by silencing nestlings with alarm calls, and nestlings can crouch or becoming silent when they detect predators nearby (Magrath et al. 2010).

We examined the predation risk of nestling calling at active white-browed scrubwren, *Sericornis frontalis*, nests. Scrubwrens are an appropriate species for this study because nestlings beg when adults visit and also call between visits. Furthermore, scrubwrens use behavioural adaptations to manage nest predation risk: adults silence young with alarm calls, and nestlings go silent in response to the acoustic cues of a predator walking (Platzen & Magrath 2004; Haff & Magrath 2010). We assessed whether playback of nestling vocalizations at natural rates over a relatively short period (1h) attracted predators to nests. We also examined whether adults and nestlings behaved in ways that could minimize risk when predators were present.

METHODS

We conducted playback experiments in the Australian National Botanic Gardens in 2009. Scrubwrens are small, dome-nesting songbirds whose primary predators across much of Southeastern Australia are pied currawongs, *Strepera graculina* (Higgins & Peter 2002). Currawongs are territorial, omnivorous songbirds that hunt by sight and sound (Platzen & Magrath 2004). Scrubwren nests are extremely cryptic, and acoustic cues are probably a principal way that predators detect nests.

Nestlings call when parents visit the nest (begging calls: 200-800 ms, with sidebands and harmonics), as well as when parents are away (repeat calls: 50-150 ms, often without sidebands; Magrath et al. 2010). Begging calls are usually louder than repeat calls (below) but only last several seconds, whereas bouts of repeat calls often go on for tens of minutes. Both call types can be audible from over 2 m away (T.M. Haff personal observations 2008-9). The rate and amplitude of begging and repeat calls increase as nestlings become hungrier (Maurer et al. 2003).

We played back nestling vocalizations and control sounds at 21 nests containing 7-10 day old nestlings. Playbacks of nestling vocalizations mimicked a brood of three, and consisted of 12 s of begging calls, played only during adult visits, and repeat calls, played continuously when adults were not at the nest, at a natural rate of three per second. Control sounds consisted of continuous amplified background noise, and tested whether nestling vocalizations or background noise affected the behaviour of predators, adults or nestlings. Nestlings were never completely silent, however, and so our playbacks contrasted hungry broods to average broods, instead of hungry broods to silent ones. Nestling calls and background sounds were recorded at each experimental nest when the young were 4-5d old. Repeat and begging calls were played back at 65 dB and 80 dB at 20 cm, respectively, both at the upper natural range for 8 day old nestlings, and background noise was amplified to the same level as the background between amplified repeat calls (average 32 ± 2 dB among replicates). Vocalization playbacks were deliberately at the upper range of call rate and amplitude in order to mimic a hungry brood, as predation risk is predicted to increase with begging intensity (Godfray 1995).

All recordings and playbacks took place within the Australian National Botanic Gardens in Canberra, Australia, 35° 160' S, 149° 060' E. We recorded sounds at nests using a Marantz PDM 670 solid-state digital recorder, sampling wave files at 44.1 kHz and 16 bits, connected by 15 m audio cables to two Audio-Technica ATM15a miniature cardioid condenser lapel microphones placed 12 cm from the nest entrance. One microphone faced towards the entrance, to record nestling calls, while the other microphone faced away from the nest entrance, to record adult calls. We recorded sounds when nestlings were 4-5 days old in order to create playbacks using calls from each nest's young. Background noise was taken from recording periods when neither adults nor nestlings were vocalizing, with loud or abrupt sounds removed.

We edited nestling calls from each nest into unique 5 min (repeat call) or 12 s (begging call) playback tracks. For repeat call playbacks, we selected clean recordings between 10 s and 1min long, edited those selections to create playbacks containing approximately 3 calls/second, and then used these sections to create 5min playback loops. Individual call exemplars were repeated within loops, and we digitally altered the order and arrangement of those calls so that exemplar order was variable. All begging call tracks contained unique exemplars of calls, and averaged 46.8 ± 4.8 calls per track. We created 2-3 begging call tracks per nest, so that adults were not repeatedly presented with the same begging call exemplars. We played back recordings using an Edirol R-09HR solid-state digital player controlled from a hide at least 10 m from the nest. Equipment was placed when no predators were present, at least 30 min before playback began.

Playbacks were 30 min long and were presented at nests twice on a single day, with at least 60 min between bouts, so that each nest was exposed to a total of 60 min of playback. We used the same playback at a nest on a single day in order to avoid carryover effects of brood noisiness on adult behaviour, and presented the alternate playback type the following day. Playback presentation order was alternated between nests, which were distributed across the 40 ha study site.

We measured predator attraction to nests as approach within 2 m. As controls, we measured: (1) adult activity, as the number of nest visits; and (2) nestling vocal activity, as the total number of calls, mean duration (s) of measured calls, and mean maximum power (dB) of calls. We tallied nestling calls in a subset of 5 randomly selected minutes of each playback trial in Raven 1.3, and measured call properties for 2 of those minutes, also randomly selected. In total, we tallied 27,687 and measured 11,275 calls. We compared whole broods, as we could not separate the calls of individuals. We also measured antipredator behaviour of nestlings and adults (mobbing calls by adults, silence by nestlings) by comparing calling during the 60 s after a predator arrived to calling during the same minute of the replicate playback at the same nest on the same day, when no predator was present. To minimize predation risk we placed predator exclosures around nests, and ceased playback if a predator approached within 2 m. We analyzed data using nonparametric statistics and a generalized linear model (GLM) with a binomial distribution and logit link function, conducted in SPSS 17.1 and R 2.1.

RESULTS

Predators, all currawongs, approached nests exclusively during nestling vocalization playbacks (fig. 2.1; 7 visits nestling vocalization, none during background playback; two-tailed binomial test $p = 0.016$). No nest was approached more than once. Currawongs approached nests on foot, except for one individual that flew between perches. Combined playback and natural nestling calling during the vocalization playback approached the top of the range for natural broods (this study), and was greater than calling during the background playback (mean number of calls per minute ± s.e.: vocalization playback and natural calls combined 236.1 ± 18.6, background 125.2 ± 21.9, Wilcoxon $Z = -3.88$, $p < 0.0001$; mean duration combined calls: 0.12 ± 0.01 s, background 0.09 ± 0.05 s, $Z = -2.0$, $p = 0.05$; mean maximum power: combined calls 66.8 ± 0.9 dB, background 62.2 ± 1.3 dB, $Z = -3.32$, $p = 0.001$).

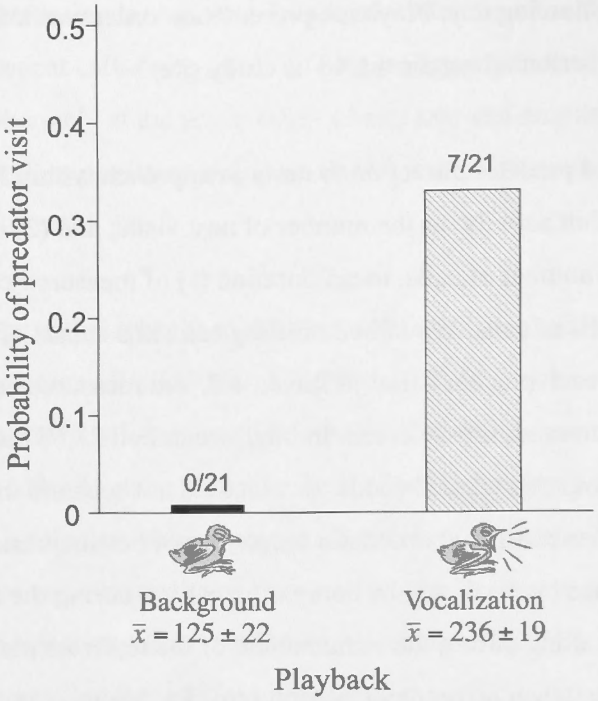

Figure 2.1: Probability of predator visits to nests, comparing mean number of calls per minute (±s.e.) during background and nestling vocalization playbacks.

Predator attraction to nestling calling was not confounded by changes in adult behaviour or nestling activity between treatments. There were no differences in scrubwren activity between treatments (mean adult visits: vocalization 10.9 ± 0.9, background 12.0 ± 1.0, paired t-test, $t_{20} = -1.1$, $p = 0.3$; mean number of nestling calls per minute: vocalization 104.0 ± 15.2, background 125.2 ± 21.9 $Z = -1.04$, $p = 0.3$; mean call duration: vocalization 0.10 ± 0.06s, background 0.09 ± 0.05 s $Z = -8.52$, $p = 0.4$; mean maximum power: vocalization 62.5 ± 1.2 dB, background 62.2 ± 1.3 dB $Z = -0.3$, $p = 0.8$). Further, predator visits were not due to between-nest differences in adult or nestling activity (binomial GLM including parental visits and nestling activity, $\chi^2_4 = 0.69$, $p = 0.95$; mean parental visits, vocalization playback: predator visit 12.0 ± 1.4, no visit 12.0 ± 1.5; mean number of natural nestling calls per minute, vocalization playback: predator visit 89.3 ± 26.5, no visit 111.3 ± 18.9; mean duration: predator visit 0.11 ± 0.02 s, no visit 0.11 ± 0.02 s; mean maximum power: predator visit 61.1 ± 2.6 dB, no visit 62.86 ± 1.4 dB). Predators arrived an average of 16.3 ± 4.6 min after the start of playback, with two approaches on Day 1 and five on Day 2 (binomial test p = 0.45).

Adults and nestlings used defensive behaviours when a predator was near the nest. Adults gave alarm calls only when they saw a predator near the nest (mean number of alarms: currawong present 40.9 ± 27.6, not present 0.0, Wilcoxon Z = -2.02, p = 0.04), and nestlings tended to call less when a predator was nearby (mean number of calls: currawong present 5.7 ± 4.8, not present 28.7 ± 10.3, Z = -1.86, p = 0.06).

DISCUSSION

Nestling vocalizations attracted avian predators to nests attended by parents. Neither adult nor natural nestling activity differed between playback types, indicating that predators were attracted by nestling calls alone. To our knowledge, this is the first experimental study demonstrating that nestling calling at active nests can attract predators. Further, we show that the cost of nestling calling can be incurred over short periods. This contrasts with previous studies, which have documented high predation rates after extended playback periods (Haskell 1994; Leech & Leonard 1997; Dearborn 1999; McDonald et al. 2009). No nest was completely silent during 'quiet' playback treatments, yet predators only visited nests when calling was highest, confirming the begging model assumption that costs increase with signal exaggeration, so maintaining signal honesty (Godfray 1995). Furthermore, because begging intensity varies in response to nestling hunger (Maurer et al. 2003), risk will fluctuate temporally. Thus,although the daily predation rate on nests with young at our study site is 4% (Platzen & Magrath 2004), risk to hungry broods is much higher (fig. 2.1).

Adults gave mobbing calls, which silence young, when a predator was at the nest, and nestlings tended to call less during predator visits, consistent with results of previous playback experiments (Platzen & Magrath 2004; Haff & Magrath 2010). Nestling detection of danger was imperfect, however, and some broods continued to call when a predator was nearby. This occurred when adults were not present to alarm call and the predator flew to a nearby perch, instead of approaching on foot (Haff, T., personal observations 2009). We conclude that nestlings are most vulnerable when they are hungry, when parents are absent, and when predators approach nests silently.

Our study suggests that begging can incur predation costs, and shows that past studies have not simply measured the "ghost of predation past" (Haskell 2002). Future studies at active nests incorporating incremental changes in nestling vocalizations, and separating out the relative influences of begging and repeat calling, will be valuable in helping to evaluate the true risks that nestlings take in crying out to be fed.

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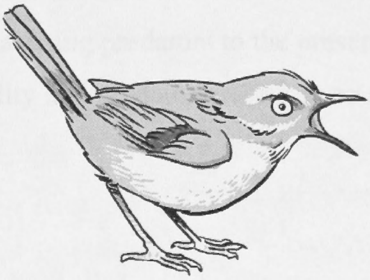
CHAPTER 3

To call or not to call: parents assess the vulnerability of their young before warning them about predators



SUMMARY

Communication about predators can reveal the effect of both conspecific and heterospecific audiences on signalling strategy, and so provide insight into signal function and animal cognition. In species with alarm calls, parents face a fundamental dilemma resulting from the presence of both intended and eavesdropping audiences. Calling can silence noisy offspring, but can also alert predators to the presence of nearby young. Parents could reduce this dilemma by being sensitive to the current vulnerability of offspring and calling only when they are most at risk. Testing whether offspring vulnerability affects parental strategy has proved difficult, however, because more vulnerable broods are often also more valuable to parents. We tested experimentally whether white-browed scrubwren, *Sericornis frontalis*, parents took brood noisiness into account when alarm calling in response to a nearby predator. Parents gave more alarm calls when playbacks simulated noisy compared to quiet broods when a model predator was nearby, yet brood noisiness did not affect adult calling in response to a control model. Parents were therefore sensitive to the tradeoffs between silencing young and alerting predators to the presence of nests. Our study shows that receiver vulnerability and predator presence can affect signalling decisions in species other than primates.

INTRODUCTION

An animal's audience can affect the way it communicates (Marler & Evans 1996; Ridley et al. 2007; Zuberbühler 2008), revealing the function and underlying costs and benefits of signalling. Audience effects on signalling can occur in a range of contexts (Marler et al. 1986b, a; Doutrelant et al. 2001; Striedter et al. 2003; Vignal et al. 2004), including communication about danger (Karakashian et al. 1988; Wich & Sterck 2003; Ridley et al. 2007; Le Roux et al. 2008; Zuberbühler 2009), where the audience can include both intended receivers and eavesdropping predators. Audience effects depend on variation in the costs and benefits of communication, and so may be particularly strong in alarm signalling about predators, as these signals can be variably costly to send (Sherman 1977; Sherman 1985), and benefits to receivers are likely to vary depending on receiver state and predator location at the time the signal is sent. For example, receivers in exposed positions should profit more from information about predators than those already in cover.

Previous studies have shown that the value of the intended audience can affect signalling about danger (Cheney & Seyfarth 1985; Sullivan 1985; Le Roux et al. 2008), but we know little about the importance of audience vulnerability. Male fowl, *Gallus gallus*, for example, pay attention to audience value, and so give more alarm calls for females than for rival males (Gyger et al. 1986; Marler et al. 1986a; Kokolakis et al. 2010), and alarm call the most for females to which they have recently mated (Wilson & Evans 2008). In other cases, both audience value and vulnerability could affect alarm calling, but disentangling the two has proved difficult. For example, fork-tailed drongos, *Dicrurus adsimilis*, foraging with pied babblers, *Turdoides bicolor*, give alarm calls in response to terrestrial predators to which only babblers are vulnerable, but also occasionally use false alarms to kleptoparasitize food from babblers (Ridley et al. 2007). It is therefore possible that calling is selected because of the value of babblers as a resource to drongos (Ridley et al. 2007; Radford et al. 2011). Overall, the influence of audience vulnerability alone on alarm calling has seldom been tested (Zuberbühler 2008), and to our knowledge has been demonstrated in only one species of primate (Papworth et al. 2008; Zuberbühler 2008).

Parent-offspring communication provides an excellent model for studying audience effects in alarm signalling because the intended audience, in this case offspring, varies both in value to parents and vulnerability to predators. Adults are more likely to give alarm calls to warn young of danger when they are more closely related and therefore more valuable to parents (Sherman 1977; Cheney & Seyfarth 1985; Wich & Sterck 2003; Griesser & Ekman 2004; Le Roux et al. 2008; Colombelli-Negrel et al. 2010). Yet offspring vulnerability to predators, which can be affected by the behaviour of young, might also influence alarm signalling by parents (Curio 1978; Harvey & Greenwood 1978; Serra & Fernandez 2011). In birds, for example, the intensity of nestling begging affects their conspicuousness to predators (McDonald et al. 2009; Haff & Magrath 2011), and parents of many species can reduce risk to nestlings by using alarm calls to prompt young to become silent (reviewed in Magrath et al. 2010). Separating the relative influence of offspring vulnerability and value on parental behaviour has proved difficult, however, because both brood conspicuousness to predators and value to parents increase as offspring age (Montgomerie & Weatherhead 1988). For example, American goldfinch, *Carduelis tristis*, parents gave more alarm calls when potential predators threaten older broods, but older broods are both noisier and more valuable than younger offspring (Knight & Temple 1986). Parents may also use other information about offspring behaviour, such as their ability to escape predators by jumping from the nest, when making decisions about alarm calling (Gill & Sealy 1996; Kleindorfer et al. 1996; Suzuki 2011), but no study that we are aware of has isolated the effect of offspring behaviour independent of brood value.

A flexible parental response to nestling behaviour in broods of constant value should allow a test of whether brood vulnerability itself affects parental signalling. Parents face the tradeoff that alarm calls can silence young, the intended audience, but can also alert eavesdropping predators to the presence of a nearby nest (Krama & Krams 2005; Krams et al. 2007). One way that parents could minimize risk to nests is by actively monitoring offspring activity, and making decisions about when to alarm call based on nestling behaviour (Harvey & Greenwood 1978; Grieg-Smith 1980; Redondo & Carranza 1989; reviewed in Magrath et al. 2010). If nestlings are silent, parents should remain quiet when a predator is nearby, so as to not alert the predator to the presence of a nest (Krama & Krams 2005; Krams et al. 2007). By contrast, if nestlings are hungry and therefore calling loudly, parents should use alarm calls to silence offspring, as begging calls offer clearer cues of nest location than adult alarm calls (Bradbury & Vehrencamp 1998; Peake 2005; Searcy & Nowicki 2005; McDonald et al. 2009; Haff & Magrath 2011). Such dynamic risk assessment would represent a powerful, short-term tactic adults could use to reduce nest predation risk, and would demonstrate that audience effects in alarm calling can be sensitive to audience vulnerability to predation.

We tested experimentally whether nestling vulnerability to predators affected parental alarm calling independent of brood value. White-browed scrubwrens, *Sericornis frontalis,* provided an ideal model because nestling calling is known to attract predators (Haff & Magrath 2011), and parental alarm calls silence noisy young in this species (Platzen & Magrath 2004, 2005; Haff & Magrath 2011). Playback of nestling vocalizations was combined with presentation of model predators to test whether parental alarm calling varied in response to brood conspicuousness to predators. Matched experiments within broods ensured that we manipulated the parents' perception of brood conspicuousness and risk of predation while holding brood value constant.

METHODS

Study site and species

We studied a colour-banded population of white-browed scrubwrens in the Australian National Botanic Gardens, Canberra, 35° 160' S 149° 060' E, in 2009. Scubwrens are small (14 g) passerines that build well-concealed domed nests about 15 cm in diameter on or near the ground (Magrath et al. 2000; Higgins & Peter 2002). They are facultative cooperative breeders in which a single female incubates an average of 3 eggs for 18 days (Magrath et al. 2000). The dominant pair and up to three beta males assist in feeding young, which are in the nest for an average of 15 days (Higgins & Peter 2002).

The primary predators of scrubwren nests in the Gardens are pied currawongs, *Strepera graculina* (Major et al. 1996; Wood 1998). Currawongs are large (300 g), omnivorous passerines that hunt by sound as well as by sight (Major et al. 1996; Higgins & Peter 2002), and can use nestling vocalizations to locate scrubwren nests (Haff & Magrath 2011). Daily nest predation rates jump from about 1% during incubation to 5% after hatching (Platzen & Magrath 2004), a magnitude of increase that is high compared to most other passerines (Clark & Wilson 1981). These data suggest that nestling vocalizations, parental activity, or a combination of the two betray the location of otherwise cryptic nests.

Scrubwrens have a wide repertoire of calls used at or near the nest. Nestlings call when adults visit the nest with food (begging calls or ‘whines’: 200-800 ms, with sidebands and harmonics), as well as between feeding visits when parents are not present (fig. 3.1; repeat calls or ‘peeps’: 50-150 ms, often without sidebands; Magrath et al. 2007). Peeping bouts often continue for tens of minutes or longer, and can be audible 2 m or more from the nest (Haff & Magrath 2011). The rate and amplitude of both whines and peeps increase as nestlings become hungrier (Maurer et al. 2003). Adults give contact calls, which stimulate nestling peeping, when coming to and from the nest (‘chips’: 20-30 ms, 6-8 kHz; Magrath et al. 2007). Adults often use alarm calls when predators are near the nest (fig. 3.1; ‘buzz’ alarms: 120-180 ms, 3-12 kHz; Platzen & Magrath 2005). Nestlings respond to buzz alarms by becoming silent, therefore decreasing their risk of being overheard by nearby predators (Platzen & Magrath 2004, 2005; Haff & Magrath 2011).

Study design

We combined nestling call playback with model predator presentation to test whether adults were more likely to give alarm calls to a predator if nestlings were noisy. We predicted that adults would give proportionally more buzz alarms in response to playback simulating noisy compared to quiet offspring when a model predator was near the nest, but not when a control model was nearby. We further predicted that increased adult calling when model predators were presented during noisy nestling playbacks would be specific to alarm calling and not an increase in calling overall, and so chip call rates would not differ between treatments. We conducted experiments at 20 nests containing broods of three 7-10 day old nestlings.

We presented taxidermic models at nests in order to manipulate parents’ perceptions of threat to nestlings. Models were either: 1) a predator, a currawong; or 2) a control, a crimson rosella, *Platycercus elegans,* a harmless parrot common in the Gardens. Models were placed on the ground 2 m from the nest, and presented for 2 minutes. We chose to place models 2 m from the nest because at this distance potential predators might not notice a nest if nestlings were silent, but would be able to overhear young if they were calling loudly. We chose 2 minutes as the length of model exposure to mimic a realistic situation while minimizing the chance of more than one adult responding to the model at a time, and to avoid habituation to the model.

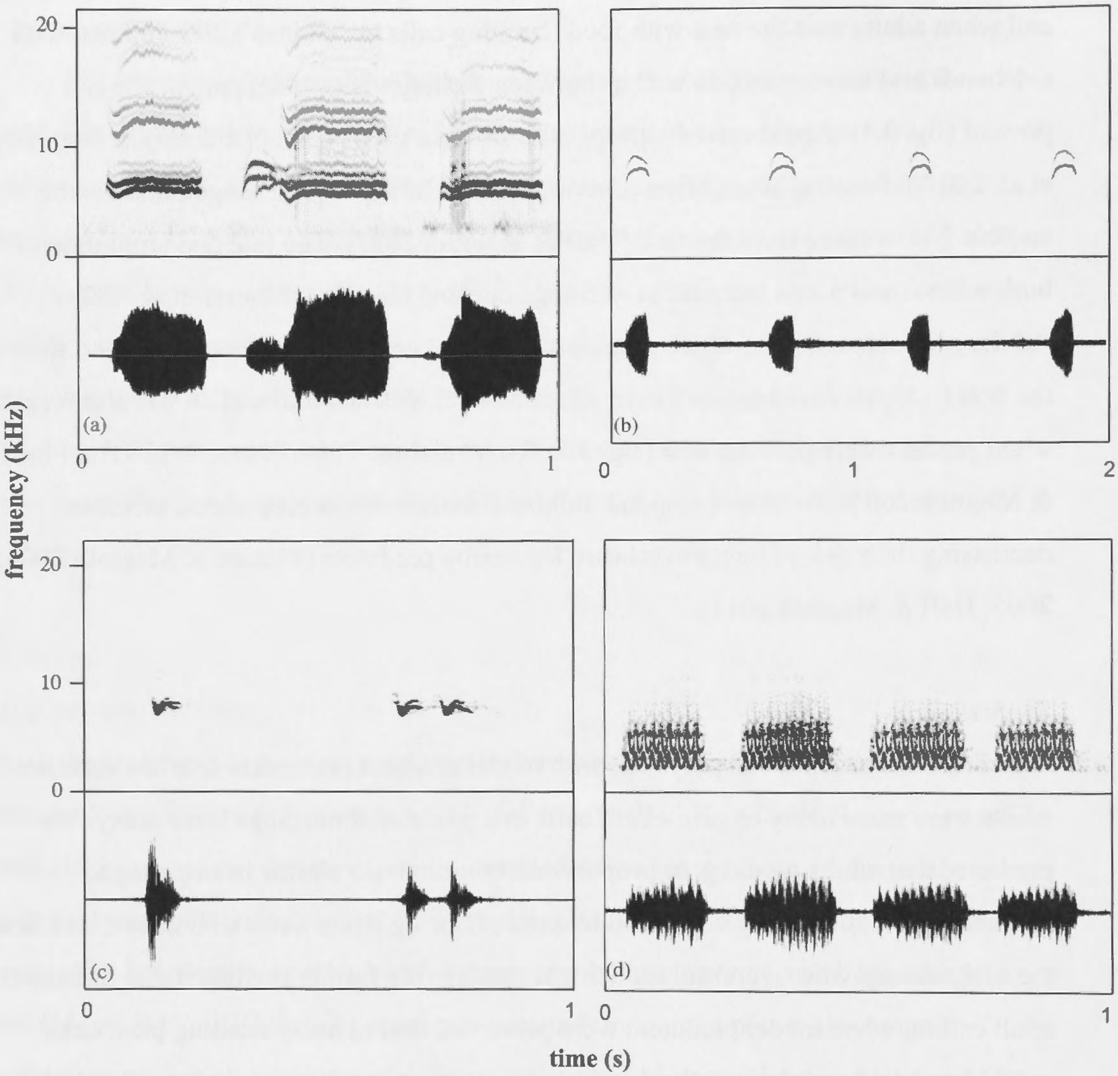


Figure 3.1: Examples of a) nestling begging calls (first published in Haff & Magrath 2010); b) nestling peep calls; c) adult chip contact calls; d) adult buzz alarm calls. Upper panels contain sonograms created in RavenPro 1.3 using settings described in the text for call analysis; lower panels show waveforms.

In order to simultaneously manipulate parents' perception of brood noisiness we also presented parents with playbacks of nestling calling. Nestling vocalization playbacks were designed to mimic a hungry brood of three, and consisted of about three peep calls per second played continuously when adults were not directly at the nest, and

12 s of nestling whines, the average length of nestling calling during feeding visits (Haff and Magrath, unpublished), played only during adult feeding visits. Peeps were played back when adults were not at the nest because of the potential for these calls to convey information to adults without adults having to be directly present at nests (Magrath et al. 2010). All peep and whine playbacks were of parents' own nestlings. To ensure that parents were responding to playback of nestling vocalizations and not the properties of background sounds in the recordings, we also presented control playbacks consisting of amplified background noise. No broods were completely silent during the background noise playback, and so we effectively compared adult response to nestling calling at high rates with response at moderate or low rates of nestling calling. Playbacks were presented continuously for at least 30 min, or until both the female and alpha male visited the nest, to allow adults time to assess brood noisiness.

Each nest received all four combinations of playback treatment and model type (table 3.1). In order to control for potential carryover effects of playbacks on adult behaviour, we presented parents with both model types in a single day, but kept playback type the same. We judged this design to be more realistic than manipulating brood noisiness within a day, as very hungry broods are likely to be consistent in their behaviour over the course of several hours, while the presence of other species near the nest can fluctuate over short periods. Nests were left undisturbed for at least 60 minutes between playback trials. Each nest received the second playback type with model presentations the subsequent day. We alternated playback and model presentation order between nests to control for order effects or effects of brood value (Montgomerie & Weatherhead 1988). This matched design allowed us to measure differences in adult calling within each nest under different levels of perceived vulnerability and predation risk.

We assessed the response of a single focal parent instead of both members of the pair because we could only control the length of model exposure to a single individual. We focused on the first parent (female or alpha male) to approach the nest after the first 30 min playback period and then maintained that adult as the focal individual for all subsequent trials.

Table 3.1: Playback and model presentation design. Playbacks were presented continuously for at least 30 min prior to presentation of each model, which lasted 2 min. Within a day, nests were left undisturbed for at least 60 min between trials. Playback and model presentation order were switched between nests.

Day 1: Nestling vocalization playback	Day 2: Background noise playback
Predator presentation	Predator presentation
Control presentation	Control presentation

Recording, playback and model presentation methods

We recorded sounds for playbacks at each nest when nestlings were 4 or 5 days old, using two Audio-Technica ATM15a miniature cardioid condenser lapel microphones connected by 15 m audio cables to a Marantz PMD670 solid state digital recorder sampling wave files at 44.1 kHz and 16 bits. Recording nestlings at this age allowed us enough time to prepare playbacks for experiments. We examined all recordings on spectrograms in Raven Pro 1.3 (Charif et al. 2008), and selected sections for peep, whine, and background playbacks. We filtered out sounds below 1 kHz in recordings of peep calls and background sounds, but did not filter whine calls because of their broad frequency range. For all playbacks we removed loud calls or other abrupt noises in the background.

We broadcast peeps and whines at 65 dB and 80 dB at 20 cm, respectively, which are at the upper ranges of natural amplitude of these calls for 7-8 day old nestlings (Haff & Magrath 2011). Background noise playbacks were amplified to the same level as the background between amplified peep call playbacks (average 32 ± 2 s.e. dB among replicates). Playbacks were broadcast from 16-bit wave files using a Sony MDR-A106 headphone speaker placed directly above and facing the same direction as the nest entrance, connected by a 15 m cable connected to an Edirol R-09HR solid-state digital player.

At least one day before experiments we placed dummy microphones and speakers at nests to habituate adults to their presence. At this time we also secured a garden mesh dome covered with camouflage cloth 2 m from the nest, and placed models under these domes at least 1.5 h before presentation. Adults quickly resumed normal behaviour after we placed equipment. We replaced dummy equipment with recording and playback equipment on the day of experiments, which we ran from a hide 10-15 m from the nest.

We presented models to focal parents during stage 2 of the experiment by using a fishing line to pull the camouflage cloth off the model dome at a constant rate of approximately 30 cm/s when parents were 10 m from nests. We used three different currawong and two rosella models. There were no differences in how adults treated different taxidermic mounts of predators (number of buzz alarms: Kruskal Wallis $\chi^2_2 = 0.74$, $p = 0.69$; minimum approach to models: $\chi^2_2 = 0.81$, $p = 0.67$; minimum approach to nests: $\chi^2_2 = 0.31$, $p = 0.86$), or controls (number of buzz alarms: $X^2_1 = 1.58$, $p = 0.21$; minimum approach to models: $\chi^2_1 = 0.11$, $p = 0.75$; minimum approach to nests: $\chi^2_1 = 0.06$, $p = 0.81$; see *Measurement of response*, below).

We recorded nestling calls during model presentation using the same methods described above for recording playback sounds. We recorded adult vocalizations using a Sennheiser ME62 omni-directional microphone covered in camouflage cloth and placed next to the model. We also recorded a commentary on adult behaviour during model presentation using an audio recorder.

In order to minimize our impact on predation rates, we used wire predator exclosures that allowed adults free access to nests, but kept out mid-sized predators such as currawongs (Haff & Magrath 2010). Exclosures were installed before recording or playback at nests. Parents generally ignored the exclosures, and no nest was abandoned after caging.

Measurement of response

We measured adult response to playback and model presentation using vocal and other behavioural responses. We used Raven Pro 1.3 spectrograms to count all calls, with settings as in Magrath et al. (2007). In total, we analysed 8,532 buzz and 1,408 chip calls. For each focal parent at each trial we recorded: (1) number of buzz alarms; (2) number of chip calls; (3) the closest distance that adults approached models, to the nearest 0.25 m; (4) the closest distance that adults approached nests, to the nearest 0.25 m; and (5) whether or not adults dropped or ate the food they were carrying to the nest.

We measured nestling calling to examine the impact of natural nestling calling on adult behaviour, as well as to measure nestling response to adult alarm calling. In order to test for variation in brood noisiness between playback treatments we tallied nestling calling in a subset of 5 randomly selected minutes distributed throughout each 30 min playback trial prior to model presentation. To measure response to adult vocalizations we also measured nestling calling during stage 2. We measured nestling calls using the processes described above for adult calls. In total, we analysed 27,687 nestling calls in stage 1, and 6,586 nestling calls in stage 2 of the experiment. We used the brood as the level of analysis, as we were not able to separate the calls of different nestlings.

Statistical analysis

We were not able to improve normality of data through transformation, and so we used nonparametric statistics. We used a matched design with Friedman ANOVA and Wilcoxon signed rank tests to compare differences in adult call rates between model and playback treatments, Kruskal-Wallis one-way ANOVA for independent samples to test for differences in adult response to model replicates, and Spearman's correlation to test for relationships between natural nestling calling prior to model presentation and adult alarm calling during model presentation. Comparing differences within adults allowed us to control for variation among individuals due to factors such as nest exposure or personality (Andersson et al. 1980; McLean et al. 1986 ; Hollander et al. 2008). We tested the specific *a priori* prediction that adults would give more alarm calls when nestlings were noisy specifically during presentation of predator compared to control models. We therefore calculated the difference in calling as the number of adult alarm calls during nestling calling playbacks minus the number of adult alarm calls during background playbacks, and compared these differences between predator and control model presentations. This allowed us to test the prediction that adults alter their behaviour in response to nestling vulnerability to predators. We predicted that nestlings should reduce calling in response to adult buzz alarm calls. We used an alpha level of 0.05 and two-tailed statistics for all tests, which we carried out in SPSS Statistics 19.0. The sample size was 20 for all tests.

RESULTS

Adults treated model currawongs but not rosella controls as predators, demonstrating that our experiment manipulated the parents' perception of risk (fig. 3.2). Parents gave more buzz alarms, which suppress nestling calling, and fewer chip contact calls, which stimulate nestling calling, during presentations of predators than control models (fig. 3.2; playback treatments combined, number of buzz alarms: Wilcoxon $Z = -3.85$, $p < 0.0001$; number of chip calls: $Z = -2.28$, $p = 0.02$). Parents also stayed farther away from both nests and models during model predator than control presentations (playback treatments combined, minimum approach to models: $Z = -3.74$, $p < 0.0001$; minimum approach to nest: $Z = -2.8$, $p = 0.005$). Parents dropped or swallowed food only in response to model predators (20 drops or swallows during one or both predator presentations, 0 during control presentations, two-tailed sign test $p < 0.0001$).

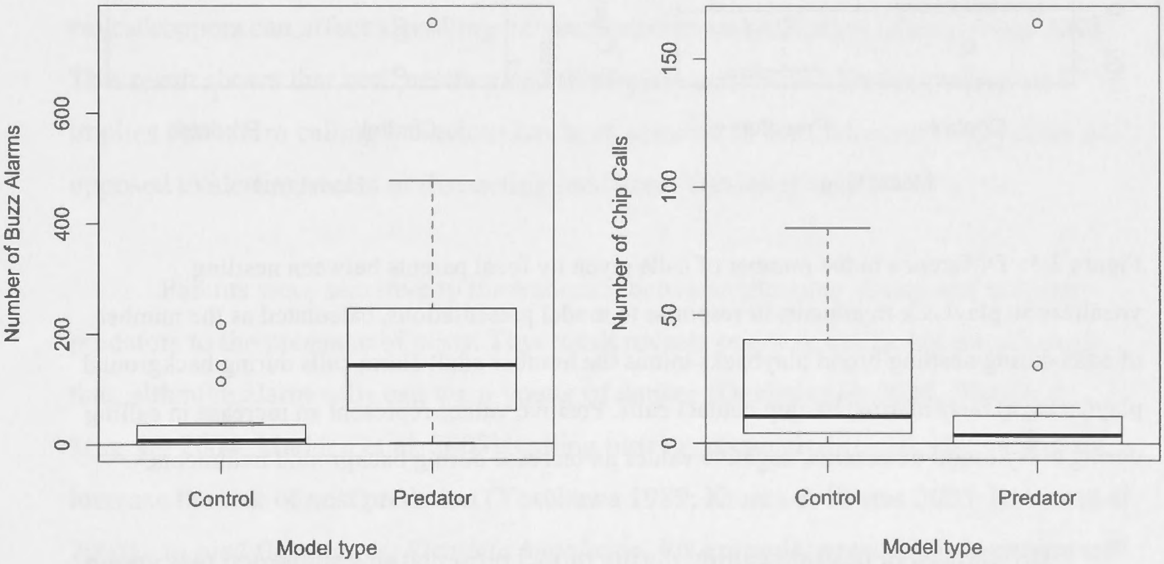


Figure 3.2: Vocal response by focal parents to control and predator models, playback treatments combined; a) buzz alarms; b) chip contact calls.

Supporting our key prediction, brood noisiness affected adult alarm calling only when model predators were near nests. Parents gave more alarm calls when playbacks were of noisy broods if the model was a predator, but not if the model was a harmless parrot (fig. 3.3; Wilcoxon $Z = -2.94$, $p = 0.003$). This response was not due to differences in calling in general, as there was no difference in the number of chip callsbetween nestling playback types when model types were combined (fig. 3.3; Z = -

1.21, p = 0.23). Adult response was not due to natural nestling calling, as nestling behaviour prior to model presentation did not differ between treatments (Friedman ANOVA number of calls per minute $\chi^2_3 = 3.3$, p = 0.35; call duration $\chi^2_3 = 2.34$, p = 0.51; call amplitude $\chi^2_3 = 4.02$, p = 0.26), and there was no relationship between natural nestling calling prior to model presentation and adult alarm calling during model presentation (model predator presentations: Spearman's r = -0.23, p = 0.15).

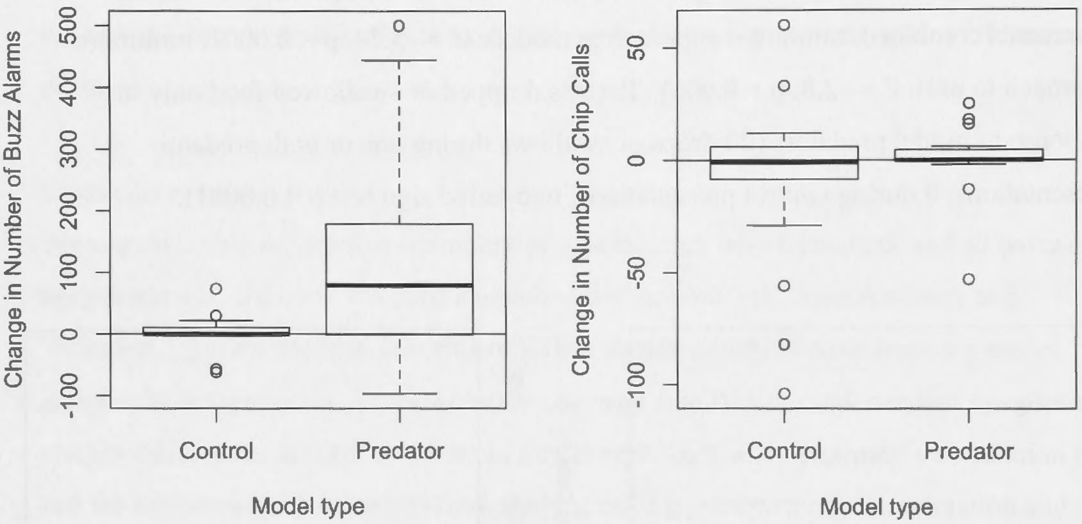


Figure 3.3: Difference in the number of calls given by focal parents between nestling vocalization playback treatments in response to model presentations, calculated as the number of calls during nestling brood playbacks minus the number adult alarm calls during background playbacks; a) buzz alarms; b) chip contact calls. Positive values represent an increase in calling during noisy brood treatments, negative values an increase during background treatments.

Differences in nestling calling during model presentations suggested that young monitored parental alarm calls and vocalized least when parents gave more alarm calls. Nestlings gave fewer calls during predator than control model presentations (median and IQR calls predator 24.0, 3.75 – 86.0 IQR, control 66.0, 20.5 – 182.25; Wilcoxon Z = -2.88, p = 0.004), and also gave fewer calls during noisy than quiet brood playback treatments when model predators were presented (median and IQR calls noisy 14.5, 2.25 – 51.25, quiet 47.0, 6.25 – 119.0; Z = -2.13, p = 0.03), in both cases reflecting differences in adult alarm calling during those treatments. Similarly, as expected from adult calling, there was no difference in the number of nestling calls between playback treatments during control model presentations (median and IQR calls noisy 50.0, 17.0 – 234.20, quiet 111.50, 27.75 – 328.70; Z = -1.16, p = 0.25). Differences in nestling calling were not due simply to response to playbacks of nestling calls, as offspring calling prior to model presentation did not differ between treatments (above).

DISCUSSION

Parents gave the most alarm calls when a model predator was nearby and playbacks simulated noisy broods vulnerable to eavesdropping. By contrast, playback of noisy nestlings did not affect alarm calling when control models were near nests. These results control for brood value and suggest that adults take nestling vulnerability into account when assessing the tradeoff between warning young of danger and betraying the location of nests. To our knowledge this is the first experimental study to demonstrate that offspring behaviour can affect alarm signalling by parents (Zuberbühler 2009; Magrath et al. 2010), or to show that the presence of heterospecific eavesdroppers can affect signalling between parents and offspring (Zuberbühler 2008). This result shows that both nestling and third-party audiences affect signaling, and implies that alarm calling behaviour has been selected to communicate with young, as opposed to alerting mates or distracting predators (Davies et al. 2004).

Parents were sensitive to the tradeoffs between silencing young and alerting predators to the presence of nests. This result reveals one way to resolve the dilemma that, although alarm calls can warn young of danger (Davies et al. 2004; Platzen & Magrath 2004; Madden et al. 2005), calling near nests can also alert predators and so increase the risk of nest predation (Yasukawa 1989; Krama & Krams 2005; Krams et al. 2007). In pied flycatchers, *Ficedula hypoleuca*, for example, nests receiving alarm call playbacks were depredated at higher rates than nests receiving control playbacks (Krama & Krams 2005). Furthermore, nests receiving alarm call playbacks at high intensities were depredated at higher rates than those receiving low intensity playbacks (Krams et al. 2007). Our results show that parents balance the risk of alarm calling with the benefit of silencing offspring by alarm calling at high levels only when nestlings are at high risk of discovery by predators.

Adults did not give more alarm calls when nestlings were noisy simply to ensure that young were able to detect their calls, which might be expected if nestling calling masked parental vocalizations (Wiley 1994; Wollerman & Wiley 2002; Mockford & Marshall 2009). If this had been the case, playback of noisy broods during control model presentations should have led to an increased number of adult chip calls, which stimulate young and prepare them for parental arrival at the nest (Magrath et al. 2007; Haff & Magrath 2010). Instead, chip call rates were similar between playback types during control model presentations.

This study provides strong evidence that parental alarm calling behaviour has been selected to reduce risk to young. Although parents probably always consider predators near nests a threat, predators that hunt using acoustic cues pose a particular risk to noisy broods (Haskell 1994; McDonald et al. 2009; Haff & Magrath 2011). In the present system, the risk of currawongs detecting scrubwren nests is significantly higher for noisy broods than for broods calling at low to moderate rates (Haff & Magrath 2011). Silencing young through alarm calls is therefore likely to be an important way in which parents can reduce nest predation risk, although potentially alarm calls could also reduce risk by masking the calls of unresponsive nestlings. Nestlings in this study called the least when parents alarm called the most, providing further observational support that parental calling can reduce nestling vocalizations, and thereby conspicuousness to predators (Platzen & Magrath 2004, 2005; Haff & Magrath 2011). Furthermore, whereas most theoretical models assume the direct costs of signalling are borne by the sender alone (Maynard Smith & Harper 2003; Searcy & Nowicki 2005), these results demonstrate an alarm signalling system in which the major costs and benefits of signalling are likely to be born by receivers.

Parents typically still gave some alarm calls when a model predator was near the nest even when playbacks were of quiet broods, yet this low level of calling probably entailed relatively little risk to young. Evidence from pied flycatchers suggests that it is the most intense parental alarm calling that is riskiest to broods (above; Krams et al. 2007). Further, given that scrubwren nestlings may vocalize while parents are away from the nest, a conservative strategy to reduce risk to young by parents may be to give some alarms when predators are near nests in case young are vocalizing, but to avoid escalating calling unless broods are noisy.

The results of this study support previous work demonstrating that parent birds can have flexible behavioural responses to both offspring behaviour and nest predation risk. For example, parents typically adjust provisioning rates in response to small changes in nestling begging (Bengtsson & Ryden 1983; Ottosson et al. 1997; Price 1998; Grieco 2001). Further, parents can mediate risk to nests by responding to changes in environmental predation risk and altering reproductive strategies such as nest placement, clutch size, nest attentiveness, egg resource allocation, and feeding rates to young depending on predator abundance (Martin 1995; Martin et al. 2000; Ghalambor & Martin 2001; Eggers et al. 2006; Fontaine & Martin 2006; Massaro et al. 2008; Martin & Briskie 2009). Here, we show that parents can also synthesize information about both current nestling behaviour and nest predation risk in order to mitigate short-term changes in offspring vulnerability.

Few studies have shown that vulnerability of the intended audience can affect alarm calling (Zuberbühler 2008, 2009). Male blue monkeys, *Cercopithecus mitis stuhlmanni*, for example, monitor the level of threat to their audience, and give more alarm calls when group members are closer to playbacks of conspecific alarm calls indicating an avian predator (Papworth et al. 2008). In Thomas langurs, *Presbytis thomasi*, males continue to alarm call in response to a terrestrial predator until all group members call in response, possibly to ensure all are aware of the risk of descending to the forest floor (Wich & de Vries 2006). Our study demonstrates that animals other than primates can also adjust alarm calling based on audience vulnerability to detection by predators. Given the tradeoffs that can arise between alarm calling and audience predation risk (Krama & Krams 2005; Krams et al. 2007), such assessment of audience vulnerability is probably widespread.

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Chapter 4

Vulnerable but not helpless: nestlings are fine-tuned to cues of approaching danger

Haff, T.M. and R.D. Magrath. 2010. *Animal Behaviour* 79, 487-496.

SUMMARY

Vocalizing nestlings are vulnerable to eavesdropping by predators, but may reduce risk through behavioural tactics such as responding with silence to adult alarm calls. Nestlings may also assess danger independently, although there has been little investigation of this possibility. Additionally, nestlings might also use parental signals to modify their response to possible cues of danger in order to reduce the likelihood of going silent to harmless stimuli. Nestling white-browed scrubwren, *Sericornis frontalis*, cease calling in response to both parental alarms and the acoustic cues of a predator. However, it is unknown if their response to the predator cue (a pied currawong, *Strepera graculina*, walking on leaf litter) is specific to the predator's sound, or whether it is a response to broadband, atonal sounds in general, to a 'walking tempo', or simply to any novel sound. Using field playback experiments of synthetic and natural sounds we show that nestlings are finely tuned to cues of danger. Nestlings suppressed calling most strongly to the sound of a real predator, and less strongly to broadband sounds. They did not respond to either novelty or a 'walking' tempo alone. Nestlings responded just as strongly to the predator's sound if they first heard the sound of a parent nearby, suggesting that they could discriminate predator cues from the sound of parental arrival, or that their interpretation of sounds was 'adaptively pessimistic'. Overall, scrubwren nestlings showed specific and independent assessment of predator sounds, which appeared unaffected by cues of parental presence.

INTRODUCTION

Nestling birds are subject to both welcome attention from parents and unwelcome attention from predators, yet they are neither passive recipients of parental care nor helpless victims of predation. Research on parent-offspring conflict shows that nestlings influence parental provisioning (Trivers 1974; Zahavi 1977; Godfray 1991; Burford et al. 1998; Davies et al. 1998; Godfray & Johnstone 2000; Budden & Wright 2001; Kilner & Hinde 2008). Less work, however, has focused on how nestlings might reduce their risk of predation. The response of nestlings to parental cues about danger has received some attention (Kleindorfer et al. 1996; Davies et al. 2004; Platzen & Magrath 2004), yet other cues that nestlings themselves use to independently detect danger remain largely unexplored (Magrath et al. 2007). Studies of how nestlings assess danger could help us understand what role they play in avoiding predation, how they make behavioural decisions, and how subtle their awareness is of cues indicating danger.

One way in which nestlings may lower their risk of predation is by responding to alarm calls from their parents. For instance, nestling moustached warblers, *Acrocephalus melanopogon* (Kleindorfer et al. 1996), reed warblers, *Acrocephalus scirpaceus*, dunnocks, *Prunella modularis*, European robins, *Erithacus rubecula* (Davies et al. 2004), white-browed scrubwrens, *Sericornis frontalis* (Platzen & Magrath 2004), and red-winged blackbirds, *Agelaius phoeniceus* (Madden et al. 2005) all fall silent when they hear playbacks of their parents' alarm calls. Even brood parasites such as common cuckoos, *Cuculus canorus*, stop begging when they hear their host's nest alarms (Davies et al. 2006). Nestling response to parental alarms can even be timed to match the risks that nestlings face at different stages of their development. For example, nestling scrubwrens respond to parental alarms that indicate predators hunting on the ground and attuned to acoustic cues, but not to those that indicate predators in flight, which hunt primarily by sight and pose relatively little threat to stationary, well-concealed nestlings (Platzen & Magrath 2005). By contrast, young respond to adult alarms that signal flying predators as soon as they fledge (Magrath et al. 2006). The sensitivity of such responses demonstrates that young birds can have a refined response to signals of danger from parents.

Parents are not always around the nest to warn nestlings of danger, however, and so nestlings may also benefit from assessing risk independently by listening for cues created by predators. Studies of acoustic or seismic detection of predators have focused primarily on invertebrates and amphibians, while birds have received minimal attention (Warkentin 2005; Catania 2008; Lohrey et al. 2009). For example, earthworms, *Diplocardia mississippiensis*, surface from their burrows when they detect the vibrations of digging moles, *Scalopus aquaticus*, a major worm predator (Catania 2008), and wolf spiders, *Schizocosa acreata*, freeze when they detect acoustic or seismic cues made by predatory birds (Lohrey et al. 2009). The few early studies of predator detection in nestling birds suggest nestlings may independently assess risk using sight or seismic cues, but simultaneous parental alarm calls confound the interpretation of these results (Schaller & Emlen 1961; Kleindorfer et al. 1996).

How nestling birds respond to acoustic cues may be particularly relevant because many nestlings have a limited field of view due to both gradual visual development and to constraints caused by nest structure, and even young nestlings with their eyes still closed can respond to acoustic stimuli (Clemmons 1995; Leonard et al. 1997). Response to sounds may therefore allow more opportunity for nestlings to react in time to avoid predation. We know of only one study that has tested the response of nestling birds to acoustic cues of a predator (Magrath et al. 2007). Seven-day-old nestling scrubwrens, which frequently call even when no adults are at the nest (Maurer et al. 2003), went completely silent to the sound of a predator walking on leaf litter. By contrast, parental food calls and the calls of other bird species either stimulated begging, or did not change calling. These calls were voiced and tonal, while the sound of the predator walking was atonal, and had a broad frequency range, with irregular amplitude peaks that correspond to a quick succession of three or four footsteps (Magrath et al. 2007).

What attributes of the sound of a predator walking could nestlings use to assess risk? The sound is potentially novel to nestlings, and they may therefore simply follow a general rule of 'turning off' to any novel acoustic cue, thereby reducing the likelihood of begging to inappropriate sounds. The sounds of a nearby predator are likely much less common than many other potentially unfamiliar sounds, such as harmless bird songs or calls, and novelty therefore may serve as an appropriate cue to silence naive nestlings. Indeed, novelty has been found to be an important component of a fear response in some birds, mammals and invertebrates (Bomford & O'Brien 1990; Darrow

& Schivik 2009; Hemmi & Merkle 2009). Going silent to all novel sounds may be costly, however, if nestlings respond inappropriately to adult vocalizations or mistakenly turn off to novel but harmless sounds, such as a new bird song, and are consequently unprepared to compete at the next parental visit (Muller & Smith 1978; Davies et al. 1998). Instead, nestlings may optimize the balance between responding to non-threatening stimuli with silence, and mistakenly vocalising to sounds that represent danger (Davies et al. 2004), by tuning in to specific sound properties that may indicate a predator approaching the nest. Such cues may include the atonal rustle of vegetation, or the erratic pattern of a predator's footsteps.

Even if nestlings' responses to environmental cues are fine-tuned, there may be times when the meaning of a sound is ambiguous; for example, the rustle of vegetation may be made by wind or by parents approaching the nest, rather than by a nearby predator. Nestlings might therefore benefit from being able to adaptively change their responses to cues of danger when those cues are preceded by 'safe' sounds that indicate nearby adult activity. Evidence for behavioural modification based on cue context comes from both reed warblers and pied babblers, *Turdoides bicolor*. Adult reed warblers change their interpretation of the likelihood of brood parasitism based on perceived risk, and are more likely to reject cuckoo eggs when they see a cuckoo near the nest (Davies & Brooke 1988). In pied babblers, sentinel birds give continuous 'surveillance calls', which vary in intensity from 'calm' to 'disturbed' based on the detection of heterospecific alarm calls (Bell et al. 2009). Foraging individuals adjust their own vigilance behaviour based on the intensity of sentinel surveillance calls, and are more likely to flee to cover after a sentinel alarm call that follows a 'disturbed' surveillance call, as opposed to a 'calm' surveillance call. Behavioural modification in nestlings based on cue context might be expected if 1) cues from parents, who have more information about the local environment, override nestling interpretation of a sound, even if that sound is unlike sounds that parents may make near the nest (such as an atonal rustle, as opposed to a voiced call), or 2) cues from parents change nestling response to a sound, particularly for sounds that are ambiguous and could be interpreted as produced either by a parent or by a predator (such as the rustle of a predator as opposed to the rustle of a parent). Demonstration of the capacity of nestlings to refine their response to cues of danger based on cue context could imply an opportunity for offspring to learn about threats while still in the nest.

In this study we used playback experiments on scrubwrens to examine how fine-tuned nestlings are to cues of a predator walking nearby. Scrubwrens are a good model for research on nestling response to sounds because nestlings call even when no adults are at the nest, and so both call suppression and stimulation can be measured. We carried out a series of playbacks using natural and synthetic sounds to examine nestling response to different acoustic attributes of the sound of a predator walking on leaf litter, and tested the role of sound context in nestling risk assessment.

METHODS

Study Site and Species

We studied a colour-banded population of white-browed scrubwrens in the Australian National Botanic Gardens in Canberra (35° 160’ S 149° 060’ E) during the breeding season (July through December) of 2008. The Botanic Gardens consist of both native planted (27 ha) and natural vegetation (13 ha), and are adjacent to the Black Mountain Reserve, a large area (9 km^2) of natural woodland where scrubwrens also breed (Magrath 2001).

Scrubwrens are small (12-15g) passerines in the ‘old endemic’ Australian family Acanthizidae (Schodde & Mason 1999). Adults breed primarily as pairs or as groups consisting of a single female and generally two males. Female scrubwrens build a domed nest (15 cm diameter) in a well-hidden location in or underneath vegetation or leaf litter, with access through a small (4 cm diameter) side entrance (Magrath et al. 2000). Females lay an average of three eggs, which they incubate for a mean of 18 days (Magrath et al. 2000). Nestlings may be fed by all group members, although assistance by helper males is variable (Magrath & Wittingham 1997). Fledging occurs at around day 15 (Magrath et al. 2000).

We found nests during the building or incubation period, and monitored their progress daily. In order to minimize any impact of our activities at nests on predation rates we enclosed them in green wire ‘cages’ as soon as females started incubation. Cages allowed free access to parents and small birds (and smaller predators), but excluded larger predators such as currawongs. Adults treated the cages as if they were part of the surrounding vegetation, and often used them as perches as they approached the nest. No nest was abandoned after it was caged.

Nestlings typically give two types of calls: 'whines' and 'peeps' (Magrath et al. 2007). 'Whines' are equivalent to begging calls, and are given in response to adult arrival at the nest. They are between 200-800 ms in duration, and typically include sidebands and harmonics. Nestlings also intermittently produce a regular 'peep' call, both immediately before and after adult feeding visits, as well as when adults are not at the nest. These calls are shorter (50-150 ms) than whines, and often without sidebands. Peeps in the absence of parents are often given at a regular tempo without an obvious prompt, with an average frequency of about 1 per second (Platzen & Magrath 2005). Bouts of peeping can go on from a few seconds to up to tens of minutes at a time. Although their adaptive function is unknown, laboratory experiments have shown that peep rate increases with nestling hunger (Maurer et al. 2003).

Adult scrubwrens give several calls that stimulate nestling calling, including 'food' calls, given at the nest, and 'chips' calls, given when adults approach the nest (Magrath et al. 2007). Food calls vary from structurally simple to complex calls that vary in length (<50 ms to > 300 ms), amplitude and bandwidth, and include elements of song, territorial calls, and mimicry, as well as other elements of unknown origin (Platzen 2004). The full function of scrubwren food calls is unclear, but they do incite young to beg (Platzen 2004; Magrath et al. 2007). Chips are structurally simple calls that are given singly or in quick succession with increasing frequency as adults approach the nest (Horn, Leonard and Magrath unpublished data). Whether these calls are intended to convey information to nestlings or to other adults is unclear, but previous studies have demonstrated that chips excite young to increase peeping, or even to whine (Magrath et al. 2007). Adults also give ground alarm 'buzz' calls in the presence of predators, to which nestlings respond with silence (Platzen & Magrath 2005).

The primary predator of scrubwren nestlings in the Botanic Gardens is the pied currawong, *Strepera graculina* (Prawiradilaga 1996; Platzen & Magrath 2004; Magrath et al. 2006), a large (280-320 g), omnivorous passerine that hunts using both visual and acoustic cues (Major et al. 1996; Wood 1998; Higgins & Peter 2002). Other potential predators at the site include Australian Magpies, *Cracicus tibicen*, laughing kookaburra, *Dacelo novaeguineae*, common brush-tailed possums, *Trichosurus vulpecula*, eastern brown snakes, *Pseudonaja textilis*, and water dragons, *Physignathus lesueurii*. The reaction of nestlings to sounds made by predators other than currawongs has not been assessed, but nestling reaction to the footsteps of other avian nest predators is not expected to differ, as most similarly sized species in the gardens are at least opportunistic nest predators (Higgins & Peter 2002).

Experimental Design and Predictions

Experiment 1: nestling response to sound properties

This experiment was designed to test which qualities of the sound of a predator walking are used as cues of danger by nestlings: novelty, acoustic structure, or tempo. We played 3 s examples of six different sounds to 20 broods of 7 or 8 day old nestling scrubwrens. Sounds played to broods were: 1) a computer-generated series of tones; 2) a computer-generated, atonal, smooth broadband sound; 3) a computer-generated, atonal, erratic broadband sound; 4) a parental food call; 5) the sound of a currawong walking in leaf litter; and 6) 'bell' calls of a crimson rosella, *Platycercus elegans* (fig. 4.1). Each nest received a unique example of each of these playbacks.

Each playback was designed to test a specific response in nestlings. The 'tonal' playback consisted of a series of short, smooth tones of varying frequency, arranged in an irregular temporal pattern and spanning a large frequency range. If nestlings use novelty alone as a cue of danger, then we predicted that they should go silent to this playback. If nestlings use cues specific to the sound of a predator, however, then the novel tonal playback should not stop nestlings from vocalizing. The 'smooth broadband' playback was a broadband white noise that gradually increased and subsided in amplitude. The 'erratic broadband' playback was a broadband white noise with irregular amplitude peaks inserted at intervals similar to the peaks in walking currawong recordings. If nestlings go silent to the non-voiced, broadband nature of rustling leaf litter or vegetation, then we expected both the smooth broadband and the erratic broadband playbacks to turn nestlings off equally. If nestlings use the irregular pattern of footsteps as an additional cue of danger we predicted they should turn off more strongly to the erratic broadband playback than to the smooth broadband treatment. If instead they use tempo alone as a cue, then they should turn off to both the tonal and erratic broadband playbacks, but not the smooth broadband treatment.

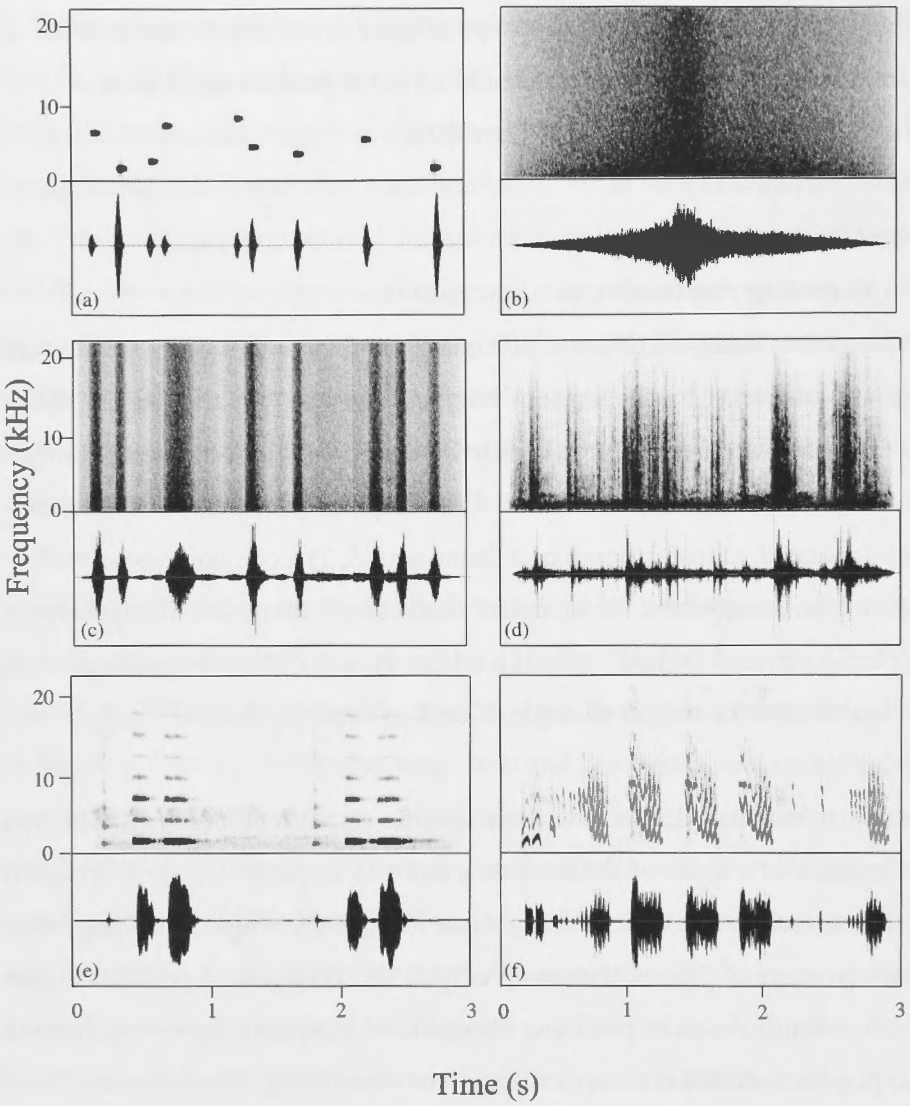

Figure 4.1: Examples of playbacks to individual broods of scrubwren nestlings in experiment 1. (a) Computer-generated tonal sounds, (b) computer-generated smooth broadband sound, (c) computer-generated erratic broadband sound, (d) currawong walking in leaf litter, (e) crimson rosella bell call, (f) scrubwren food call. Upper panel contains sonograms created in RavenPro 1.3 using settings described in the text for call analysis; lower panels show waveforms. Each set of six playbacks was unique for each brood, and scrubwren food calls were recorded from parents.

We created the synthetic playbacks using Adobe Audition 3. Tonal playbacks were made by creating a range of 8 ms tones between 2 and 8 kHz (within the range of nestling hearing). Each tone was placed in a curve-pulse envelope and arranged in a temporal pattern that matched the tempo of the walking currawong playback received by that nest. Amplitude between tones varied within the range of elements in scrubwren food calls. The sound was quite unlike the calls of scrubwren or any other species at the study site, and so was a novel, tonal sound. Smooth broadband playbacks were created using the 'pink' noise selection at an 'intensity' of 40. 'Intensity' in Adobe Audition scales from 2 to 40, and higher intensities create sounds that are louder, harsher, and more erratic. The broadband playbacks were then cut to 3 seconds and placed in an individually modified 'smooth' sound envelope. Erratic broadband sounds were similarly created, but were placed in a sound envelope that was modified to have amplitude peaks at intervals that mimicked the tempo of the walking currawong treatment received by that nest. Both broadband sounds were filtered at 0.3 kHz. In order to avoid pseudoreplication, synthetic playbacks were created individually for each nest, so while the overall pattern of each treatment was similar between nests, no pattern was identical.

We also presented nestlings with a range of control playbacks. Food call playbacks were composed of segments of calls given by a single parent at each nest, played at a natural tempo, and were used as a 'positive' control to ensure that nestlings begged as expected to a known positive stimulus. Currawong walking sounds were recorded from currawongs walking on leaf litter at the study site, and were used as a 'negative' control to ensure that nestlings 'turned off' as expected from a previous study (Magrath et al. 2007). The bell calls of the crimson rosella, a harmless parrot, were used as a 'neutral' control. These calls are given commonly throughout the study site, and previous studies have shown that nestlings have little or no reaction to their playback (Platzen & Magrath 2005; Magrath et al. 2006; Magrath et al. 2007). For details on how natural sounds were recorded and prepared see 'Recording and Playback Methods' below.

Experiment 2: behavioural modification

This experiment was designed to examine whether or not nestlings can adaptively change their response to a cue of danger if the sound is preceded by a 'safe' sound that indicates parental activity near the nest. We broadcast 8 s playbacks, each consisting of a 3 s sound, followed by 2 s of silence, followed by a 3 s playback, of three different combinations of sounds to 19 broods of 8 or 9 day old nestlings. The sounds broadcast

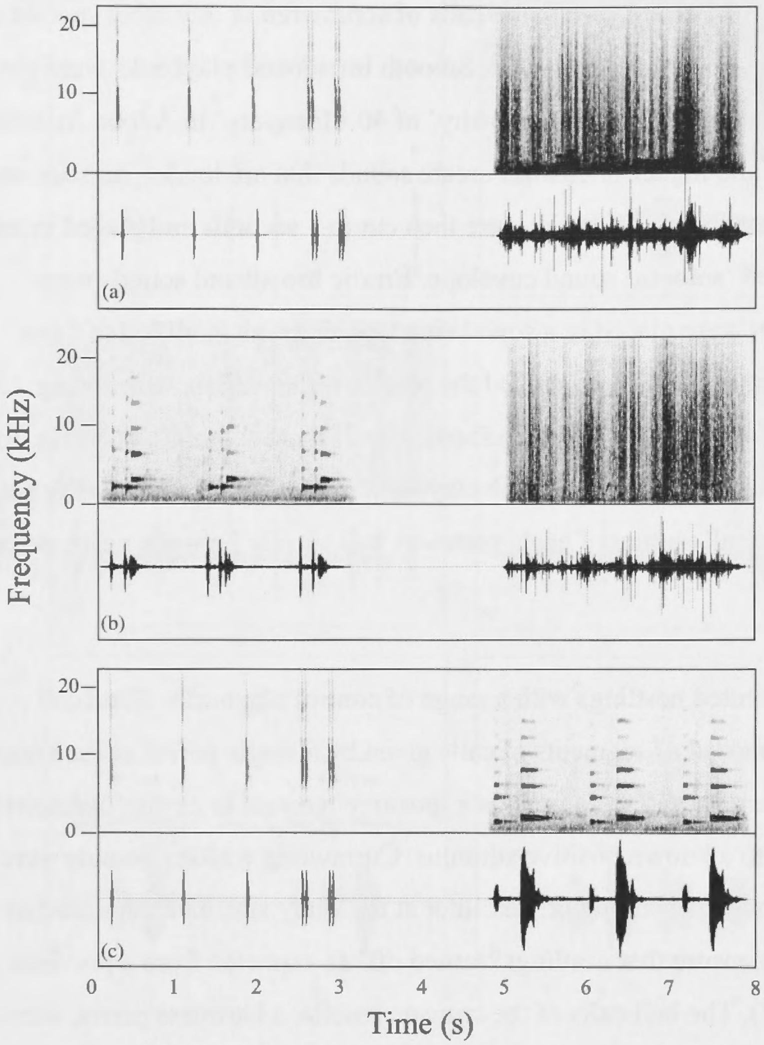

Figure 4.2: Examples of playbacks to individual broods of scrubwren nestlings in experiment 2. (a) Scrubwren chip contact calls followed by a currawong walking in leaf litter, (b) crimson rosella bell call followed by a currawong walking in leaf litter, (c) scrubwren chip calls followed by crimson rosella bell calls. Upper panel contains sonograms with the same settings as in fig. 4.1; lower panels show waveforms. Each set of playbacks was unique for each brood, and currawong and rosella recordings were not repeated either within one brood or between this experiment and experiment 1. Scrubwren chip contact calls were recorded from parents.

to nests were: 1) a series of parental chips followed by the sound of a currawong walking; 2) chips followed by rosella bell calls; and 3) rosella bell calls followed by the sound of a currawong walking (fig. 4.2). We used different examples of currawong and rosella playbacks at each nest within this experiment and between this experiment and experiment 1, so that nestlings were not habituated to specific recordings. The nests used for this experiment were the same as used for experiment 1. Broods were never subject to more than one experiment on a single day.

Playback design and rational were as follows. The 'chip-currawong' playback consisted of three single chips, followed by two couplets of chips in quick succession (designed to mimic an adult scrubwren approaching the nest), followed by the sounds of a currawong walking in natural leaf litter. If nestlings are able to change their interpretation of rustling leaves from the sound of a predator to the sound of a parent arriving at the nest depending on cue context, then we expected nestlings to increase or maintain their call rate after a 'chip-currawong' playback. The 'chip-rosella' playback was comprised of the same series of parental chips, followed by rosella bell calls. This treatment was included as a control to test the specificity of the response of nestlings to the 'chip-currawong' treatment; if nestlings treat rosella calls neutrally, as expected, then we predicted a slight increase in call rate after this playback, as nestlings respond to the chip and ignore the rosella bell calls. The 'rosella-currawong' playback consisted of rosella bell calls followed by the sound of a currawong walking in leaf litter. We used this treatment as a control, and expected nestlings to respond by turning off as strongly as to a currawong-walking playback alone (tested in experiment 1), as the rosella call provides no information on safety.

Recording and Playback Methods

Sounds used in the playbacks for both experiments were recorded at the study site using a Marantz PMD670 solid state digital recorder sampling wave files at 44.1 kHz and 16 bits. Parental food calls and chips were recorded at each nest when the nestlings were 4 or 5 days old, using two Audio-Technica ATM15a miniature cardioid condenser lapel microphones covered in camouflage mesh cloth and connected to a Marantz on 15 m audio cables. Both microphones were placed 12 cm from the nest entrance; one was pointed towards the nest, to record food calls, and one was pointed away from the entrance, to record adult chip calls on their way to the nest. The currawong walking and rosella bell calls were recorded in 2006 using hand-held Sennheiser ME66 or ME67 directional microphones. Recordings were transferred digitally to a Macintosh computer, and prepared using RavenPro 1.3 (Charif et al. 2008) and Adobe Audition 3. We examined all recordings on sonograms in RavenPro 1.3 to ensure there were no overlapping background sounds. We filtered recorded sounds (food call, chip, currawong walking and rosella bell calls) for playback at 0.5 kHz, cut them to 3 s, and smoothed the sound ends to avoid noisy crackles and abrupt starts and stops.

All playbacks were transferred as wave files to an Edirol R-09HR solid state digital recorder-player, and were broadcast at about 70dB at 20 cm, within the natural range of adult food calls, so that nestling reactions to playbacks were based on sound quality rather than amplitude. Playbacks were broadcast using a Sony MDR-A106 headphone speaker placed 20 cm from the nest entrance, connected by a 15 m cable connected to the Edirol player, and recorded on a Marantz connected by a 15 m cable to an Audio-Technica lapel microphone placed 12 cm from the nest entrance. We placed dummy microphones and speakers at all nests at least 24 h before the experiments, to ensure that adults were habituated to their presence. Placing equipment at the nest caused some disturbance to parents, but in all cases they quickly resumed their normal behaviour.

On the day of the experiment, we placed equipment at the nest, and retired to a discrete location 10 –15 m from the nest. We used a hide on the rare occasion that adults reacted to our presence. We did not start experimental treatments until adults had resumed normal feeding behaviuor at the nest. Treatment order was randomized by pulling numbers from a hat. Treatments were separated by at least 5 minutes, or by a natural feeding visit by an adult. Before any playbacks were performed we waited until nestlings were peeping regularly (approximately one peep per second for one minute or more), adults were least 15 m from the nest and not vocalizing, and there were no other loud or irregular sounds in the background. If a parent called or returned to the nest during a treatment, that recording was discarded, and the treatment was moved to the end of the experiment.

Nestling Call Analysis

We measured the timing and properties of all vocalizations produced by broods during the10 s period before playback started and in the 10 s period after the playback ended. The specific measurements of calls were: time at the start and end; frequency range (Hz), between the lowest and highest tonal component, excluding harmonics; and maximum power (dB). If broods were silent during the 10 s after playback, we continued recording for up to two minutes so that we could measure the time when calling resumed. Calls were measured from sonograms produced in RavenPro 1.3, with sonogram settings as in Magrath et al. (2007): Blackman filter at 582 samples, and 3 dB filter bandwidth, 2.27 ms grid time, 21.5 Hz frequency grid, and 12 Hz of window scaling and 1s per line. True call amplitude was calibrated against sound files of known amplitude, as measured by a sound pressure level meter. We measured each of the 5325 calls, even when they overlapped with calls of other nestlings.

We analysed four measures of brood response based on the measurement of individual calls: (1) brood calling effort; (2) mean frequency range (Hz) ; (3) mean maximum power (dB) ; and (4) duration of call suppression after each playback (s), calculated as the time from the end of the playback to the first call, up to a maximum of 120 s later. Brood calling effort was the first principle component from an analysis including the number of calls and the total duration of individual calls, which were themselves strongly correlated (eigenvalue 1.834, component extraction 0.958 for both number of calls and total duration of calls). For the first three measures, the brood's response was calculated as the value in the 10 s sample period after playback minus the value in the 10 s sample period before playback, so that positive values indicate an increase in brood response, and negative values a decrease. These measures controlled for differences in base peep rate between nests, and have been used in previous playback experiments with nestlings (Platzen 2004; Magrath et al. 2007). For frequency and amplitude measurements we lumped calls that overlapped in time and frequency, and considered these variables as representative of the brood call output as a whole. Because all broods were peeping regularly before playback, we simply used the measured duration of call suppression after the playback as the response, rather than subtracting any pre-playback value. We used the brood as the level of analysis because we could not tell individual nestling calls apart.

Statistical Analysis

The measures of brood response were not all normally distributed , and it was not always possible to normalize through transformation, so we used nonparametric analyses throughout. For both experiments we used two-tailed Wilcoxon signed rank tests to test for differences in brood response between the rosella control treatment and all other treatments. Nestlings did not respond to rosella calls for any variable tested (below), and so we considered differences in brood response between a treatment and the rosella playback to indicate a reaction to the playback being tested. We used Cochran Q or McNemar tests to examine differences in the probability of complete suppression of calling, or giving whine calls, in the 10 s after the currawong walking and computer-generated treatments.

Although some of our analyses involved multiple comparisons of nestling response, we chose not to perform statistical adjustments such as Bonferroni procedures because they may make interpretation of results less clear, reduce statistical power, increase the likelihood of Type II errors, and contribute to publication bias (Nakagawa 2004). Instead, we present uncorrected statistical tests here, so that readers may independently assess the biological and statistical significance of test results. Furthermore, our interpretation of results is based on overall patterns of nestling response, instead of on isolated ‘significant’ results that may simply be the result of a Type I error. All statistics were carried out in SPSS Statistics 17.0 (SPSS Inc., Chicago, Illinois, USA) using a significance level of 0.05.

RESULTS

Experiment 1: nestling response to sound properties

Novelty alone was not sufficient to silence calling nestlings (fig. 4.3). Nestling response to the novel computer-generated tonal treatment did not differ from their response to the familiar rosella control for most measures. In fact, call frequency range increased, and brood calling effort tended to increase, indicating that this novel sound was perceived as slightly stimulating to nestlings (Wilcoxon signed rank test comparing response to tonal treatment with the rosella treatment: brood calling effort $Z = -1.87$, $p = 0.06$, frequency range $Z = -2.02$, $p = 0.04$, maximum power $Z =- 0.37$, $p = 0.71$; call suppression $Z = -1.624$, $p = 0.1$).

In contrast to the lack of importance of novelty, nestlings decreased calling in response to both computer-generated broadband treatments similarly, suggesting that a broadband cue, but not an erratic pattern that might indicate footsteps, determined response (fig. 4.3; Wilcoxon signed rank test for response to mean combined broadband treatments versus rosella treatment as the neutral control: brood calling effort $Z = -2.80$, $p = 0.005$; frequency range $Z = -0.31$, $p = 0.75$; maximum power $Z = -0.78$ $p = 0.94$;

call suppression $Z = -3.36$, $p = 0.001$). There was no difference in response to the smooth and erratic broadband playbacks (fig. 4.3; Wilcoxon signed rank test: brood calling effort $Z = 0.40$, $p = 0.69$; frequency range $Z = -1.41$, $p = 0.16$; maximum power $Z = -0.47$, $p = 0.64$, call suppression $Z = -1.307$, $p = 0.19$). While nestlings did not always suppress calling completely in the 10 s after the broadband treatments (4 of 20 stopped calling for at least 10 s to the smooth broadband, and 7 of 20 did so for the erratic broadband treatment), they did so more than for all other playbacks (0 of 20 for rosella, tonal, and food call treatments), with the exception of the currawong playback (17 of 20; Cochran's Q comparing combined broadband treatments to rosella, tonal and food call treatments $Q_3 = 9.0$, $p = 0.03$).

Although nestlings generally went silent to the erratic broadband treatment, their response was not as uniform as to the smooth broadband treatment. Six broods increased calling, and three of those broods responded by whining. No nestlings whined after the smooth broadband treatment, and only two of 20 broods increased calling after that treatment (McNemar test comparing whether or not nestlings were more likely to increase calling after the erratic broadband playback, relative to the smooth broadband treatment $Q_1 = 4.0$, $p = 0.046$).

Supporting the hypothesis that nestling response to acoustic cues is fine-tuned, the computer-generated broadband treatments did not suppress nestling calling as strongly as the sound of an actual currawong walking (fig. 4.3; Wilcoxon signed rank test comparing response to combined broadband treatments versus currawong treatment: brood calling effort $Z = -3.66$, $p < 0.0005$; call suppression $Z = -3.40$, $p = 0.001$). The sound of a currawong's footsteps in leaf litter strongly suppressed nestling calling (fig. 4.3; Wilcoxon signed rank test comparing response to the currawong treatment versus rosella treatment: brood calling effort $Z = -3.92$, $p < 0.0005$; call suppression $Z = -3.92$, $p < 0.0005$), and was excluded from analysis of frequency and amplitude variables because too few broods called during the 10 s after the playback. In fact, the predator playback suppressed nestling calling so strongly that 85% (17 of 20) of broods did not call at all in the 10 s following the playback (Cochran's Q comparing currawong to rosella, tonal and food call treatments $Q_3 = 51.000$, $p < 0.0005$), significantly more than in the broadband treatments (Cochran's Q comparing calling in

10 s after currawong playback to combined broadband treatments $Q_1 = 14.0$, $p < 0.0005$).

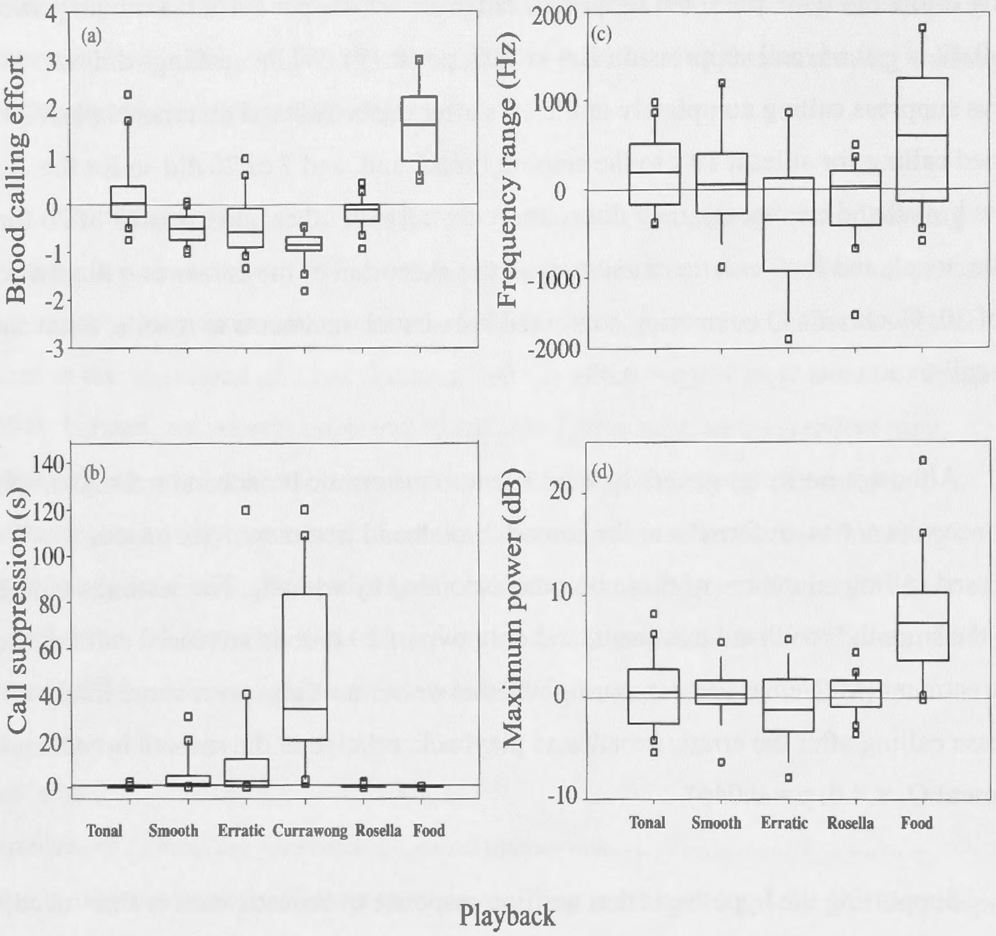

Figure 4.3: Nestling responses to playbacks in experiment 1. (a) Brood calling effort, the first component extracted from a PCA of number of calls and mean total duration of calls; (b) call suppression (s); (c) mean frequency range (Hz); (d) mean maximum amplitude (dB). Currawong treatment not included in (c) or (d). All measurements except call suppression are differences of calling from the 10 s before to the 10 s after the playback, with positive values representing an increase. Box plots show the median and inter-quartile range, whiskers represent the 10th and 90th percentiles, and other symbols show outliers. N = 20 for all playbacks in (a) and (d); N = 13 for erratic, N = 16 smooth, and N = 20 for all other playbacks in (b) and (c).

Nestlings reacted to the neutral (rosella) and positive (food call) control playbacks as expected based on past experiments (Platzen & Magrath 2004, 2005; Magrath et al. 2007). Nestlings did not respond to the rosella playback for any variable measured (fig. 4.3; Wilcoxon test of calling before compared to after rosella playback: brood calling effort $Z = -0.34$, $p = 0.79$; frequency range $Z = -0.45$, $p = 0.65$; maximum power $Z = -1.0$, $p = 0.28$). Parental food calls stimulated nestling calling in all variables measured (fig. 4.3; Wilcoxon ranked sign test comparing response to food call playback versus rosella control: brood calling effort $Z = -3.92$, $p<0.0005$; frequency range $Z = -2.73$, $p = 0.006$; maximum power $Z = -3.62$, $p < 0.0005$; call suppression $Z = -2.315$, $p = 0.02$).

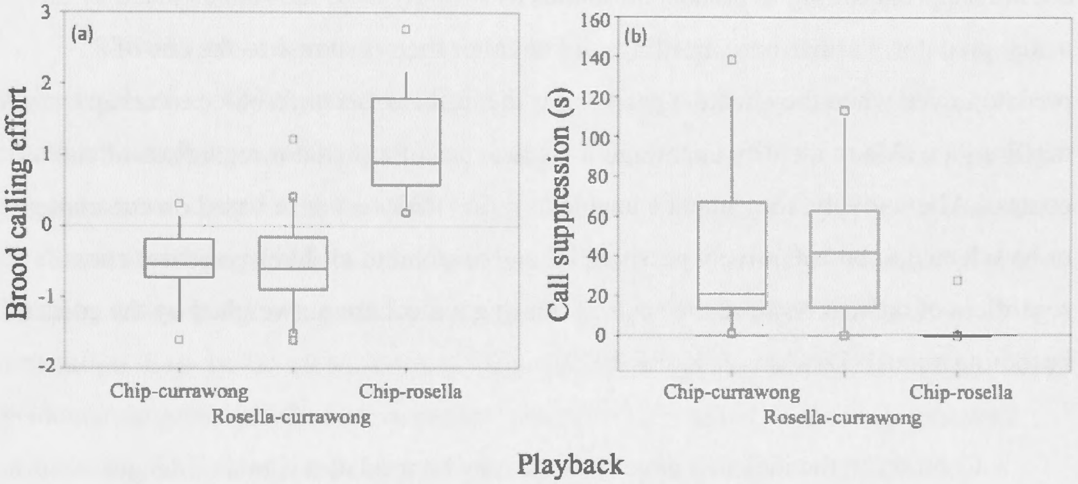

Figure 4.4: Nestling responses to playbacks in experiment 2. (a) Brood call effort, showing the difference from the 10 s before to the 10 s after the playback, with positive values representing an increase; and (b) call suppression (s). Box plots show the median and inter-quartile range, whiskers represent the 10th and 90th percentiles, and other symbols show outliers; N = 19 in all cases.

Experiment 2: Behavioural modification of nestling response to danger

Nestlings did not change their reaction to the sound of a currawong walking in response to hearing their parents near the nest shortly before (fig. 4.4; Wilcoxon signed rank test comparing chip-currawong to rosella-currawong playbacks: brood calling effort $Z = -0.121$, $p = 0.9$, call suppression $Z = -0.24$, $p = 0.81$). Both of the currawong walking treatments strongly suppressed nestling calling compared to the neutral chip-rosella control (fig. 4.4; Wilcoxon signed rank chip-currwong versus chip-rosella: brood calling effort $Z = -3.83$, $p < 0.0005$, duration of call suppression $Z = -3.82$, $p < 0.0005$; rosella-currawong versus chip-rosella: brood calling effort $Z = -3.66$, $p < 0.0005$, duration of call suppression Z = -3.58, $p < 0.0005$). Too few nestlings called in the 10 s after the chip-currawong (3 of 19) and rosella-currawong (3 of 19) treatments to analyze frequency and amplitude variables. In fact, the only treatment in which nestlings called regularly in the 10 s after the playback was the chip-rosella playback (18 of 19).

DISCUSSION

Nestlings were finely tuned to their acoustic world, and responded appropriately to sounds of danger nearby. Nestlings did not suppress calling simply to novel sounds, and did not suppress calling to broadband sounds as strongly as to the sounds made by an actual predator. Furthermore, nestlings did not alter their response to the cue of a predator, even when they heard a parent near the nest two seconds before. Perhaps nestlings are able to identify unambiguously the cues of a predator regardless of cue context. Alternatively, they may be unable to refine their response based on cue context, or be selected to be 'adaptively pessimistic' and respond to all likely predator cues regardless of context because the costs of missing a meal are outweighed by the costs of becoming a meal (Dawkins & Krebs 1979).

Contrary to the idea that novelty alone may be used as a signal of danger (Schaller & Emlen 1961; Curio et al. 1978), the playback of novel tonal sounds did not turn nestlings off. In fact, call frequency range increased after the playback, and there was a tendency towards an increase in brood calling effort after the treatment. This response does not seem to be a general rule of response to all tonal sounds, as nestlings ignored rosella bell calls, which are also tonal. Because the treatment included short tones strung together over a broad range of frequencies, the tonal playback may have contained some properties in common with parental food calls, which could explain this slight increase in nestling response. On the whole, however, nestlings seemed to treat the tonal playback as if it were just another harmless birdcall in the background. This result is contrary to studies on humans (Warr 1990) and other mammals (Bomford & O'Brien 1990; Darrow & Schivik 2009), which have shown novelty to be an important component of frightening stimuli. Fewer studies have explicitly examined the importance of novelty as a potential stimulus for alarm (Curio et al. 1978; Rydén 1978), although recent studies have found that prey do not react strongly to 'non-threatening' stimuli (such as a 'loud noise' in the case of wolf spiders; Lohrey et al. 2009), which are also likely to have been novel. Considering the wide variety of novel but harmless tonal sounds such as bird, insect and frog calls that nestlings are likely exposed to as they grow and their senses develop (Schaller & Emlen 1961; Khayutin 1985), the lack of a reaction or even an increased alertness after tonal sounds seems adaptive, as nestlings that treated every novel tonal sound as if it represented immediate danger could miss out on competing for food. Nestling response to novel sounds may therefore be expected to change as they grow older and fewer sounds are novel. Further work examining nestling response to novel sounds at different developmental stages would be helpful in illuminating how nestling perception of danger changes as they age.

Both the smooth and erratic broadband playbacks suppressed nestling calling in a similar manner. We expected nestlings might respond to the smooth broadband treatment relatively weakly, as smooth broadband sounds, such as the rustle of wind in vegetation, are common at the study site. Perhaps nestlings may be wary of broadband or atonal sounds in general, or the smooth broadband treatment approximated a sound made by a non-avian nest predator, such as a snake sliding through leaf litter or vegetation. Eastern brown snakes are relatively common at the study site, and anecdotal evidence suggests that they are important predators of scrubwren nestlings (personal observations). Although call suppression would be unlikely to prevent snake depredation because snakes do not hunt acoustically[1], a concomitant reduction in movement, such as crouching or huddling, might help prevent chemical and visual detection by snakes. Further work is necessary to understand what the acoustic properties of snake slithering are, and whether or not slithering is a cue of danger that nestlings recognize.

Although mean nestling reaction to the smooth and broadband treatments were indistinguishable, nestling reaction to the erratic broadband treatment was more variable. While some nestlings reacted to the erratic playback with silence, others increased calling, and nestlings in three broods begged to the sound. Perhaps the irregular sound structure of the erratic playback was similar to the rustle of vegetation that some nestlings might hear as a parent approached the nest. Since scrubwrens nest in a variety of locations, from on the ground under leaf litter to dense tangles of vines,

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[1] Note: At close range snakes can use vibrations cause by sound to locate prey. Consequently silence, along with a concomitant reduction in movement, might help reduce detection by snakes.

shrubs or grass (Higgins & Peter 2002), some nestlings might have had higher levels of exposure to 'rustling' or erratic broadband sounds caused by parents, and therefore had a lower propensity to treat such sounds as cues of danger. The variable response of nestlings to this playback highlights the difficulty that nestlings may face in detecting and appropriately responding to stimuli from predators that, unlike stereotyped communication signals from parents or conspecifics, are potentially less predictable, and may not be distinct from background sounds (Leonard et al. 2005; Warkentin 2005).

The response of scrubwren nestlings to cues of danger contrasts with that of nestling tree swallows, *Tachycinetta bicolor*, which beg to the atonal scratching sounds made by both common grackles, a potential nest predator, and to the calls plus atonal scratching sounds of parents as they land on the roof of a nest box (Leonard et al. 2005). One possibility is that the atonal components of the sounds of both of these species landing on the nest box may be acoustically similar, and therefore provide ambiguous cues to nestlings. Alternatively, cavity-nesting species may be "adaptively optimistic" because nest predation is typically less intense than for cup nesters (Martin 1995; Fontaine et al. 2007). Further work on nestling response to predator cues in both cup and cavity nesters is necessary to understand how the potentially opposing forces of nestling competition, hunger, and the risk of predation affect nestling risk assessment.[2]

Playback of the sound of a currawong walking suppressed calling more strongly than the computer-generated broadband treatments, supporting the idea that nestlings respond to cues that indicate high likelihood of immediate danger. In fact, not only did nestlings suppress calling effort after they heard the currawong playback, but in most cases they suppressed all calling for more than 10 s after the treatment, and often did not call at all until a parent arrived at the nest (personal observations). The latency to resume behaviour after exposure to a cue of danger is positively correlated with

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[2] The extent to which these results are generalizable to other species vulnerable to similar threats is unknown, but it seems probable that nestlings across a broad range of taxa, particularly those that reside in cup nests placed on or near the ground, would benefit from similar responses to predator walking sounds. Indeed, the fact that nestlings of many species are silent when approached by human observers suggests that young may be using acoustic cues to detect and respond to potential cues of danger near nests.

perceived risk in birds (Lima 1998), and so it is likely that the longer period of call suppression after the currawong-walking playback reflects nestling perception of extreme risk. While further study is required, we suspect that the difference in nestling response to the computer-generated broadband treatments and the currawong playback is due to the extremely narrow, sharp frequency peaks that correspond to leaf 'crackles' that were present in the currawong walking playback, but not in the computer-generated treatments.

Our results contribute to a growing body of evidence that young animals can independently assess risk and respond adaptively (Sih & Moore 1993; Chivers et al. 2001; Laurila et al. 2002; Relyea 2003; Warkentin 2005). Many young aquatic animals, such as salamanders and fish, are able to respond to chemical cues of predators and alter their optimal hatch date accordingly (Sih & Moore 1993; Chivers et al. 2001). Red-eyed treefrogs, *Agalychnis callidryas*, lay terrestrial eggs, and have embryos that respond to mechanical (vibrational) stimuli. Larvae hatch early in response to the vibrations of snakes attacking egg masses, but not to tropical thunderstorms, which also vibrate egg masses (Warkentin 2005). Previous work on scrubwren nestlings demonstrated that they respond to playback of the sound of a predator walking (Magrath et al. 2007), but that experiment did not reveal what acoustic attributes of the sound nestlings use as cues of danger. To the best of our knowledge, ours is the first study that has tested the specificity of nestling bird responses to acoustic cues produced by a predator, and shows that nestlings can be highly tuned to cues of danger in their environment.

Can the calls of parents modify nestlings' independent assessment of cues of danger? This study suggests that they may not. Nestlings responded with silence to the sound of a currawong walking, even when it was preceded by a parental contact call near the nest. This may be because nestlings are so finely tuned to acoustic cues from predators that they are not 'fooled' by cue context, or because there are stronger selection pressures on avoiding predation than on gaining an extra meal so that they respond with silence to any ambiguous cues (Dawkins & Krebs 1979). The role of experience may still be relevant in reinforcing behaviour or in decreasing recognition errors, at least for some species (Davies & Brooke 1988; Davies et al. 2004).[3]

The study of nestling response to acoustic cues is critical in developing a better understanding how both nestlings and fledglings avoid predation, and may help redefine what the true costs of begging may be, at least in terms of nest predation. Nestling response to acoustic cues of danger may also affect parent-offspring communication. Hesitancy to call after hearing a potential predator may select for more extreme displays by parents (Leonard et al. 2005), for example, and how nestlings perceive their acoustic environment may affect parental decision rules about when to communicate to their young about danger (Kleindorfer et al. 1996; Krama & Krams 2005; Magrath et al. 2007). Further work illuminating the aspects of acoustic cues that nestlings use to detect danger will therefore inform our understanding of the dynamics of parent-offspring communication and conflict, and will help shed light on the evolutionary forces that have shaped the behaviour and communication networks of young animals.

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[3] Removed from text: For birds such as scrubwrens that build nests whose protection relies upon crypsis (Higgins & Peter 2002), however, the costs ignoring a cue that indicates danger may be greater than unnecessarily suppressing calling when a parent arrives with food.

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Chapter 5

Learning to listen? Nestling response to heterospecific alarm calls

SUMMARY

Many nestling birds go silent in response to parental alarm calls, potentially lowering their risk of being overheard by predators. Parents are not always nearby, however, and so offspring could also benefit if they could respond to the alarm calls of other species. Response could be innate, particularly if heterospecific alarm calls are acoustically similar to conspecific alarms, or learned through experience or association with parental behaviour. We investigated the responses of both young (5-6 days old) and older (10-11 days old, close to fledging) nestling white-browed scrubwren, *Sericornis frontalis*, to the alarm calls of three heterospecifics whose nests are vulnerable to similar predators. Brown thornbills, *Acanthiza pusilla*, produce the most similar alarm calls to scrubwrens, while superb fairy-wren, *Malurus cyaneus*, and New Holland honeyeater, *Phylidonyris novaehollaniae*, produce alarm calls that are more distinct. Model predator presentations demonstrated that nestlings were likely to overhear the alarms of all three species. In support of innate response, nestlings suppressed calling after hearing both thornbill and parental alarms even when young. However, young nestlings ignored or increased calling to fairy-wren and honeyeater alarms. Older nestlings continued to suppress calling to thornbill and parental alarm calls, but also suppressed calling to honeyeater and fairy-wren alarms, a change that may be due to learning. This study thus demonstrates that nestlings can respond to the alarm calls of other species, and that these responses may be enabled through both innate mechanisms and learning.

INTRODUCTION

Information about danger is critical to survival for most animals, and many gather relevant information by eavesdropping on the alarm cues or signals of other species (Goodale et al. 2010). In terrestrial vertebrates eavesdropping on heterospecific alarm calls is widespread (Nuechterlein 1981; Hurd 1996; Shriner 1998; Zuberbühler 2000; Forsman & Monkkonen 2001; Goodale & Kotagama 2005; Magrath et al. 2007b), including examples of birds responding to mammals and mammals to birds (Hauser 1988; Rainey et al. 2004; Randler 2006; Flower 2011), and even lizards eavesdropping on birds (Vitousek et al. 2007; Ito & Mori 2010). Some species can also extract complex messages from heterospecific alarm calls, such as predator size and type, or urgency of response (Zuberbühler 2000; Templeton & Greene 2007; Fallow & Magrath 2010). Given the vulnerability of young animals to predators (Sih 1982; Lima & Dill 1990; Meri et al. 2008), there should also be strong selection pressures on offspring to respond to relevant alarm calls, but we know little about how and when individuals develop appropriate responses to other species' alarm calls.

Young animals might respond appropriately to heterospecific alarm calls without the need for prior experience or through learning, or a combination of both. Responses without the need for prior experience benefit young by enabling early response, and minimize the need to learn about predators through trial and error (Hollén & Radford 2009). Species communities vary both geographically and temporally, however, and so even response through fine-scale genetic adaptation to local species' alarm calls is probably not enough to allow response to the full range of relevant alarm calls to which an animal is exposed (Griffin 2004; Magrath & Bennett 2012). Learning could allow individuals to develop appropriate responses to novel alarm calls and to thereby fine-tune their anti-predator responses to the local environment (Lima & Dill 1990; Griffin 2004). Further, young could learn to associate social cues such as alarm calls or other parental behaviours with heterospecific alarms, thereby reducing the costs of trial and error learning (Griffin 2004; Hollén & Radford 2009). Response to alarm calls either without prior experience or through learning are not necessarily mutually exclusive, and young that are able to use both mechanisms could be the most successful at escaping predation.

Expression of unlearned responses to heterospecific calls could be either immediate or delayed. Immediate response would benefit young by allowing them to respond correctly upon first exposure to a threat, and in fact immediate response to conspecific alarm calls is widespread (reviewed in Hollén & Radford 2009; Magrath et al. 2010). Such responses to conspecific calls could facilitate similar reactions to heterospecific alarm calls that are acoustically similar (Marler 1967; McCracken & Sheldon 1997; de Kort & ten Kate 2001; Johnson et al. 2003; Rendall 2003; Russ et al. 2004; Hollén & Radford 2009; Rendall et al. 2009; Fallow et al. 2011). Yet a delayed or gradual acquisition of adult-like responses to alarm calls does not necessarily imply learning (Hollén & Radford 2009). Delayed responses could be due to physiological maturation, which can constrain how young are able to perceive and thus react to signals of danger (Espmark & Langvatn 1985; Korneeva et al. 2006; Hollén & Radford 2009; Wiedenmayer 2009). For example, many young nestlings are unable to detect high frequency sounds (Khayutin 1985; Dmitrieva & Gottlieb 1992; Brittan-Powell & Dooling 2004), which may limit their response to high-pitched alarm calls (Magrath et al. 2006; Hollén & Radford 2009). Young might also generalize learned responses to acoustically similar novel sounds (ten Cate 2000; Fallow et al. 2011). Adaptive timing of appropriate response to age-specific threats could also explain delayed responses of offspring to alarm calls (Magrath et al. 2006).

A gradual acquisition of responses to both conspecific and heterospecific alarm calls by young could also be explained by learning (Hollén & Radford 2009). Learned responses can develop gradually, particularly when repeated exposure to predators or cues indicating danger is required (Griffin 2004). Learning about heterospecific alarm calls appears to be widespread in adult birds and mammals (Hurd 1996; Shriner 1999; Ramakrishnan & Coss 2000; Forsman & Monkkonen 2001; Griffin 2004; Davies et al. 2006; Magrath et al. 2009a; Magrath & Bennett 2012), and is important in facilitating appropriate responses by young to conspecific alarm calls (Miller et al. 1990; Mateo & Holmes 1997). Learning probably also enables response by young to heterospecific alarms. For example, young vervet monkeys, *Chlorocebus pygerythrus*, gradually acquire appropriate responses to the aerial alarm calls of superb starlings, *Lamprotornis superbus*, and those on territories with higher starling abundances develop responses more quickly, suggesting that opportunities to learn play a critical role in the timing of development of response by young (Hauser 1988).

Altricial nestlings are a good system for studying how young develop appropriate responses to heterospecific alarms (Rydén 1978; Davies et al. 2004; Hollén & Radford 2009; Anderson et al. 2010). In many species vocalizing nestlings are both vulnerable to eavesdropping predators (Haskell 1994; Leech & Leonard 1997; McDonald et al. 2009; Haff & Magrath 2011) and responsive to parental alarm calls (Halupka 1998; Davies et al. 2004; Platzen & Magrath 2004; Madden et al. 2005a). However, young could also benefit from responding to the calls of heterospecifics vulnerable to similar predators, as parents are not always present to warn of danger (Roulin et al. 2000; Leonard & Horn 2001; Dor et al. 2007; Bulmer et al. 2008; Haff & Magrath 2010; Magrath et al. 2010).

Despite the potential tractability of this system, few studies have examined the response of nestlings to heterospecific alarm calls, and none have tested how nestling response changes over time. Common cuckoos, *Cuculus canorus*, are innately pre-tuned the alarm calls of reed warbler, *Acrocephalus scirpaceus*, hosts, but require exposure to respond appropriately (Madden et al. 2005b; Davies et al. 2006), while brown-headed cowbirds, *Molothrus ater*, respond innately to the alarm calls of one closely related species (Madden et al. 2005b). Similar responses outside brood parasites are generally unknown (but see Anderson et al. 2010). Cross-fostering experiments have not revealed learning about heterospecific alarm calls (Davies et al. 2004), yet if young learn through association with parental behaviour then cross-fostering may not provide appropriate learning opportunities. However, learning in general while still in the nest can occur (Kedar et al. 2000; Grodzinski et al. 2008; Raihani & Ridley 2008). For example, very young cuckoo nestlings in both Europe and Australia learn through experience to accurately mimic host species begging calls (Madden & Davies 2006; Langmore et al. 2008). These results suggest that learning to recognize the alarm calls of other species may also be possible.

We studied the response of nestling white-browed scrubwrens, *Sericornis frontalis*, to the mobbing alarm calls of three species that overlap with scrubwrens in habitat use, predator vulnerability and geographic range: superb fairy-wren, *Malurus cyaneus*, brown thornbill, *Acanthiza pusilla*, and New Holland honeyeater, *Phylidornis novaehollandiae*. Nestling scrubwrens can detect and respond to sounds near the nest, and go silent to parental mobbing alarm calls indicating nearby predators (Platzen &

Magrath 2004; Haff & Magrath 2011). Adults respond to aerial alarm calls, which are produced in response to predators in flight, of both fairy-wrens and honeyeaters (Magrath et al. 2007b, 2009b), and probably also thornbills (Fallow et al. 2011), but the response of young scrubwrens to heterospecific alarm calls of any type is unknown. We examined nestling response to heterospecific alarm calls using call playback when nestlings were several days old, and again when they were closer to fledging, in order to test if non-parasitic offspring respond to the alarms of other bird species, and if so, how those responses change over time.

METHODS

Study site and species

We conducted experiments in the Australian National Botanic Gardens in Canberra (35° 160' S, 149° 060' E) between September and December 2010. The 40 ha gardens consist of both planted (27 ha) and natural (13 ha) vegetation, and are adjacent to Black Mountain Nature Reserve, a 9 km^2 area of natural vegetation. All experiments were conducted under permits from the Environment ACT, the Australian Bird and Bat Banding Scheme, the Australian National Botanic Gardens, and the Australian National University Ethics Committee.

Scrubwrens are small (14 g), facultatively cooperative breeding songbirds that build well-concealed domed nests on or near the ground (Higgins & Peter 2002). Females lay and incubate an average of 3 eggs, and young are attended by the female, the dominant male, and up to 3 male helpers, who are often offspring from previous years (Magrath & Wittingham 1997). Nestlings fledge at about 15 days old, and are dependent upon adults for approximately 6-7 weeks (Magrath et al. 2000).

Both nestlings and adult scrubwrens use a range of calls at or near nests. Nestlings give begging calls or 'whines' when parents arrive at the nest with food (200-800 ms, with sidebands and harmonics), as well as repeat calls ('peeps') in the absence of parents (fig. 5.1; 50-150 ms, often without sidebands; Maurer et al. 2003). The rate and amplitude of both whines and peeps increase as nestlings become hungrier (Maurer et al. 2003). Adults give 'buzz' mobbing alarm calls (fig. 5.2; 120-180 ms in duration, 3-12 kHz) when predators are on the ground or perched near the nest, and vocalizing nestlings respond to these calls with silence (Platzen & Magrath 2004, 2005; Haff &

Magrath 2011). Adults also use a variable set of provisioning calls (5-665 ms in duration, 4.6-6.6 kHz) when arriving at the nest with food (Platzen 2004).

We found nests primarily in the building and incubation period, and monitored nests daily. In order to reduce our impact on predation rates we used green garden mesh to build predator exclosures around nests. Exclosures kept out mid-sized predators, but allowed adults free access to and from nests. Adults generally resumed normal behaviour soon after the exclosures were in place.

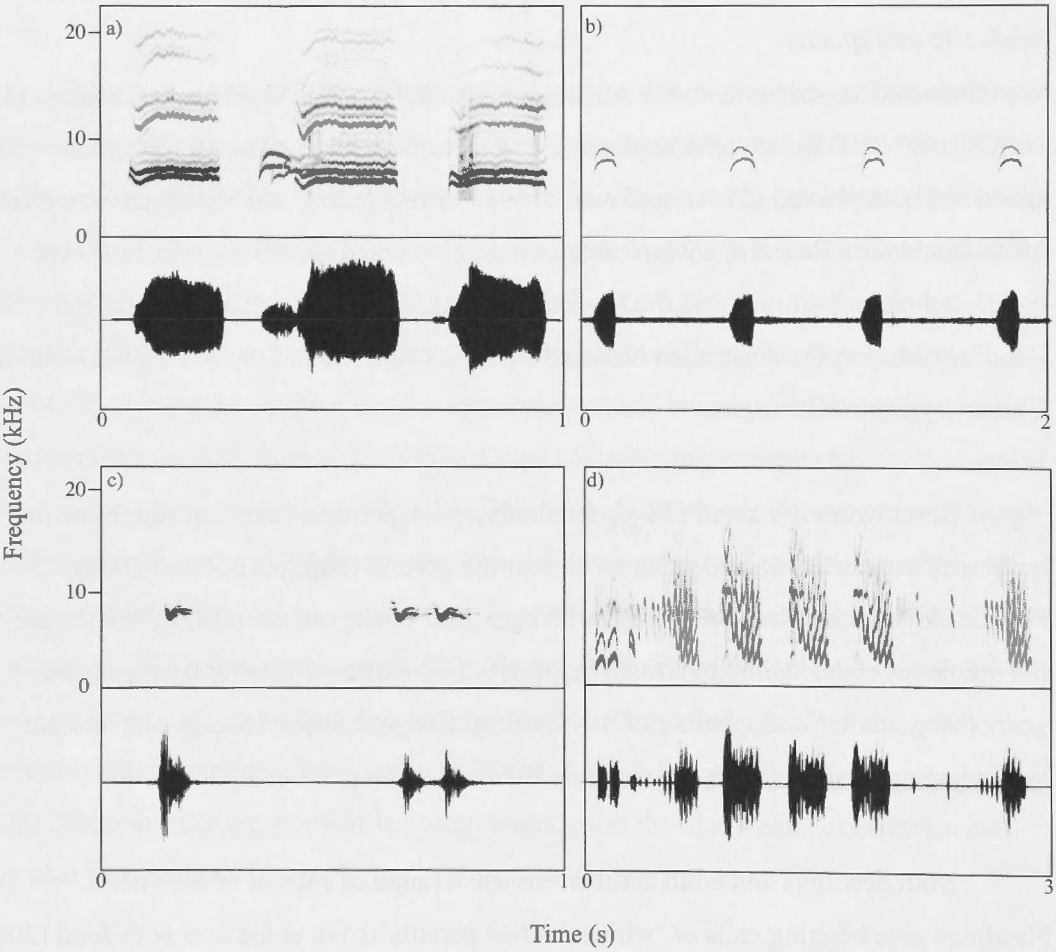

Figure 5.1: Vocalizations given by scrubwren nestlings and adults: a) nestling whines; b) nestling peeps; c) adult chip calls; d) adult provisioning calls. Upper panels show spectrograms, lower panels waveforms, both created in Raven 1.3 using settings described in the text.

The pied currawong, *Strepera graculina*, is a major predator of scrubwrens and other small songbirds in the Gardens and throughout southeastern Australia (Major et al. 1996; Wood 1998). Currawongs are large (300 g), omnivorous songbirds that hunt by sight and sound, and that can use nestling calling to locate nests (Haff & Magrath 2011). In fact, nestling scrubwrens treat the sound of a currawong walking in leaf litter as a cue of danger, and cease calling in response to its playback (Magrath et al. 2007a; Haff & Magrath 2010). In the Gardens, and probably throughout southeastern Australia, brown thornbills, superb fairy-wrens, and New Holland honeyeaters also suffer high rates of nest predation due to currawongs (Prawiradilaga 1996; Higgins et al. 2001; Higgins & Peter 2002); B. Igic, personal communication). All three of these species nest in similar habitats, often have overlapping territories with scrubwrens, give mobbing alarm calls in response to currawongs and other predators near nests, and join scrubwrens in mobbing predators (this study).

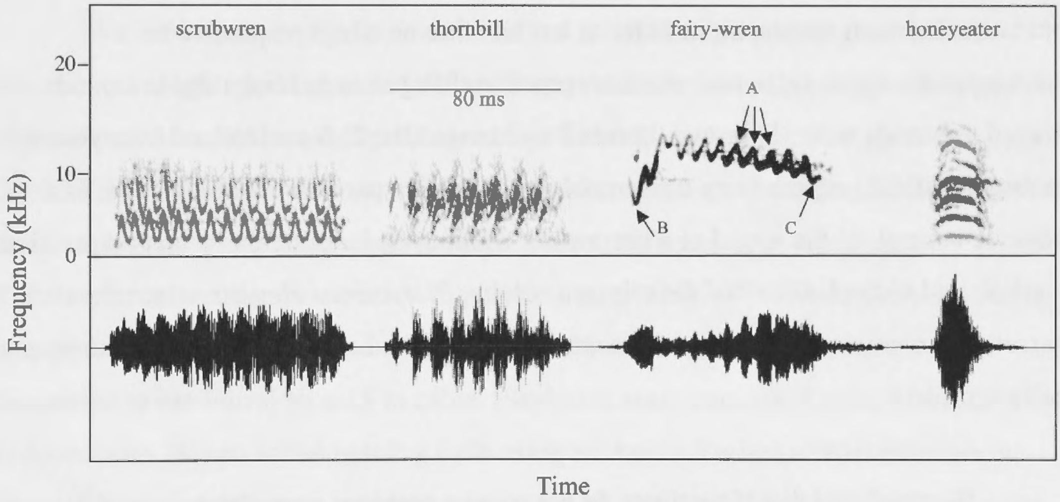

Figure 5.2: Examples of mobbing alarm calls used in playbacks: white-browed scrubwren, brown thornbill, superb fairy-wren and New Holland honeyeater. A indicates frequency cycles, used to calculate frequency modulation rate; B and C indicate low frequency points used in frequency change measurements; same methods used for measurement of all calls; see Methods for more detail. Upper panels show spectrograms, lower panels waveforms, created in Raven 1.3 using settings described in text.

Scrubwrens, thornbills, honeyeaters and fairy-wrens are all members of the Meliphagoidea superfamily (Gardner et al. 2010), but their mobbing calls vary widely. The genera *Acanthiza* (thornbills) and *Sericornis* (scrubwrens) are sister taxa (family Acanthizidae). Like scrubwren alarms, thornbill mobbing calls are broadband and of moderate duration (fig. 5.2; 60-120 ms, 1-12 kHz). Honeyeaters are in the Meliphagidae, sister to the Acanthizidae. Their mobbing alarms are broadband but short (fig 5.2; 30-40 ms, 0.6-13 kHz). Fairy-wrens are in the Maluridae, which is sister to all other groups within the Meliphagoidea. Their mobbing alarms sweep up in frequency before sweeping back down, have a narrow frequency range compared to the other species tested here, and are of moderate duration (fig 5.2; 85-115 ms, 3.4-11.6 kHz).

Experiment 1: playback design and predictions

We presented six different playbacks to nestlings at 24 nests when nestlings were five to six days old and again five days later (10-11 days old; four nests were lost due to predation between test days), in order to test whether nestlings responded to heterospecific alarm calls, and whether response changed as nestlings aged. Sounds played to broods were: 1) brown thornbill mobbing calls; 2) New Holland honeyeater mobbing calls; 3) superb fairy-wren mobbing calls; 4) a parent's mobbing calls, as a positive control; 5) the sound of a currawong walking on leaf litter, as a second positive control; and 6) the bell call of the crimson rosella, *Platycercus elegans*, a harmless parrot, as a neutral control. Playbacks were 10 s long, and each brood received unique call exemplars.

We predicted that if nestlings do not require previous exposure to respond appropriately to other species' alarm calls, young should go silent to heterospecific alarm playbacks upon first exposure. If call structure enables response through similarity to conspecific calls, we predicted that nestlings at both ages should go silent in response to thornbill alarms, which are most similar to scrubwren alarms, but not honeyeater or fairy-wren playbacks, neither of which are similar to scrubwren alarms. Delayed response to heterospecific alarms would suggest either sensory development or learning. If learning or expression of response not requiring experience does not occur until after young have left the nest, nestlings should not go silent in response to any heterospecific alarm calls.

Recording and playback construction methods

We recorded playback sounds in Canberra using a hand-held Sennheiser ME66 or ME67 directional microphone connected to a Marantz PDM670 solid-state digital recorder, sampling wave files at 44.1 kHz. We examined sonograms in Raven Pro 1.3 (Charif et al. 1995), and selected segments of calls with clean recordings for playback. We constructed honeyeater and scrubwren playbacks so there were six call elements per second, which is within natural rates for these species (personal observations). Thornbills and fairy-wrens tend to call at a slightly lower rate, and we therefore constructed those playbacks so there were 5 calls per second. Ten seconds of continuous rosella calling or currawong walking is atypical, and we therefore created those playbacks so that they consisted of 3 s of sound, followed by a brief silence, followed by 1s of sound, and a brief pause followed by 3 s of sound, so that the entire 10s playback period was spanned. We filtered scrubwren, thornbill, and fairy-wren calls below 1 kHz, and honeyeater, rosella, and currawong sounds below 0.5 kHz.

We broadcast playbacks from an Edirol R-09HR solid state digital recorder-player at an amplitude of about 65 dB at 20 cm, which is towards the upper range of the natural limit of scrubwren buzz call alarms as heard from the nest (Platzen & Magrath 2005; T.M. Haff personal observations). We maintained a constant amplitude across treatments to ensure that nestling reactions were to differences in the sounds themselves, rather than to variation in playback amplitude. We broadcast sounds using a Sony MDR-A106 headphone speaker placed 20 cm from the nest entrance and connected to the Edirol by a 15 m cable. Playbacks were controlled from a hide 10-15 m from nests. We recorded nestling calls using an Audio-Technica lapel microphone placed 12 cm from the nest entrance, connected by a 15 m cable to a Marantz recorder. We placed dummy equipment at nests the day before experiments in order to habituate adults to its presence.

We started experiments once adults resumed normal feeding behaviour at nests. Treatment order was randomized, and separated by at least 5 minutes or by a feeding visit by an adult. We waited to perform playbacks until nestlings were peeping regularly, adults were at least 15 m from the nest and not vocalizing, and there were no other loud or abrupt noises nearby. We discarded recordings if a parent called or returned to the nest during a treatment, and repeated the playback at the end of the experiment.

Call analysis

We measured time intervals and nestling calls in Raven Pro 1.3, with the sonogram settings: Blackman filter at 582 samples, and 3 dB filter bandwidth, 2.27 ms grid time, 21.5 Hz frequency grid, and a window scaling of 12 kHz and 1s per screen (Magrath et al. 2007a). We calculated true call amplitude using sound files of known amplitude. We used the brood as the level of analysis, as we could not tell individuals apart, and measured 6,614 nestling calls.

For each playback, we measured the: 1) number of calls in the 10 s before and after each playback, a measure that allowed us to conduct paired analyses and that controlled for differences in call rates between broods; and 2) latency to the first call after the end of each playback (s), up to 120 s after the end of a playback. If no nestling called in the 2 min after the playback we scored latency as 120 s. These variables can be used as a measure of response even when nestlings suppress calling after a playback. We also measured 3) whether or not broods gave begging (whine) calls after hearing playbacks, measured as any call ≥ 200 ms duration (above), in order to quantify whether nestlings mistakenly begged in response to playbacks.

We measured three adult mobbing alarm calls for 10 individuals of each species in order to quantify similarities between scrubwren and heterospecific calls. Specifically, for each call we measured low frequency (Hz), peak frequency (Hz), call duration (ms), and frequency modulation rate, measured as the number of frequency cycles in each call per second (fig. 5.2). We chose these measurements as they have high repeatability and are robust to variation in recording environment (Fallow et al. 2011). We also measured call frequency change, calculated as the difference in low frequency (Hz) at the end of each call minus the low frequency at the start of each call (fig. 5.2). We then used a Principal Component Analysis and extracted the first two dimensions for analysis. Aspects of call frequency contributed primarily to the first component extracted ('call frequency': eigenvalue 2.72, extraction 0.95 for low frequency, 0.82 for frequency change, and 0.60 for peak frequency), while call duration and frequency modulation contributed to the second dimension extracted ('call structure': eigenvalue 1.88, extraction 0.82 for duration and 0.72 for modulation). Together, these components accounted for 92.0% of the variance in call measurements.

Experiment 2: model presentation

We presented model predators at 21 nests between the younger and older nestling stages of experiment 1 as an assay of the presence and responsiveness of heterospecifics near individual nests. This also allowed us to test whether heterospecific calling during model presentation resulted in changes in the behaviour of older nestlings. When nestlings were 7-9 days old and parents were away, we placed a model currawong on the ground 0.5 m from and facing towards nests, and recorded both parental and heterospecific vocal response for 5 min once any heterospecific individual approached within 5 m of the nest, or when parents returned to within 5 m of the nest, whichever came first. To measure heterospecific response we recorded: 1) what species approached to within 5 m and visually inspected the model; and 2) whether or not individuals that approached nests also gave mobbing alarm calls. We measured heterospecific response through visual observations, and by recording calls using a Sennheiser ME62 omnidirectional microphone placed next to the model, and connected by a 15 m cable to a Marantz recorder. Mobbing responses by heterospecifics can be temporally patchy, depending on which species or individuals are nearby when a mobbing event begins, and so we attempted to gather a broader picture of what species were likely to join mobbing choruses by repeating model exposure three times at each nest in a single day, with at least one hour between presentations. A species was counted as present if it approached during at least one of the three model presentations per nest.

Statistical analysis

We examined scrubwren, thornbill, honeyeater and fairy-wren mobbing alarm calls by plotting call components extracted from principal component analysis (above) on a canonical variates plot and by comparing squared Mahalanobis intra-centroid distances, both generated using linear discriminant function analysis. We tested for similarities between mobbing alarm calls using one-way ANOVAs of PCA components. To compare nestling responses to playbacks in experiment 1 we analyzed 1) the difference in the number of calls given in the 10 s after the playback to calling in the 10 s prior to the playback as well 2) as log-transformed call latency (ms), both using generalized linear mixed models (GLMM) with a normal distribution and identity link function. Variables used in the model were playback type (thornbill, fairy-wren, honeyeater, scrubwren, currawong and rosella), nestling age (5 or 10 days old) and the interaction between playback type and nestling age as fixed terms, with nest identity as a random term. GLMMs allow for unbalanced designs, and so we included all 24 nests in the analysis even though data for four nests were unpaired. We measured call suppression to heterospecific alarm call playbacks by comparing values to the neutral control using pairwise comparisons generated from GLMMs. We tested for differences in the number of whine calls between playback treatments and between nestling ages using McNemar and Cochran tests with pairwise comparisons for nonparametric data. All p-values reported for pairwise comparisons are adjusted for multiple comparisons using Bonferroni corrections. For experiment 2 we used chi-square contingency tests to check for differences in the likelihood of thornbills, fairy-wren and honeyeaters mobbing at scrubwren nests, and Mann-Whitney tests to examine whether nestlings the behaviour of older nestlings was affected by exposure to heterospecific mobbing calls during model predator presentations. We used two-tailed statistics and an alpha level of 0.05 for all tests, and conducted statistics in SPSS 19.0.

RESULTS

Call structure

Although scrubwren mobbing alarm calls were statistically distinguishable from all heterospecific mobbing calls, they were most similar to brown thornbill calls (table 5.1, fig. 5.2 & 5.3). Scrubwren calls occasionally overlapped in acoustic properties with thornbill calls (fig. 5.3), but not with those of honeyeaters or fairy-wrens, and intra-centroid distances were shorter between thornbill and scrubwren calls (squared Mahalanobis distance 12.79 ± 5.73 s.d.) than between any other groups (honeyeater to thornbill 26.14 ± 4.07; fairy-wren to scrubwren 84.39 ± 16.78). Nonetheless, mean scrubwren calls differed significantly from means of all other species in features of both call frequency (table 5.1; one-way ANOVA, PCA component 1: $F_3 = 320.87$, $p < 0.0001$; Tukey test: scrubwren vs. thornbill $p < 0.0001$; scrubwren vs. honeyeater $p < 0.0001$; scrubwren vs. fairy-wren $p < 0.0001$) and call structure (table 5.1, fig. 5.3; one-way ANOVA, PCA component 2: $F_3 = 64.65$, $p < 0.0001$; Tukey test: scrubwren vs. thornbill $p < 0.0001$; scrubwren vs. honeyeater $p < 0.0001$; scrubwren vs. fairy-wren $p < 0.0001$).

Table 5.1: Mobbing alarm call features (means ± s.e.). N = 10 individuals per species, 3 calls per individual.

Species		Low frequency (Hz)	Peak frequency (Hz)	Frequency change (Hz)	Duration (ms)	Modulation (# of frequency cycles/s)
Scrubwren	Mean	2238.60	5329.46	70.23	160	90
	SD	121.34	297.90	32.92	9	8
Thornbill	Mean	1533.06	6050.83	118.23	120	70
	SD	78.57	172.14	62.56	6	5
Honeyeater	Mean	1046.05	5677.53	-30.50	50	0
	SD	26.95	243.40	31.55	2	0
Fairy-wren	Mean	3955.32	7479.20	2524.93	110	90
	SD	73.96	161.90	109.76	4	10

Experiment 1

Nestlings' response to playbacks depended on their age, particularly for heterospecific sounds of danger that were acoustically distinct from their own species' alarms (fig. 5.4; GLMM: effect = playback x nestling age; difference in number of calls, $F_{20,5} = 4.47$, $p = 0.001$; latency, $F_{20,5} = 5.26$, $p < 0.0001$). Offspring became much more likely to suppress calling after hearing honeyeater and fairy-wren playbacks when they were older (fig. 5.4a). Young nestlings ignored honeyeater alarm calls, and actually increased calling in response to playback to fairy-wren alarms (table 5.2, fig. 5.4a). By contrast, older nestlings strongly suppressed calling in response to honeyeater playbacks, and took longer to resume calling after hearing fairy-wren alarms, compared to rosella bell calls (table 5.2, fig. 5.4). Offspring at both ages strongly suppressed calling to thornbill alarm playbacks, as well as to the positive controls of parental mobbing and the sound of a predator walking, and ignored rosella bell calls, the neutral control (table 5.2, fig. 5.4). Although offspring always suppressed calling in response to both thornbill and scrubwren alarms, these responses strengthened slightly between ages (table 5.2, fig.

5.4a). By contrast, nestling response to the sounds of a predator walking strengthened considerably with age (table 5.2, fig. 5.4).

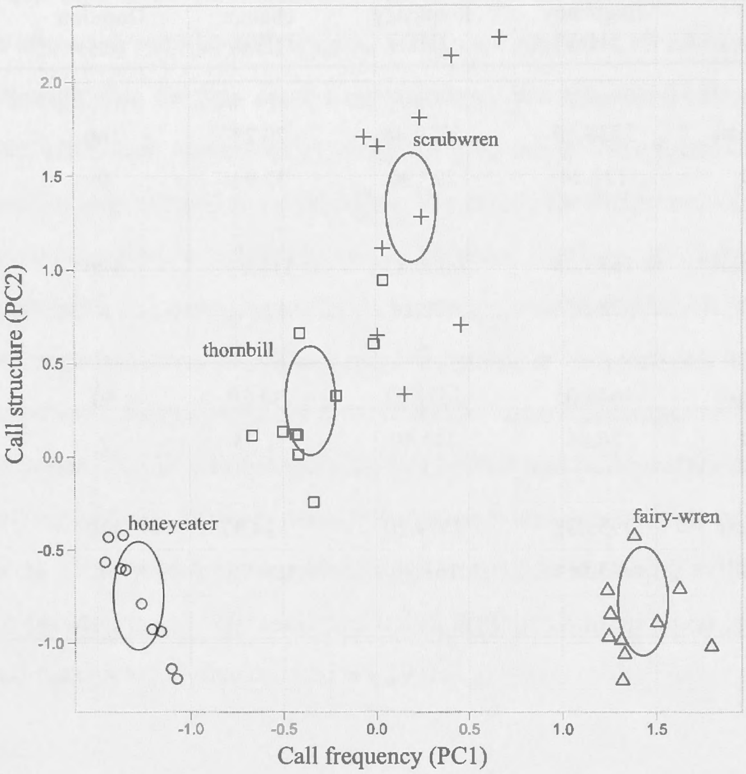

Figure 5.3: Plot of the first two principal components in an analysis of measurements of honeyeater (circles), fairy-wren (triangles), thornbill (squares) and scrubwren (crosses) mobbing alarm calls. Circles represent 95% confidence intervals for means.

The change in nestling response with age specifically to honeyeater and fairy-wren playbacks can be partly explained by a reduction in mistaken begging (fig. 5.4a). Young nestlings begged significantly more often to fairy-wren and honeyeater playbacks than any other playbacks (table 5.3; Cochran test comparing mistaken begging by younger broods: $T_5 = 27.12$, $p < 0.0001$; McNemar: scrubwren vs. honeyeater $\chi^2 = 3.11$, $p = 0.028$; scrubwren vs. fairy-wren $\chi^2 = 4.28$, $p < 0.0001$; scrubwren vs. thornbill $\chi^2 = -0.39$, $p = 1.0$; scrubwren vs. currawong $\chi^2 = 1.56$, $p = 1.0$, rosella $\chi^2 = 1.17$, $p = 1.0$). In contrast to young nestlings, older nestlings made few mistakes, and only ever mistakenly begged to fairy-wren alarms (table 5.3; Cochran test comparing mistaken begging among treatments by older broods: $T_5 = 16.74$, $p = 0.005$).

Table 5.2: Pairwise contrasts from GLMMs comparing nestling response to playbacks alarm calls (and the sound of a predator walking) to the neutral control, contact calls of the crimson rosella, for both young (5-6 days old) and older (10-11 days old) nestlings in experiment 1 for: the difference in the number of nestling calls in the 10 s before minus 10 s after playback; and call latency, measured as the length of time nestlings took to resume calling after playbacks. All p values are adjusted for multiple comparisons using least significant differences. See figure 5.4 for data.

		Difference in number of calls		Call latency	
Nestling age	Playback type	Response	p	Response	p
Young	Honeyeater	Unchanged	0.49	Unchanged	0.14
	Fairy-wren	Increase calling	<0.0001	Unchanged	0.25
	Thornbill	Decrease calling	<0.0001	Longer latency	<0.0001
	Scrubwren	Decrease calling	<0.0001	Longer latency	<0.0001
	Currawong	Decrease calling	0.002	Longer latency	<0.0001
Older	Honeyeater	Decrease calling	0.007	Longer latency	<0.0001
	Fairy-wren	Unchanged	0.82	Longer latency	0.001
	Thornbill	Decrease calling	<0.0001	Longer latency	<0.0001
	Scrubwren	Decrease calling	<0.0001	Longer latency	<0.0001
	Currawong	Decrease calling	0.002	Longer latency	<0.0001

Experiment 2

Nestlings were exposed to the mobbing calls of other species during model predator presentations, suggesting young had the opportunity to learn about heterospecific alarm calls. Heterospecifics approached models at 18 out of 20 nests, and a thornbill, honeyeater or fairy-wren gave mobbing alarm calls at 14 of these nests (table 5.4). There was no significant difference in the proportion of nests mobbed by the three target species ($\chi^2_2 = 2.96$, $p = 0.23$). We found no association between the change in nestling response across ages and whether or not a thornbill, honeyeater or fairy-wren mobbed near the nest during model predator presentations for either nestling calling (table 5.5).

Table 5.3: Number of nests in which offspring gave begging calls in response to playbacks. Total broods = the total number of broods in sample.

	Nestling age	
Playback type	Young (5-6 days old)	Older (10-11 days old)
Honeyeater	8	0
Fairy-wren	11	4
Thornbill	1	0
Scrubwren	0	0
Currawong	4	0
Rosella	3	0
Total broods	24	20

DISCUSSION

This study demonstrates that nestlings can respond to heterospecific alarm calls, and suggests that different mechanisms may be responsible for the timing of response to different species' alarm calls. Despite being statistically distinguishable, thornbill alarms overlapped in acoustic features with parental alarm calls, and nestlings suppressed calling to the two playbacks similarly (table 5.2, fig.5. 4). By contrast, honeyeater and fairy-wren calls alarms were acoustically distinct from scrubwren alarms, and nestling response to these alarms was also dissimilar to their response to parental alarm calls. While young nestlings ignored or even begged in response to honeyeater and fairy-wren playbacks, older nestlings generally decreased calling (fig. 5.4). Results from model predator presentations demonstrated that young had the opportunity to eavesdrop upon and potentially learn about heterospecific alarm calls while in the nest. Together, these results suggest that both response without need for prior exposure and learning help nestlings respond appropriately to heterospecific alarm calls, and demonstrate that nestlings can respond appropriately to a variety of heterospecific alarms. To our knowledge, this is also the first study to demonstrate that response to mobbing alarm calls can change rapidly as young birds age.

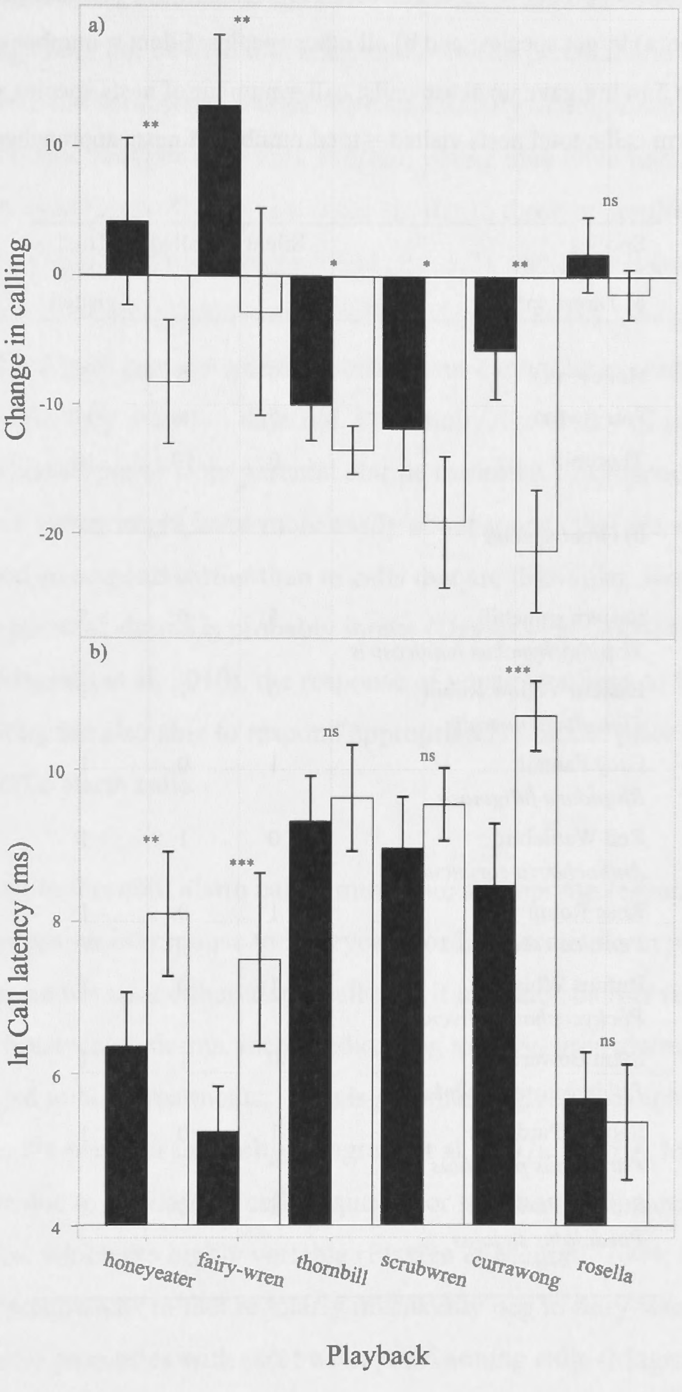

Figure 5.4: Nestling response to playbacks (mean ± 95% C.I.): a) change in calling, the difference in the number of nestling calls in the 10 s before minus the 10 s after playback, where values > 0 represent an increase in calling, and < 0 a decrease in calling; and b) call latency, the time nestlings took to resume calling after playback (ms, log transformed), where longer times represent a stronger negative response. Black bars represent young nestlings (5-6 days old), and white bars older nestlings (10-11 days old); ns = not significant, * 0.05 ≥ p ≤ 0.03, ** 0.03 ≥ p ≤ 0.002, and *** p ≤ 0.0001 based on pairwise comparisons from GLMMs.

Table 5.4: Species that approached nests at least once during model predator presentations (experiment 2), for: a) target species; and b) all other species. Silent = number of nests species approached within 5 m but gave no alarm calls; call = number of nests species approached and gave mobbing alarm calls; total nests visited = total number of nests approached. N = 20 nests.

Species a) Target species	Silent	Called	Total nests visited
Honeyeater	0	5	5
Fairy-wren	5	6	11
Thornbill	0	10	10
b) Other species			
Eastern spinebill *Acanthorhynchus tenuirostris*	5	0	5
Eastern Yellow Robin *Eopsaltria australis*	0	1	1
Grey Fantail *Rhipidura fuliginosa*	1	0	1
Red Wattlebird *Anthochaera carunculata*	0	1	1
Rose Robin *Petroica rosea*	1	0	1
Rufous Whistler *Pachycephala rufiventris*	1	0	1
Satin Bowerbird *Ptilonorhynchus violaceus*	0	1	1
Spotted Pardalote *Pardalotus punctatus*	1	0	1
Striated Pardalote *Pardalotus striatus*	1	0	1

Nestling response to thornbill playbacks suggests that young may not require previous exposure to respond appropriately to these heterospecific alarm calls. As with response to parental alarm playbacks, broods at both ages strongly suppressed calling in response to playback of thornbill alarms. Response to conspecific alarm calls is probably innate (Herzog & Hopf 1984; Davies et al. 2004; Platzen & Magrath 2004, 2005), and this innate response could have been generalized to thornbill alarms as well (de Kort & ten Kate 2001; Johnson et al. 2003; Madden et al. 2005b; Fallow et al. 2011), or nestlings may not be able to distinguish between parental and thornbill alarms. Although thornbill and scrubwren alarms were statistically distinguishable, they overlapped in acoustic features (fig. 5.3). Further, young may have focused on a subset of acoustic features in thornbill calls that were similar to those of scrubwrens. For example, alarms of both species are broadband (fig. 5.2), an acoustic cue that tends to suppresses calling in nestling scrubwrens (Haff & Magrath 2010). The potential for early learning about both parental and thornbill alarms cannot be excluded, as nestlings were not tested until they were 5-6 days old. Potentially, the ability of young to generalize a learned response from parental alarms to similar heterospecific calls may occur early on, or young might learn more easily about sounds that are similar to parental calls, and so respond earlier than to calls that are dissimilar. However, given that response to parental alarms is probably innate (Davies et al. 2004; Hollén & Radford 2009; Magrath et al. 2010), the response of young nestlings to thornbill alarms suggests that young are also able to respond appropriately without prior exposure to some heterospecific alarm calls.

In contrast to thornbill alarm calls, immediate appropriate response cannot explain call suppression in response to honeyeater or fairy-wren alarm playbacks. Young nestlings did not treat either alarm call as if it indicated danger (fig. 5.4), and instead ignored honeyeater alarms, increased calling to fairy-wren alarms, and even mistakenly begged to both treatments. This is surprising, given the high potential costs of such mistakes if a predator is nearby (Magrath et al. 2007a; Haff & Magrath 2011). Mistakes may be due to overlaps in call frequency or structure with parental provisioning calls, which are highly variable (Platzen & Magrath 2004; Magrath et al. 2007a). Young scrubwrens in fact regularly mistakenly beg to fairy-wren song, a sound that shares acoustic properties with scrubwren provisioning calls (Magrath et al. 2007a). In contrast to the response of young offspring, older nestlings strongly suppressed calling in response to honeyeater alarm calls, and did so weakly to fairy-wren alarms, suggesting that older offspring had begun to perceive these sounds as cues of danger (fig. 5.4).

Table 5.5: Differences in older nestling response to playbacks between nests that were exposed to focal heterospecific alarm calling during model predator presentations and nests that were not. Change in call rate represents the difference in the number of calls in the 10 s after playback minus the 10 s before playback, were more negative numbers represent stronger call suppression. Call latency represents the number of seconds nestlings took to resume calling after playback, where higher numbers represent stronger call suppression. Statistics are from Mann-Whitney U tests.

Response measure	Playback type	Heterospecific called mean ± s.d.	Heterospecific did not call mean ± s.d.	Statistics	
				U	p
Change in call rate	Honeyeater	-11.40 ± 2.56 N = 5	-13.73 ± 4.21 N = 15	0.61	0.55
	Fairy-wren	-27.5 ± 12.08 N = 6	-14.21 ± 5.57 N = 14	-0.19	0.40
	Thornbill	-2.5 ± 3.52 N = 10	-4.2 ± 1.16 N = 10	1.41	0.17
Call latency (s)	Honeyeater	6.92 ± 4.18 N = 5	14.75 ± 8.57 N = 15	-0.22	0.87
	Fairy-wren	20.40 ± 10.22 N = 6	13.60 ± 6.71 N = 14	0.17	0.90
	Thornbill	24.0 ± 16.57 N = 10	11.89 ± 11.61 N = 10	0.15	0.88

Compared to when they were young, older nestlings suppressed calling more strongly to all playbacks except the neutral control. Potentially, a change with age could be due to sensory constraints that prevent appropriate response in very young offspring. For example, young nestlings may simply have been unable to detect playbacks containing high-pitched sounds (Khayutin 1985; Dmitrieva & Gottlieb 1992; Clemmons 1995; Brittan-Powell & Dooling 2004). This was not the case here, however. Not only are the low frequencies of honeyeater and fairy-wren mobbing alarm calls within the range of hearing described for young passerines (0.1-5 kHz for 4-7 day old young; Khayutin 1985), but honeyeater alarms are actually lower in frequency than both thornbill and scrubwren alarms, and well within the hearing range described for young birds. Indeed, young nestlings often mistakenly begged to both honeyeater and fairy-wren treatments, demonstrating that they were able to detect these calls. Although it is possible that poor hearing could have reduced the abilities of young nestlings to discriminate between sounds, leading to inappropriate responses early on, older nestlings also suppressed calling more strongly to playbacks to which they responded appropriately early on, such as the sounds of a predator walking and parental alarm calls. This pattern suggests that improvement in call discrimination alone does not explain the change in nestling response to playbacks with age. Likewise, a generalized increase in caution as nestlings age in response to sounds near the nest does not adequately explain the patterns found here, as older offspring did not change their response to crimson rosella bell calls, the neutral control.

Learning, potentially through association with concomitant parental alarm calls and other acoustic cues of danger, could potentially explain the pattern of strengthened call suppression with age. The pattern found here of strengthened response with age to playbacks of parental alarms and the sound of a predator walking is consistent with previous findings that even innate response to conspecific alarm calls are strengthened through learning (Davies et al. 2004; Madden et al. 2005b). Indeed, the increased nestling response to playbacks of the sound of a predator walking strongly suggests learning. Initial response to these playbacks might be innate (Haff & Magrath 2010), yet call suppression strengthened considerably with age. Although how often nestlings were exposed to predators on foot approaching nests is unknown, all broods were exposed to walking sounds when observers approached nest during experiment set-up and take-down, and these may be acoustically similar to currawong walking sounds. Human approach was also sometimes accompanied with parental mobbing (T.M. Haff 2010, personal observations), and these secondary associations, as well as the primary association of acoustic cues with a potential predator at the nest, could have presented opportunities for nestlings to associate the sound of footsteps with danger. Although we do not know how often young had the opportunity to associate heterospecific mobbing with parental behaviour (below), learning could have affected their change in response to playbacks over time. Indeed, the pattern of gradual acquisition of appropriate response by nestlings to honeyeater and fairy-wren alarm calls fits well with previous studies of offspring response to both conspecific and heterospecific alarms. Such experiments have demonstrated that young slowly acquire appropriate responses to alarm calls, but that those responses develop more quickly the more exposure young have to opportunities for social learning (reviewed in Hollén & Radford 2009).

All three heterospecifics whose calls were tested in this study joined mobbing choruses near scrubwren nests, demonstrating that nestlings have the opportunity to learn about other species' calls. Although we were unable to detect an influence of heterospecific mobbing during model presentations on the behaviour of older nestlings, these trials may not have been sufficient to capture the effects of heterospecific mobbing on nestling response, particularly if natural mobbing events near nests were spatially and temporally variable. Furthermore, differences in such potential learning events could have affected the response of older nestlings to playbacks. For example, fairy-wrens tend to alarm call to a wider variety of potential aerial threats than scrubwrens or honeyeaters (Magrath et al. 2009a). If the same holds true for mobbing alarm calls then it could be difficult for nestlings to associate fairy-wren mobbing alarms with parental alarm calls or any other cue of danger. Future experiments using playbacks combined with parental mobbing are needed to understand whether nestlings use social cues to learn about sounds that indicate danger.

Overall, we demonstrate that very young animals can respond appropriately to a variety of heterospecific alarm calls while still in the nest, and that these responses can develop within the nest. This study thus reinforces the idea that young are not simply passive victims of predation, but instead have a variety of mechanisms that can help reduce predation risk (Haff & Magrath 2010; Magrath et al. 2010). Our results also suggest that learning about cues of danger by young could be an insightful avenue of future research. Future studies will be important in elucidating the extent to which young animals can respond to heterospecific alarm calls, and defining exactly how such responses are enabled.

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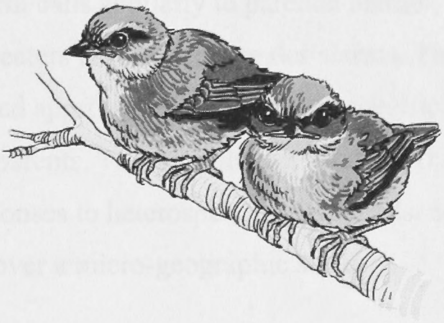
CHAPTER 6

Fearful neighbours: fledglings learn to respond to heterospecific alarm calls



SUMMARY

Young birds and mammals suffer from a high risk of predation, and should be under strong selection for early response to cues indicating danger, including the alarm calls of other species. Despite this prediction, there has been little investigation of the development of response by young animals to heterospecific alarm calls, and none on fledgling songbirds. We examined the responses of fledgling white-browed scrubwren, *Sericornis frontalis*, at three ages to playback of the aerial alarm calls of sympatric superb fairy-wren, *Malurus cyaneus*, and New Holland honeyeater, *Phylidonyris novaehollaniae*. Fairy-wren and scrubwren alarms are acoustically similar, while honeyeater alarms are distinct; adult scrubwrens respond to both. Recently fledged young responded strongly to scrubwren alarms, but quite weakly to heterospecific alarms. Only two weeks after leaving the nest, however, most fledglings treated fairy-wren and honeyeater alarm calls similarly to parental alarms. However, fledglings in territories without honeyeaters ignored honeyeater alarms. Three weeks later, fledglings on all territories responded appropriately to all heterospecific alarms, an identical response to that of their parents. These results demonstrate that fledglings quickly develop appropriate responses to heterospecific alarm calls, and present strong evidence that response is learned over a micro-geographic scale.

INTRODUCTION

The alarm calls of other species contain detailed information about predators, and eavesdropping on these calls is widespread among vertebrates, especially in birds and mammals (Caro 2005; Goodale et al. 2010). Some birds even eavesdrop upon mammals (Rainey et al. 2004; Flower 2011), and mammals upon birds (Hauser 1988; Randler 2006; Müller & Manser 2008). This understanding may be mutual (Nuechterlein 1981; Hurd 1996; Shriner 1998; Zuberbühler 2000b; Forsman & Monkkonen 2001; Goodale & Kotagama 2005; Magrath et al. 2007b), or it can be unidirectional, such as when non-vocal lizards eavesdrop on the alarm calls of birds (Vitousek et al. 2007; Ito & Mori 2010). Eavesdroppers can gather information not just on the presence or absence of predators, but also on the type of predator nearby, as well as the degree of danger (Zuberbühler 2000b; Templeton & Greene 2007; Fallow & Magrath 2010).

Young animals are likely to benefit from responding to heterospecific alarm calls, yet most work has been done on adults. Indeed, young are often poor at identifying threats and are more vulnerable to predation than adults (Seyfarth & Cheney 1980; Sih 1982; Lima & Dill 1990; Mateo 1996; Clutton-Brock et al. 1999; Kullberg & Lind 2002; Meri et al. 2008), and so there are probably strong selective pressures for offspring to respond to heterospecific alarm calls at an early age. Despite the widespread nature of heterospecific eavesdropping, however, we know almost nothing about when or how young animals develop appropriate responses to other species' alarm calls (Hollén & Radford 2009).

Evidence from adult animals suggests that response to heterospecific alarm calls can either occur without prior exposure, or be learned. For example, structural similarity in alarm calls can facilitate response without prior exposure, particularly in closely related species (Johnson et al. 2003; Russ et al. 2004; Fallow et al. 2011). Innate or generalized responses could enable appropriate response early on, and thus increase the survivorship of even very young animals (Lind & Cresswell 2005). However, animal communities can vary over small distances or short periods of time, potentially limiting the value of response without prior exposure (Lima & Dill 1990; Griffin 2004; Hollén & Radford 2009; Magrath & Bennett 2012). Indeed, response to heterospecific alarm calls can vary depending on whether or not populations of alarm callers and eavesdroppers are sympatric, suggesting that learning is important in the development of appropriate response. For example, adult bonnet macaques, *Macaca radiata*, only respond to the alarm calls of heterospecifics where their populations frequently overlap (Ramakrishnan & Coss 2000), and superb fairy-wrens, *Malurus cyaneus*, only respond to the aerial alarm calls of white-browed scrubwrens, *Sericornis frontalis*, within species sympatry (Magrath et al. 2009b). Learning is also the most logical explanation for differences in response to heterospecific alarm calls observed over very small spatial scales; within single populations of superb fairy-wren, anti-predator responses to the alarm calls of noisy miners, *Manorina melanocephala*, mirror micro-geographic structure in species overlap (Magrath & Bennett 2012). Thus, learning appears to be important in enabling appropriate response to other species alarm calls, and may even result in territory-specific responses.

Young animals typically have both less experience with predators and less exposure to heterospecific alarm calls than adults, and are thus particularly useful for the study of whether responses to other species alarm calls are likely to be innate or learned. If responses do not require prior exposure, young animals could respond appropriately upon first exposure, while learned responses require experience (Hollén & Radford 2009). Although sensory and neurological development may also delay response, pinpointing when animals begin to respond to heterospecific alarms will help target periods of behavioural change, and thus potential periods of learning.

The fledging period in birds is an outstanding time for examining the role of experience in appropriate response to heterospecific alarms, and presents an opportunity to examine response development in a very specific life-history period. Fledglings emerge from their nests into a ‘new’ world, one with exposure to new predators and little chance to learn about appropriate response before leaving the nest (Newton & Marquiss 1982; Magrath et al. 2006). In fact, fledglings suffer extremely high predation rates (Sullivan 1989; Naef-Daenzer et al. 2001; Leedman & Magrath 2003), a pattern that could in part be due to their inability to recognize appropriate cues of danger, as well as to limited motor skills, particularly for very young fledglings (Sullivan 1989; Kullberg & Lind 2002). This life stage is therefore a likely time that learning about heterospecific alarm calls could occur. Yet despite this clear prediction, we are aware of no experiments on the response to heterospecific cues of danger during the fledgling period.

We examined the ontogeny of response by fledgling white-browed scrubwren to heterospecific aerial alarm calls, which are given to predators in flight and signal the need to immediately freeze or flee to cover (Caro 2005; Bradbury & Vehrencamp 2011). New Holland honeyeater, *Phylidonyris novaehollandiae*, and superb fairy-wren are sympatric with scrubwrens in many locations, and all three species are vulnerable to similar predators. Adult scrubwrens in sympatry respond equally strongly to the aerial alarm calls of both honeyeaters and fairy-wrens by fleeing to cover (Magrath et al. 2009a), yet when this response develops is unknown. Fledglings have an extended dependency period of six to eight weeks (Magrath et al. 2000), during which they may have time to learn to recognize honeyeater and fairy-wren aerial alarm calls. We tested whether fledglings responded to the alarm calls of these heterospecifics and how their response changed over time, using call playback experiments at three different fledgling ages that spanned the dependency period: 1) immediately upon leaving the nest, when fledglings were presumably the most naïve; again 2) when fledglings were approximately two weeks out of the nest, just as they began to leave cover and forage independently; and again 3) when fledglings were just over 5 weeks out of the nest and close to full independence.

METHODS

Study site and species

We conducted experiments on a colour-banded population of white-browed scrubwrens in the Australian National Botanic Gardens in Canberra (35° 160' S, 149° 060' E) between August and December 2011. The Gardens consist of 40ha of natural (13ha) and planted (27ha) vegetation adjacent to the Black Mountain Nature Reserve, a 9km^2 tract of natural vegetation. All experiments were conducted under permits from the Environment ACT, the Australian Bird and Bat Banding Scheme, the Australian National Botanic Gardens, and the Australian National University Ethics Committee.

Scrubwrens are small (14g) songbirds that build well-concealed domed nests on or near the ground (Higgins & Peter 2002). Females lay and incubate an average of three eggs per clutch. Adults are facultatively cooperative breeders, and young are attended by the female, the dominant male, and up to three male helpers, who are often offspring from previous years (Magrath & Wittingham 1997). Nestlings fledge at about 15 days old (Higgins & Peter 2002).

We found nests primarily in the building and incubation period, and monitored nests daily when they were close to transitions such as laying, hatching and fledging. We colour-banded nestlings nine days after hatching, which is just after pin break. In order to minimize our impact on nest survival we placed mesh cages over nests. These cages excluded medium-sized predators but allowed adults free access to and from the nest. Adults never abandoned nests because of caging, and typically resumed normal behaviour immediately after the cages were in place. Once nestlings fledged we monitored fledglings regularly for survivorship.

The behaviour of fledglings changes markedly as they age. Newly-fledged young remain in dense bushes for approximately 1-2 weeks, with occasional flights between cover (Higgins & Peter 2002; Magrath et al. 2006). Most groups undergo brood division within first two weeks of fledging, and individual young are subsequently fed primarily by a single adult (Leedman & Magrath 2003). Fledglings begin to leave cover and start to forage independently after about 12-16 days, although they are still heavily provisioned by their carer (Higgins & Peter 2002; Leedman & Magrath 2003). Over the following three to four weeks fledglings slowly gain independence, and by they time they are 30-40 days old young spend much of their time foraging on their own (Magrath et al. 2000). Fully independent young may immediately leave their parents' territory, or they may stay with their families for the better part of a year (females) or their entire lifetimes (males; (Higgins & Peter 2002).

Fledglings regularly use three different types of vocalizations. Begging calls or 'whines' are long (200-800 ms), broadband calls used when carers arrive with food (Magrath et al. 2006; Magrath et al. 2007b). When parents are not present fledglings often give 'peep' repeat calls, which are short and high frequency (50 – 150 ms duration, ~7 kHz average frequency), and are given at a rate of approximately one per second per individual (Magrath et al. 2006). 'Pipe' repeat calls are structurally similar to peep calls but are louder (~ 60 dB at 1 m) and given in short bursts of two to seven calls, generally when adults have been absent for longer periods of time (Magrath et al.

2006). While peeps tend to be quiet, fledging pipes may be heard from 30 m away or more (Magrath et al. 2006). The locatability of fledgling vocalizations has not been explicitly tested, but nestling begging and repeat calls can attract eavesdropping predators (Haff & Magrath 2011), and fledgling calls probably also increase their likelihood of being detected by predators (Magrath et al. 2006).

Adults give aerial alarm calls when predators fly over. Scrubwren aerial alarms consist of a series of similar elements that are repeated in rapid succession. The calls are high frequency, modulated calls with two bands of sound (fig 6.1; 102 ± 58 ms duration, 6.4 – 10.6 kHz frequency range, ~ 90 ± 6 Hz modulation), and cause other adults to flee to cover (Leavesley & Magrath 2005; Magrath et al. 2007b). Nestlings pay little attention to parental aerial alarm calls, but recently fledged young respond to the calls with silence, indicating that they use the calls as a signal of danger (Platzen & Magrath 2005; Magrath et al. 2006).

Two songbird species common in the Gardens that regularly alarm call to aerial threats are New Holland honeyeater and superb fairy-wren. Like scrubwren aerial alarms, both fairy-wren and honeyeater aerial alarms consist of a single element that is rapidly repeated (Magrath et al. 2009a). Fairy-wren aerial alarm calls are structurally similar to scrubwren aerial alarms, but have only a single sound band (fig. 6.1; 104 ± 32 ms duration, 8.2-10.6 kHz, 98 ± 6.3 Hz modulation; Magrath et al. 2007b). New Holland honeyeater aerial alarms are of shorter length and lower frequency (49 ± 7 ms, 3-5 kHz) than both scrubwren and fairy-wren aerial alarm calls, and are not frequency modulated, but instead simply decline in frequency (fig. 6.1; Magrath et al. 2007b). In scrubwren and fairy-wren aerial alarms, and probably those of honeyeaters as well, element number encodes urgency, with higher numbers of elements signaling more urgent threats (Magrath et al. 2009b). Playback of 4-element alarms of both honeyeaters and fairy-wrens prompts adult scrubwrens to flee to cover (Leavesley & Magrath 2005; Magrath et al. 2007b, 2009b; Fallow & Magrath 2010).

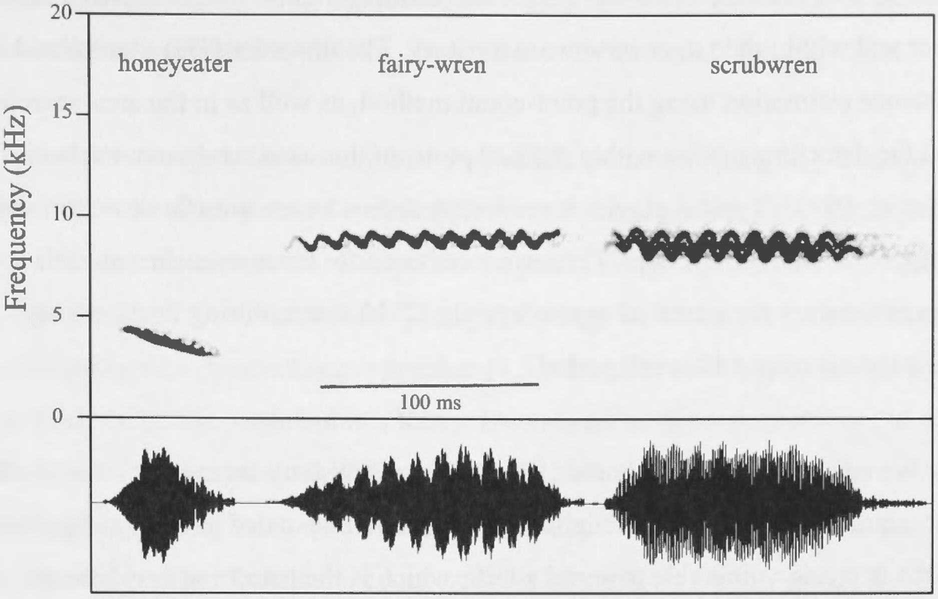


Figure 6.1: Aerial alarm calls of a) New Holland honeyeater, b) superb fairy-wren, and c) white-browed scrubwren, where upper panel displays spectrograms, and lower panel waveforms, with settings described in text.

Playback design and predictions

We presented four different playbacks to fledglings from 15 groups when young were: 1) 1-4 days fledged ('young fledglings'; mean 1.8 ± 0.9 s.d. days after fledging; N= 15); 2) 15-19 days fledged ('two-week old fledglings'; mean 16.9 ± 1.2 days after fledging; N = 15) and; 3) 31-39 days fledged ('five-week old fledglings'; mean 35.7 ± 2.3 days after fledging; N = 14) to test how fledgling response to heterospecific alarm calls changed with age. We also conducted the same playbacks on the parents of fledglings once young reached independence, to test for similarity in response between fledglings and their carers (N=15). Sounds played to fledglings were: 1) superb fairy-wren aerial alarms; 2) New Holland honeyeater aerial alarms; 3) scrubwren aerial alarms, as a positive control; and 4) the bell call of the crimson rosella, *Platycercus elegans*, a harmless parrot, as a neutral control. Each brood received unique call exemplars.

In order to estimate how likely fledglings were to hear the alarm calls of heterospecifics, we scored whether or not those species were detected by sight or sound in target scrubwren territories over the course of each playback session (four visits total to each territory). When individuals were detected by call alone we scored species presence as positive only if the call origin was estimated to be within 100m of the observer and within the target scrubwren territory. The observer (TH) was trained in call-distance estimation using the point-count method, as well as in the area-search method for detecting species within defined plots, in this case scrubwren territories (Ralph et al. 1993). Typical playback sessions and thus heterospecific detection sessions lasted approximately four hours. Thus, we monitored for heterospecifics in each scrubwren territory for a total of approximately 12-16 hours, during fairly-evenly spaced intervals over a 10-week period.

We predicted that if responses to honeyeater and fairy-wren aerial alarm calls did not require prior exposure, fledglings should have responded as soon as they were out of the nest and vulnerable to aerial attack, which is the pattern of response to conspecific aerial alarms (Magrath et al. 2006). Further, if response does not require experience, the presence of heterospecifics on scrubwren territories should not have affected fledgling behaviour. If fledglings learned to respond to heterospecific alarms, by contrast, young should have ignored heterospecific alarm calls when they were just out of the nest, but should have expressed adult-like responses later in their dependency period. Additionally, if fledgling response to heterospecific calls was learned, then response should have developed more rapidly on territories on which heterospecifics occurred more frequently.

Recording and playback methods

We recorded playback sounds using a hand-held Sennheiser ME66 or ME67 directional microphone connected to a Marantz PDM670 solid-state digital recorder, sampling wave files at 44.1 kHz. We examined sonograms in RavenPro 1.3 (Charif et al. 2008), and selected segments of calls with clean recordings for playback. Fairy-wren, scrubwren and honeyeater playbacks were constructed so that each playback contained a 4-element call. Rosella bell call elements are longer than those of aerial alarms, and so were constructed each playback to contain 2-3 elements. No playback was longer than 1 s. We filtered srubwren, and fairy-wren calls at 1 kHz, and honeyeater and rosella calls at 0.5 kHz. The ends of all playbacks were faded to avoid abrupt starts and stops. We broadcast all playbacks from an Edirol R-09HR solid-state digital recorder-player at an amplitude of approximately 64 dB at 8 m. This amplitude is towards the upper range of the natural limit of scrubwren aerial alarms (Magrath et al. 2007b), and was chosen to ensure that fledglings could hear the playbacks. Treatment order was randomized, and separated by at least 10 minutes or by two adult feeding visits.

Both the foraging tactics and anti-predator responses of fledglings change rapidly as they develop, and so we used different playback presentation techniques as well as different measurements of response for young fledglings than for two- and five-week old fledglings. For playbacks to young fledglings we broadcast sounds from 15 m away using Response Dome tweeter speaker (1.5 – 20 kHz) mounted on a tripod placed 8-10 m from fledglings, attached to a Kemo Electronics integrated amplifier (20 – 25,000 Hz) and connected to the Edirol playback device by a 15 m cable. We recorded young fledgling calling using a Sennheiser ME66 directional microphone secured on a tripod placed 5 m from fledglings, connected to a Marantz by a 15 m cable. We waited to perform playbacks until fledglings were peeping regularly, adults were at least 10 m from fledglings and not vocalizing, and there were no other loud or abrupt noises nearby. We discarded recordings if a parent called or returned to young fledglings during a treatment, and repeated the playback at the end of the experiment.

For playbacks to two- and five-week old fledglings and adults we attached the Edirol playback device, speaker and amplifier to a waist belt carried by the experimenter, in effect creating a mobile playback station (Magrath et al. 2007b). We broadcast playbacks only when fledglings were at least 20 cm from cover and foraging, and parents were more than 5 m away, out of sight from fledglings, and not vocalizing. To ensure that the responses of older fledglings were to the playbacks and not to the reactions of siblings we broadcast sounds to single young, which became the focal individual for subsequent playbacks. This ensured that any changes in response between two- and five-week old fledglings were due to changes within instead of between individuals. To examine whether or not the response of older fledglings mimicked that of their carers we tested response to playbacks by the specific carer that provided for each focal offspring.

Response analysis

Due to changes in fledgling behaviour with age we were unable to use the same response measurements for young and older fledglings (above). Instead, we used changes in fledgling calling for young fledglings, and flight and vigilance response in older fledglings as response measures to playbacks. Call suppression is a good measure of whether nestlings and young fledglings interpret sounds as cues of danger (Magrath et al. 2010), while flight and vigilance responses are a good measure for adult response to acoustic cues of danger (Magrath et al. 2007b, 2009b; Magrath & Bennett 2012).

To analyze how young fledglings responded to playbacks we counted fledgling calls and time intervals in RavenPro 1.3, with sonogram settings: Blackman filter at 582 samples, and 3 dB filter bandwidth, 2.27 ms grid time, 21.5 Hz frequency grid (Magrath et al. 2007a). In total, we tallied 3,077 calls. We used brood as the level of analysis for call response, as we could not tell individuals apart. For each playback, we calculated: 1) the difference in number of calls in the 10 s after each playback minus the number of calls in the 10 s before each playback; and 2) call latency, the time to the first call after each playback (s), calculated as the time from the end of the playback to the first fledgling call, within 2 min of the end of the playback (Haff & Magrath 2010).

To measure how two- and five-week old fledglings and adults responded to different treatments we scored their behaviour immediately after playback. For each playback we measured anti-predator response, scored as a binomial response of either: a) no reaction, if focal individuals continued foraging without visible response to the playback; or b) adverse reaction, if individuals fled to cover or increased predator vigilance by looking up and scanning for > 1 s. Flight to cover and vigilance were lumped into one response category because most target individuals that responded to playbacks fled immediately to cover (92%). When target individuals fled to cover we also recorded the length of time they spent hidden (s), for up to 1 min after the playback, as a measure of fear response (Fallow & Magrath 2010).

We used both nonparametric as well as parametric statistics to interpret fledgling response to playbacks because not all data conformed to assumptions of parametric analysis. To analyze the response of young fledglings to playbacks we used generalized linear models (GLM; family Gaussian with an identity link) to test for differences in: 1) the difference in the number of calls in the 10 s before minus the 10 s after playback; and 2) log-transformed call latency, the amount of time nestlings took to resume calling after playbacks. For older nestlings response to both control playbacks was invariable, which precluded use of parametric models. We therefore compared both the within and between age flight and vigilance responses of two- and five-week old fledglings using Cochran's Q tests with pairwise McNemar tests, which are designed for matched pair analysis. We also used these tests to examine differences in response between five-week old fledglings and their carers. We used Friedman ANOVA for paired analyses to examine differences in the time older fledglings and adults spent in cover after hearing aerial alarm playbacks. In order to compare the responses of young fledglings to those of two- and five-week old fledglings in one model we dichotomized the call rate response of young fledglings, so that no response represented an increase or no change in calling in response to alarm playbacks, compared to the neutral control, and an adverse response represented a reduction in the number of calls to less than the lower 95% confidence interval for their response to the neutral control playback. To test whether fledglings' responses to playbacks were affected by the presence or absence of heterospecifics co-occurring on target scrubwren territories we used Mann-Whitney U tests comparing differences between call latency and change in call rate for young fledglings, and Fisher's exact tests on flight responses for older fledglings. All tests were two-tailed, with an alpha level of 0.05. Pairwise multiple comparisons were adjusted using the formula pK(K-1)/2, where p = the original p-value and K = the number of pairwise comparisons (SPSS 19.0). We used SPSS 19.0 and R 2.11.1 for all analyses.

RESULTS

Vocal response of young fledglings

Young fledglings just out of the nest responded strongly to conspecific alarms but had little or no response to heterospecific aerial alarms, and ignored rosella bell calls (fig. 6.2; GLM including all playback, change in number of calls before vs. after playback: $\chi^2_3 = 81.94$, $p < 0.0001$; call latency: $\chi^2_3 = 90.62$, $p < 0.0001$). In fact, there were no differences in call rate in response to the rosella neutral control and either of the heterospecific aerial alarm playbacks (fig. 6.2a; GLM including neutral control and heterospecific playbacks: $\chi^2_2 = 2.32$, $p = 0.31$). By contrast, young fledglings strongly reduced call rate after hearing scrubwren aerial alarms (fig. 6.2a). Young fledglings took somewhat longer to resume calling in response to heterospecific aerial alarm playbacks, compared to the neutral control (fig. 6.2b; GLM including neutral control and heterospecific playbacks: $\chi^2_2 = 20.53$, $p < 0.0001$), but this pause was longest in response to scrubwren aerial alarms (fig. 6.2b).

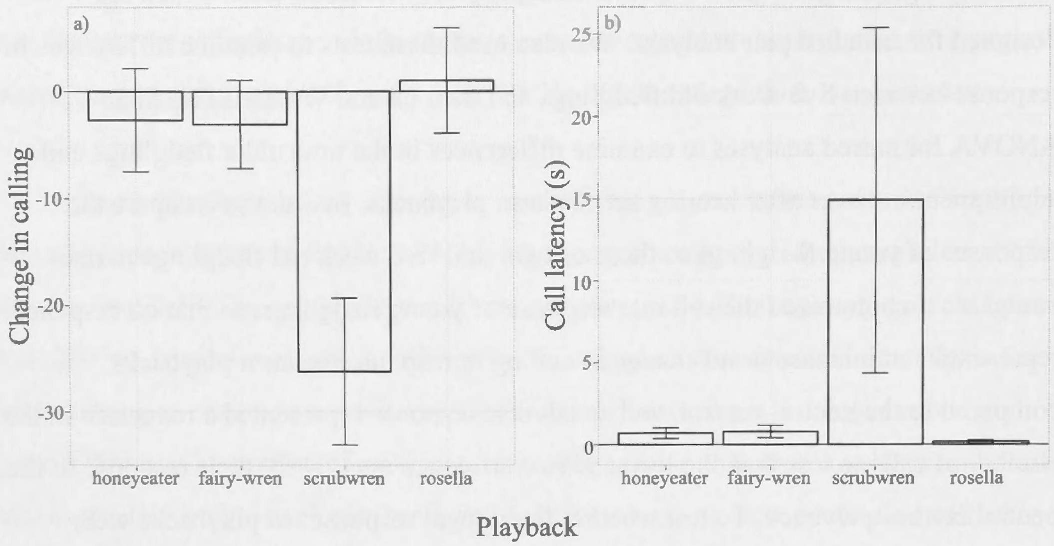


Figure 6.2: Young (1-4 days out of the nest) fledgling response to playbacks for: a) change in calling, the difference in the number of calls given in the 10 s before the playback minus the 10 s after the playback, where values above 0 represent an increase in calling, and values below 0 a decrease in calling after playback; b) call latency (s), the time young took to resume calling after playback. Values represent raw data; data for b) have been reverse-transformed for presentation.

Changes in fledgling response over time

Two-week old fledglings showed strong anti-predator responses to honeyeater, fairy-wren and scrubwren playbacks, but continued to ignore playback of rosella contact calls (fig. 6.3; Cochran's test, all playbacks: $Q_3 = 36.92$, $p < 0.0001$). In total, 11 out of 15 two-week old fledglings responded to honeyeater playbacks (10 fled, 1 scanned) and all responded to both fairy-wren (12 fled, 3 scanned) and scrubwren playbacks (15 fled), while no fledglings responded to rosella playbacks (pairwise McNemar test: honeyeater vs. rosella $\chi^2_1 = 3.85$, $p = 0.001$; fairy-wren vs. rosella $\chi^2_1 = 5.25$, $p < 0.0001$; scrubwren vs. rosella $\chi^2_1 = 5.25$, $p < 0.0001$). How long two-week old fledglings spent in cover after fleeing was not affected by playback type (Friedman ANOVA, alarm playbacks only: $\chi^2_2 = 4.44$, $p = 0.11$).

Adverse response to playback of heterospecific alarms was also strong when fledglings were five-weeks old and close to independence (fig. 6.3; Cochran's test, all playbacks: $Q_3 = 42.0$, $p < 0.0001$). All five-week old fledglings (14 out of 14) responded to honeyeater (13 fled, 1 scanned), fairy-wren (14 fled) and scrubwren (14 fled) playbacks, and none responded to rosella playbacks. Time in cover by five-week old fledglings was similar for all alarm playbacks (Friedman ANOVA, alarm playbacks only: $\chi^2_2 = 1.0$, $p = 0.61$). The response of five-week old fledglings did not differ from those of their primary carers. Adult carers responded equally strongly to honeyeater (15/15 fled), fairy-wren (12 fled, 3 scanned), and scrubwren (13 fled, 2 scanned) alarms, and ignored the neutral control, and how much time adults spent in cover after fleeing did not differ between alarm playback types (Friedman ANOVA, alarm playbacks only: $\chi^2_2 = 3.89$, $p = 0.14$; fig. 6.3).

Overall, fledgling response to heterospecific alarm playbacks changed dramatically as they aged, while their response to both scrubwren alarms and control rosella bell calls remained static. The change in fledgling response was most rapid in response to fairy-wren playbacks; while young fledglings ignored fairy-wren alarms, two- and five-week old fledglings treated the same playbacks as cues of danger (fig. 6.3; Cochran's test, binomial response to fairy-wren playbacks at all ages: $Q_2 = 22.0$, $p < 0.0001$; $N = 14$). Fledgling response to honeyeater playbacks also changed with age, but young did not have completely adult-like responses until they were five-weeks old (fig. 6.3; Cochran's test, binomial response to honeyeater playbacks at all ages: $Q_2 = 12.6$, $p = 0.002$; young vs. two-week old fledglings $\chi^2_1 = -2.32$, $p = 0.06$; young vs. five-week old fledglings $\chi^2_1 = -3.49$, $p = 0.001$; $N = 14$). Fledglings of all ages uniformly responded adversely to scrubwren playbacks. Response to the neutral control was also uniform; only two young fledglings suppressed calling in response to rosella bell calls (dichotomized response), and all two-and five-week old fledglings completely ignored their playback.

Exposure to heterospecific alarms

New Holland honeyeaters were the only species not present on all scrubwren territories (detected during 0/4 visits on 4 territories, 4/4 visits on 11 territories; fairy-wren and rosella detected during 4/4 visits on all 15 territories). We therefore used the presence or absence of honeyeaters to test if the opportunity for experience affected the rate of development of response to this species' alarm calls. Neither the call rate nor call latency of young fledglings was affected by whether or not honeyeaters co-occurred on their territories (Mann-Whitney test: difference in number of calls $U = 0.13$, $p = 0.90$;

latency U = 0.52, p = 0.60). By contrast, response by two-week old fledglings to honeyeater playbacks was significantly stronger on territories on which honeyeaters occurred than on territories where they did not (0/4 fledglings responded on territories without honeyeaters, 11/11 responded on territories with honeyeaters; Fisher's exact test, $p < 0.001$). All five-week old fledglings responded to honeyeater playbacks (above), regardless of whether honeyeaters regularly co-occurred on fledgling territories.

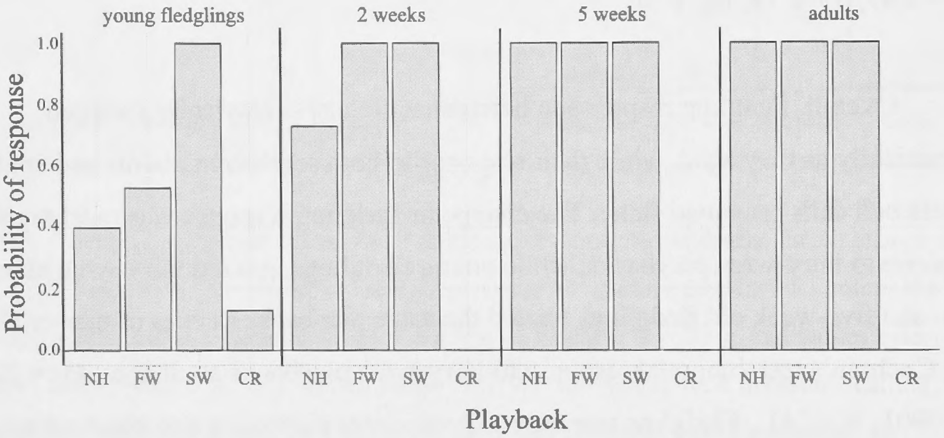


Figure 6.3: Proportion of individuals responding to playbacks for young fledglings (1-4 days out of the nest), 2-week old fledglings (15-19 days after fledging), 5-week old fledglings (31-39 days after fledging) and adults (fledgling carers), where NH = honeyeater alarm call, FW = fairy-wren alarm call, SW = scrubwren alarm call, and CR = crimson rosella contact call. Response for young fledglings represents suppression of calling greater than the 95% confidence interval for response to rosella control playbacks, while response to older fledglings and adults represents whether or not individuals fled or scanned for predators in response to playbacks.

DISCUSSION

Fledgling response to playback of heterospecific alarm calls changed rapidly over a short period. Young fledglings just out of the nest strongly suppressed calling to scrubwren aerial alarms, but were only weakly affected by playback of heterospecific aerial alarm calls, and completely ignored rosella bell calls (fig. 6.2). By the time they were just two weeks old, however, most fledglings treated both fairy-wren and honeyeater aerial alarms similarly to scrubwren alarms, and either fled to cover or scanned for predators at playback of all three species aerial alarms (fig. 6.3). The only exceptions to this pattern were in cases in which heterospecifics did not regularly co-occur on scrubwren territories, suggesting that learning is critical to the development of appropriate response to other species' alarms. By the time fledglings were five-weeks old their response to playbacks were statistically indistinguishable from those of their carers. Both mature fledglings and adults responded uniformly adversely to all three species' aerial alarm calls, and continued to ignore the neutral control. Overall, these results show that the ability to respond to heterospecific aerial alarm calls can develop early in life, probably through learning.

Recently fledged young responded strongly to conspecific aerial alarm calls, but weakly or not at all to heterospecific aerial alarms, suggesting that scrubwrens do not have an innate adverse response to honeyeater or fairy-wren alarm calls. This result is consistent with behaviour of young vervet monkeys, *Chlorocebus pygerythrus*, which do not immediately respond to playback of superb starling alarm calls, *Lamprotornis superbus*, even though adults treat the calls as a cue of danger (Hauser 1988). Similarly, nestlings of several species respond to conspecific 'nest' alarm calls, but not to those of other species (Davies et al. 2004; Madden et al. 2005a; but see Madden et al. 2005b). Interestingly, studies of the development of response by young to conspecific calls have also found that naïve young respond inappropriately or not at all (e.g. Masataka 1983; Hollén & Manser 2006; reviewed in Hollén & Radford 2009), yet young scrubwren fledglings respond immediately to conspecific alarms, and even begin to display this response late in the nestling period (Magrath et al. 2006). This suggests that response to conspecific alarms in scrubwrens is probably innate, although because it is not possible to control the experiences of wild animals we cannot exclude the possibility that young may have had opportunities to learn about conspecific calls while still in the nest (Davies et al. 2004; below).

Although young fledglings did not suppress calling overall after hearing heterospecific aerial alarm playbacks they did pause briefly, suggesting there may be salient characteristics of aerial alarm calls common between species that promote generalization or aid in rapid development of appropriate response through learning (Ghirlanda & Enquist 2003; Magrath et al. 2009b). Some bird species are innately 'pre-tuned' to conspecific calls and songs, for example, which helps to enable and strengthen learning about those sounds (Davies et al. 2004; Hultsh & Todt 2004; Davies et al.

2006). Similarly, common features of conspecific and heterospecific aerial alarm calls might promote learning about heterospecific calls. For example, while adult superb fairy-wrens flee to playback of normal but not reversed New Holland honeyeater calls, most still scan for predators when they hear reversed calls, suggesting that similarities in call features may help promote learning about novel alarms (Magrath et al. 2009b). Potentially, scrubwrens might be neurally pre-tuned to pay attention to sounds that share features with conspecific alarm calls, but require experience or social learning to develop appropriate responses (e.g. Davies et al. 2004).

Learning while still in the nest could be another explanation of why nestlings paused calling after hearing honeyeater and fairy-wren playbacks. Evidence from nestling scrubwrens suggests that young may learn about heterospecific mobbing calls while still in the nest (Chapter 5), and studies of nestling begging behaviour demonstrate that young have the capacity to learn while still in the nest. For example, even young nestlings can rapidly learn to associate their behaviour with food rewards (Kedar et al. 2000; Madden & Davies 2006; Langmore et al. 2008), and in pied babblers, *Turdoides bicolor*, older nestlings can learn to respond to parental calls used by adults to manipulate offspring behaviour after fledging (Raihani & Ridley 2008). Thus, it is possible that older nestlings could have begun to learn to associate heterospecific aerial alarm calls with danger, particularly if they heard parental and heterospecific aerial alarms in close succession, or observed parental response coupled with heterospecific alarms.

Two-week old fledglings only responded to playbacks of honeyeater alarms on territories in which honeyeaters regularly occurred, a result that is consistent with fledglings learning to respond to heterospecific alarms. This is one of the finest-scale geographic patterns of response to alarm calls that we know of (see Davies & Welbergen [2009] and Welbergen & Davies [2009] for a similarly-scaled response by hosts to brood parasites), and is similar to the pattern of correlation between species overlap and heterospecific alarm call response that have been documented in adult birds and mammals (Ramakrishnan & Coss 2000; Zuberbühler 2000a; Magrath et al. 2009b; Magrath & Bennett 2012). The pattern we describe seems to reflect differences in the speed of development, and not intrinsic differences between fledglings on different territories, as by week five all fledglings responded adversely to playback of honeyeater alarms. Potentially, young on territories without honeyeaters required more time to develop appropriate response because they had fewer opportunities to learn to associate honeyeater alarm calls with danger. Honeyeaters can be are highly mobile in search of flowering trees and shrubs (Higgins et al. 2001), and so even young on territories on which we never detected honeyeaters were probably at least occasionally exposed to the alarms of passing individuals. These results are consistent with the development of response by infant vervet monkeys to superb starling alarms, in which young on territories with high starling abundances respond to starling alarms at younger ages than offspring on territories with low starling abundances (Hauser 1988). In fact, studies of the response by young to conspecific alarm calls also suggest that how fast offspring develop appropriate responses to alarms is strongly influenced by opportunities to learn (Seyfarth & Cheney 1986; Mateo & Holmes 1997). To our knowledge, this is the first demonstration of fine-scale spatial variation in response to heterospecific alarm calls in the young of any bird species, and only the second in any species of bird or mammal.

In contrast to learning, neither developmental delays nor adaptive timing offer satisfying alternative explanations for the delay in appropriate response by young fledglings to honeyeater and fairy-wren alarm calls. Given the similarities between scrubwren and fairy-wren aerial alarms (Magrath et al. 2007b), it seems unlikely that fledglings would be able to process scrubwren calls as signals of danger, but unable to do the same for fairy-wren calls. Sensory development can limit high-frequency hearing in young passerines, which might help explain lack of response to fairy-wren alarms, but the frequency of their alarms overlaps with scrubwren alarms (Magrath et al. 2007b). Young fledglings also largely ignored honeyeater alarms, even though those calls are relatively low frequency and well within the described hearing range for young nestling songbirds (Khayutin 1985). Indeed, young paused after playback of both honeyeater and fairy-wren alarms, demonstrating that they can hear these calls. Similarly, adaptive timing seems an unlikely explanation for why young fledglings did not strongly suppress calling in response to fairy-wren and honeyeater alarm calls, as it seems implausible that recently fledged scrubwren young would not benefit from responding appropriately to the aerial alarm calls of two common species that call in response to threats dangerous to scrubwrens (Magrath et al. 2009a). Indeed, the vulnerability of fledglings to aerial predators should put a premium on responding to these alarms as early as possible (Naef-Daenzer et al. 2001; Thomson et al. 2006). We have witnessed attacks by aerial predators on fledgling scrubwrens on multiple occasions (Magrath et al. 2006; this study), and overall mortality of young is approximately 5.1% per day in the first week after leaving the nest, with avian predators responsible for most losses (Leedman & Magrath 2003). Thus, there would seem to be little benefit gained from delayed innate response to detectable cues of danger that might aid in fledgling survival.

This study demonstrates, for the first time that we are aware of, that fledgling birds can respond appropriately to the aerial alarm calls of other species, and that this response develops over very short periods of time. Further, we show that this response is probably learned. This result thus fits with an increasing range of evidence suggesting that birds and mammals largely depend upon learning to respond appropriately to the alarm calls of other species (Hauser 1988; Ramakrishnan & Coss 2000; Zuberbühler 2000a; Magrath et al. 2009b; Magrath & Bennett 2012). These results are important not only in understanding when and how young animals develop anti-predator responses, but could help explain the common pattern of rapid attrition of naïve individuals in translocation or reintroduction programs, and could thus help inform species management decisions (Maloney & Mclean 1995; Griffin et al. 2000; Griffin et al. 2001; Seddon et al. 2007). Future studies examining how fledglings learn about heterospecific alarm calls will be important in shedding light on the range of tools young have available to help them escape predation and survive to adulthood, and will help further our understanding of eavesdropping networks in general.

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Calling in the face of danger? How predation risk affects acoustic communication by parent birds and their offspring

Magrath, R.D., T.M. Haff, A.G. Horn and M.L. Leonard. 2010. *Advances in the Study of Behavior* 41, 187-253.

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I. INTRODUCTION

Anyone wanting to empathize with the lives of small birds should watch Steven Spielberg's film *Jurassic Park.* No one could forget the scenes in which predatory dinosaurs hunt human victims. The scenes are startling because we humans rarely worry about being taken by a predator while we go about our daily lives. There is no need for vigilance while engrossed in a review in *Advances*, or to sprint back to the office from lunch to avoid becoming a meal. By contrast, for many small birds a feathered raptor is just as threatening as a large carnivorous dinosaur would be to a human; indeed, the difference in body size between a human and a *Tyrannosaurus rex* is about the same as between our favorite study species and their major predators. It is not surprising, therefore, that vulnerable birds have evolved many strategies to manage risk. These strategies can be designed to thwart any stage of a predator's hunting behavior, from reducing the risk of encounter to minimizing the chance of successful consumption (Caro, 2005; Endler, 1991).

Breeding birds provide a microcosm of the challenges of living under the risk of predation. Young are extremely vulnerable to predators, in part because they are relatively defenseless compared to adults and in part because altricial nestlings are confined to a nest, which provides predators with days or weeks to discover their location. As Skutch (1976, p. 428) colourfully writes, "The nestlings of passerines and other small birds are nearly always too weak and harmless to hold aloof the animals that crave their flesh". In fact predation is the major cause of nesting failure, and has been estimated to account for an average of around 80% of failures among small birds (Martin, 1993, 1995; O'Connor, 1984; Ricklefs, 1969). The risk of nest predation selects for a diversity of adaptations in birds, including safe nest site location, cryptic egg colour, small clutch size, low feeding rates and vigorous nest defense (Kilner, 2006; Lima, 2009; Martin *et al.*, 2000a). Even after leaving the nest, young can be extremely vulnerable to predators, with some small birds suffering 5-10% mortality per day, most due to predation (Naef-Daenzer *et al.*, 2001). Parents themselves can be at risk, and so need to balance their risks against reproductive effort. Laying female zebra finches (*Taeniopygia guttata*), for example, lose more muscle mass if they lay more eggs in a clutch, which slows escape take-offs and probably increases vulnerability to predators (Veasey *et al.*, 2001). Direct defense of young can be lethal, although the evidence is anecdotal and the risk is difficult to quantify (Caro, 2005). Risks of predation can even affect global patterns of life-history evolution and anti-predator behavior (Martin *et al.*, 2000a). For example, adults of Southern Hemisphere passerine species commonly have higher annual survival and smaller clutch sizes than those of Northern Hemisphere species, and expose themselves to lower risk when defending current broods to protect investment in future broods (Ghalambor and Martin, 2001).

Breeding birds also provide an excellent model for understanding how acoustic communication is affected by the risk of predation, and how communication can itself affect risk. Most work on this issue concerns nestling begging. Young birds often give exuberant begging displays that include loud calls (Budden and Wright, 2001a; Kilner *et al.*, 1999; Wright and Leonard, 2002), which are designed to extract care from adults but potentially expose young to eavesdropping by predators (Haskell, 1999). The trade-offs faced by young birds are comparable to many other communication systems, such as the sexually selected signals that make males vulnerable to exploitation by predators and parasites (Zuk and Kolluru, 1998). In both cases, one would predict the evolution of signaling that balances effective transmission to receivers against the risk of eavesdropping. This balance can affect both the acoustic design of calls and the rules of usage, as is well illustrated by male tungara frogs (*Physalaemus pustulosus*), which change call design and timing to manage the trade-off between attracting females and avoiding predatory bats (Ryan, 1985).

While most work on parent-offspring communication has focused on young begging to adults, individuals within families may communicate with each other or even with predators. Most obviously, adults give alarm calls that can communicate with their young, other adults or predators (Caro, 2005). In this case, predators not only prompt the calls, but could influence their acoustic structure and usage, and parents can even give different alarm calls signaling different predatory threats (Zuberbühler, 2009). In addition to begging calls and alarm calls, both young and adults have other forms of acoustic communication, all of which are likely to be affected by and moderate the risk of predation, and acoustic signals of both adults and young can be affected by the other. In short, anti-predator adaptations in acoustic communication within breeding families of birds span evolutionary and ecological time-scales, and cover general themes including behavioral trade-offs, signal design and signal meaning.

In this review we consider the ways in which acoustic communication within bird families affects and is affected by the risk of predation, and how such communication can manage that risk. We focus on altricial species, but include precocial species where comparison strengthens understanding. Following the tradition of *Advances*, we use our own research – primarily on white-browed scrubwrens (*Sericornis frontalis*) and tree swallows (*Tachycineta bicolor*) – where appropriate, but have integrated our work within the broader framework of research. We start by considering calls made by young, then by adults, and subsequently integrate the two by considering the ways in which the two parties are influenced by acoustic interactions with each other. We conclude by suggesting promising avenues for future research.

II. VOCALIZATIONS BY YOUNG

The predation costs of offspring vocalizations, especially begging calls, have attracted particular interest because of the key role that costs play in theoretical discussions of parent-offspring conflict and the evolution of reliable signals (Searcy and Nowicki, 2005). Here, we outline this theoretical context and the information that begging calls are thought to convey, before considering the evidence for a predation cost to begging calls and its possible influences on call structure and delivery. We then examine offspring vocalizations given in other contexts, focusing particularly on the calls that nestlings give when parents are not at the nest, because their benefits are poorly understood yet their risks seem particularly high.

A. BEGGING AND SIGNAL HONESTY

1. Costliness and Reliability of Nestling Begging Calls

For any signal to be effective, it must first be detected by receivers, so the very nature of signaling necessitates a certain degree of conspicuousness (Bradbury and Vehrencamp, 1998). When predators are present, however, that conspicuousness risks attracting their attention, as well as the attention of the "intended" receiver (Peake, 2005). Indeed, it would be surprising if predators did not locate their prey via such "eavesdropping" – a term we use here and throughout to mean "intercepting signals intended (in an evolutionary sense) for another individual" (Peake, 2005), which is also called "interceptive eavesdropping" (Peake, 2005) or "interception" (Searcy and Nowicki, 2005). Thus, while many behaviors entail a trade-off between their benefits and the threat of predation, for signals the trade-off is particularly direct, because the very design features that enhance their benefits may also exacerbate their costs.

The trade-off is worse yet for signals in which there is an evolutionary conflict between senders and receivers – that is, when senders are more intensely selected to stimulate receivers than receivers are to respond (Maynard Smith and Harper, 2003; Searcy and Nowicki, 2005). Obvious cases of such conflict between insistent senders and reluctant receivers include contests, which accounts for the loud counter-singing duels between territorial birds, and mate attraction, which accounts for the elaboration of the peacock's train. Such situations call for signals that are more conspicuous than would otherwise be needed for detection and recognition, and that thus entail more risk of attracting the attention of predators.

Although common sense might suggest otherwise, parent-offspring communication is another situation involving sender-receiver conflict (reviewed in Kilner and Hinde, 2008; Searcy and Nowicki, 2005). Here the conflict arises because parents are on average equally related to all of their offspring, while each offspring is more closely related to itself that it is to its siblings. Individual offspring should, therefore, be selected to get more resources from parents than their parents are selected to provide. Since the offspring get resources by begging from parents, parent-offspring conflict might result in offspring begging more intensely than they would otherwise, in order to coax parents beyond their optimal level of investment. This expectation accords well with the seemingly excessive conspicuousness of nestling begging displays, which consist of exposing brightly colored gapes, stretching high, waving wings, and calling loudly.

This apparent signal exaggeration might expose begging offspring to predators. Calls in particular might increase the risk of predation, as acoustic signals can travel well beyond the confines of the nest. Indeed, in most models of parent-offspring conflict, it is costs such as energy expenditure and predation risk that place a cap on how much offspring will escalate their demands (Godfray, 1991, 1995a; Grafen, 1990; Harper, 1986). Specifically, although offspring do end up coaxing parents to give more resources, at equilibrium the benefits of obtaining those resources are balanced by the costs of begging, so that parents and offspring settle on a level of parental investment that lies somewhere between each of their optima (reviewed in Kilner and Hinde, 2008; Royle *et al.*, 2002).

Various models of the evolution of reliable signaling have addressed how parents and offspring might negotiate this level of investment, and here predation costs have played a particularly important role. Early models of parent-offspring conflict assumed that offspring can control parents, at least to some extent, by their begging, but subsequent signaling models have examined why parents respond to begging in the first place. In brief, they show that parents will respond to begging if it reliably correlates with aspects of offspring need that they cannot assess any other way, such as hunger. In the best-known models, such a reliable correlation only arises if begging is costly (Godfray, 1991, 1995b; Maynard Smith, 1991; see Parker *et al.*, 2002; Rodríguez-Gironés *et al.*, 2001 for similar conclusions based on sibling competition rather than signaling). Cost-free signaling appears possible in only limited contexts, such as when there is no conflict of interest between sender and receiver (Maynard Smith, 1991), or where the gradations of need conveyed by begging are coarse and thus less informative (Bergstrom and Lachmann, 1998). Thus, most models place particular emphasis on costs to begging, either to put a cap on its exaggeration, as in models of parent-offspring conflict, or to ensure its reliable correlation with need, as in models of reliable signaling.

Theoretical models of begging are still limited in predicting the real world despite their many elaborations, but generally propose an important role for predation (Searcy and Nowicki, 2005, provide a clear review of theoretical models). In particular, they do not take into account many of the complexities of parent-offspring communication in the real world (Royle *et al.*, 2002), most notably the fact that parents and offspring engage in repeated interactions over an extended period of time (Rodríguez-Gironés *et al.*, 1998). Nonetheless, in most of the theoretical literature, predation costs are proposed to play a particularly important role, because, unlike energetic costs of begging, which are borne only by the signaler, predation costs affect the whole brood; by attracting a predator with its noisy begging, a nestling not only risks itself but also its brood mates (Section II.B.2; but see Redondo and Castro, 1992).

A surprising possibility is that begging might not be selected to avoid predation costs, but instead to invite them. For example, Zahavi (1977) famously suggested that nestlings beg noisily to blackmail parents with this predation risk, so that the parents will quieten them by providing food. Similarly, Kilner and Hinde (2008) suggest that smaller nestlings might beg loudly to blackmail larger brood mates into backing down from their own attempts to beg for parental attention, presumably by discouraging them from begging and so making the brood still more obvious. Thus, while we focus on ways in which parents and offspring might reduce the risk of predation, an interesting caveat to this whole review is that nestlings might sometimes strategically inflate that risk to levels above those needed for efficient and reliable communication with their parents.

2. Information Contained in Nestling Begging Calls

To understand how nestlings deal with the predation risks they face when they signal, we need to understand the benefits they are trading these risks against. Nestlings call mainly to attract care from parents. Yet, despite the huge theoretical and empirical literature on begging, there are surprisingly few studies of exactly what aspects of begging calls help parents assess their nestlings' needs, and whether parents use these features to regulate their care.

Most variation in begging calls is related to hunger, age, and competition among nestlings, although begging calls can also convey information on thermal need (Choi and Bakken, 1990; Leonard and Horn, 2001a) and long-term condition (mass relative to size; Price and Ydenberg, 1995). Hungrier nestlings produce begging calls that, in virtually all cases, show features that should in theory increase the detectability and localizability of the callers, which will be a key consideration for our discussion of their predation risk below (Table 1; Section II.C.1). In addition, hungrier nestlings generally start begging more quickly (e.g., Roulin *et al.,* 2000) and call for longer when parents arrive at the nest (Glassey and Forbes, 2003; Hussell, 1988; Marques *et al.*, 2009; Price and Ydenberg, 1995), providing increased opportunity for predators to eavesdrop. Older nestlings generally give more conspicuous calls, as well, although there are exceptions (Table 1). Similarly, when nestlings call together their calls are often more obvious, for example by being louder or given at a higher rate, than when they call alone (Leonard and Horn, 2001b; Price, 1996; for an exception see Marques *et al.* 2006; see also Madden *et al.*, 2009).

Table 1: Examples of relationships (+ positive; - negative; +,- positive then negative; 0 not significant) between begging call features and hunger or age in altricial species, listed in taxonomic order [square brackets indicate relationships not directly examined, but inferable from other information in source reference].

Common name	Scientific name	Rate	Frequency	Bandwidth	Duration	Amplitude	Source
Variation in relation to hunger							
meadow pipit	*Anthus pratensis*	+	+	0			Butchart *et al.*, 2003
American dipper	*Cinclus mexicanus*	0	0	0	0	+	Fairhurst, 2006
Azure-winged magpie	*Cyanopica cyana*	+	+		+	0	Marques *et al.*, 2008
barn swallow	*Hirundo rustica*	+	0	[0]	+		Sacchi *et al.*, 2002
Spanish sparrow	*Passer hispaniolensis*	+	+	[+]		+	Marques *et al.*, 2009
dunnock	*Prunella modularis*	+	0	0			Butchart *et al.*, 2003
white-browed scrubwren	*Sericornis frontalis*	+		+	+	+	Maurer *et al.*, 2003
tree swallow	*Tachycineta bicolor*	+	0	+	+	+	Leonard and Horn, 2006
yellow-headed blackbird	*Xanthocephalus xanthocephalus*	+		[+]	+	0	Price and Ydenberg, 1995
Variation in relation to age							
great reed warbler	*Acrocephalus arundinaceus*	+	+	-			Butchart *et al.*, 2003
reed warbler	*Acrocephalus scirpaceus*	+	+	0			Butchart *et al.*, 2003
American dipper	*Cinclus mexicanus*	0	-	+	0	0	Fairhurst, 2006
little raven	*Corvus melori*		-	[-]	+		Jurisevic, 1999
common cuckoo	*Cuculus canor*	+	+	-			Butchart *et al.*, 2003
budgerigar	*Melopsittacus undulatus*		-	+,-	+,-		Brittan-Powell *et al.*, 1997
lazuli bunting	*Passerina amoena*		-	+	+		Thompson, 1974
magpie	*Pica pica*	-	-	+	+	+	Redondo, 1991
black-capped chickadee	*Poecile atricapillus*		-	+	+		Clemmons and Howitz, 1990
dunnock	*Prunella modularis*	+	+	+			Butchart *et al.*, 2003
bullfinch	*Pyrrula pyrrula*		+,-	+	+		Wilkinson, 1990
eastern bluebird	*Sialia sialis*	-	[0]	0		+	Perera, 2008
tree swallow	*Tachycineta bicolor*	+,-	-	+	+	+	Leonard and Horn, 2006
zebra finch	*Taenopygia guttata*	+	-	+	+	+	Muller and Smith, 1978
house wren	*Troglodytes aedon*		+,-	+	+	+	Sawhney *et al.*, 2006

Few studies have addressed whether parents actually use variation in call structure or delivery to make feeding decisions. Several playback experiments have stimulated higher nest visit rates with playback of nestling calls (reviewed in Hinde and Kilner, 2007), and one has reduced visit rates by muting nestlings (Glassey and Forbes, 2002). Only three studies have shown that parents use calls to select which nestling to feed (R. Brandt, pers. comm.; Kilner, 2002; Leonard and Horn, 2001c). Thus, despite claims in the literature that making calls detectable and locatable for parents is traded off against predation risks (e.g. Redondo and Arias de Reyna, 1988), there is little direct evidence that detectability or locatability affects food allocation within broods.

B. EVIDENCE THAT CALLING IS RISKY

There are two ways nestlings can attract predators to the nest by calling: indirectly, by stimulating parents to visit the nest more often, thus betraying its location, and directly, by giving predators an acoustic cue that they can use to home in on the nest. We consider each of these pathways in turn before considering the effect of predation on the design of begging calls.

1. Activity at the Nest and Risk of Predation

Skutch (1949) proposed that predation is higher during the nestling period than at other nesting stages because increased visits by parents and begging by nestlings betray the location of the nest. His hypothesis has attracted particular interest because it may explain several key aspects of avian life history, including the evolution of small brood size (Martin *et al.*, 2000a), or faster nestling growth and shorter nestling periods in species with higher predation (Remes and Martin, 2002; Roff *et al.*, 2005).

Given the interrelationship between parental feeding visits and nestling begging, both parents and offspring face inescapable trade-offs as they attempt to communicate while avoiding predation. If nestlings call more, and adults in turn visit the nest more often with food, the young might grow faster and leave the nest sooner, thus reducing the risk of predation. Conversely, however, activity around the nest will be greater, possibly increasing the risk of predation. One way out of the bind is to increase the efficiency of communication both between parents, so that visits can be optimally coordinated (such as synchronized; Sargent, 1993; Raihani *et al.*, 2010), and between parents and offspring, so that feedings can be brief and visits infrequent (Tarwater *et al.*, 2009). Most importantly, the cascade effects of these trade-offs should intensify selection for design features of signals between parents and young that hide them from predators.

Most tests for whether parental activity increases predation have been correlational and thus open to alternative explanations. In particular, since parental visits supposedly increase predation risk by making the nest more conspicuous, the inherent conspicuousness of the nest's location and structure itself must be taken into account. For example, failure to show the predicted increase in predation rates from incubation to nestling periods, when parental activity is higher (e.g., Roper and Goldstein, 1997) could occur because nests that are inherently conspicuous are taken first, thus yielding higher predation rates during incubation. Similarly, failure to find a correlation between predation and parental activity could occur because visit rate and conspicuousness interact in their effects, even in the absence of a direct correlation between predation rate and conspicuousness of the nest site (e.g., Schaefer *et al.*, 2005). Specifically, parental feeding visits might expose well-hidden nests but have no effect on conspicuous nests because they are already obvious, thus yielding no apparent effect of feeding visits overall (Martin *et al.*, 2000b).

Some studies have attempted to control for conspicuousness of nest sites by comparing predation rates at artificial nests without parents to nearby natural nests that appear similarly conspicuous but have visiting adults (e.g., Farnsworth and Simons, 1999). Even careful placement of artificial nests, however, can only roughly simulate the conspicuousness of the natural nest (Fontaine *et al.*, 2007), and using failed natural nests as controls (Halupka and Greeney, 2009) introduces additional confounding variables, such as the chance that predators will return to them. A more convincing approach was taken by Martin *et al.* (2000b), who measured the inherent vulnerability of nests by baiting the same nests with eggs after adults were finished breeding. The effect of parental activity could then be measured as the difference between predation rate with and without the adults at the same nest, and this measure indeed showed an increase in nest predation with parental activity, both within and between species, a result replicated since by other studies (Martin *et al.*, 2000a; Muchai and du Plessis, 2005).

While convincing evidence for a predation cost to parental visits rests largely on just a few studies, a wide array of experimental approaches has shown that adults visit nests less frequently when there is a greater risk that predators are nearby. Such facultative adjustment provides indirect evidence that visits to the nest are indeed risky. Predator removals have increased feeding visit rate in several species (Fontaine and Martin, 2006 a, b; Massaro *et al.*, 2008) and, conversely, presentation of a model predator has reduced nest visit rates (Peluc *et al.*, 2008) or shifted the diurnal timing of visits (Eggers *et al.*, 2005). In a particularly elegant study showing adjustments at both a behavioral and evolutionary scale, a coastal subspecies of swamp sparrow (*Melospiza georgiana*) with high natural rates of nest predation visited nests less often, vocalized less often during visits, and waited longer before approaching the nest in the presence of a model nest predator, than did an inland subspecies subject to lower predation rates (Olsen *et al.*, 2008; see also Ghalambor and Martin, 2002, for similar results on incubation feeding by cavity nesters).

An important caveat to all these studies on nest conspicuousness is that parents may also decrease predation risk through nest defense. Artificial nests are less likely to be depredated than natural nests where adults are in attendance, provided other factors are tightly controlled (Burke *et al.*, 2004; Weidinger, 2002; Zanette, 2002), and they can gain protection by being placed close to an active nest (Fontaine *et al.*, 2007; Picman *et al.*, 1988; Schmidt and Whelan, 2005), or even, in some cases, if they are simply near immobile models of adults (Opermanis, 2004; Trnka *et al.*, 2008). The availability of adults for nest defense probably explains why adults forage closer to their nest when a predator is near (Hakkarainen *et al.*, 2002; Martindale, 1982; Marzluff, 1985).

2. Evidence that Nestling Calls can Alert Predators

It seems intuitively obvious that nestling sounds will attract acoustically orienting predators, but in fact that may not be true, given the varying sensory abilities of predators, the competing demands on their time and attention, and the availability of alternative prey. It is therefore necessary to test this possibility. Unfortunately, direct tests for a predation cost of begging are few, and those that have been done apply methods that limit their results in distinctive ways. Most fall short of quantifying the marginal costs of incremental increases in calling, even though these costs are a key feature of many theoretical models of begging behaviour. Because the predation cost of begging is a key issue in understanding the risks of communication between offspring and parents, we discuss the methods used to tackle this issue, starting with correlational approaches using natural nests and then turning to experiments using playbacks of begging calls and increasingly realistic methods.

The correlational approach was first taken by Redondo and Castro (1992). They found that black-billed magpie (*Pica pica*) nests that had more begging activity, as measured by the number of nestlings gaping or calling, were more likely to be depredated. Also, predation occurred sooner the more nestlings begged, although this result was only significant for the number of gaping nestlings, while showing a trend for number of callers. Interestingly, the results also showed that among partially depredated nests, there was tendency for predators to take those nestlings that were the fastest to beg, although here no distinction between gaping and calling was made. Overall, this study provides some evidence for a predation cost to begging and also suggests that predation costs could be borne by individuals, without necessarily affecting the entire brood (Section II.A.1). It is possible, however, that the correlations between begging and predation may have been due to confounding variables. For example, perhaps parents at those depredated nests had poorer defensive abilities, or had not sufficiently concealed their nests (Moreno-Rueda, 2007). Also, begging intensity was measured at each nest by placing nestlings in a bag and stimulating begging with “a single human vocalization”, a method that might not accurately reflect begging to parents and might be vulnerable to experimenter effects.

Intervening variables might also be important in explaining the negative results of another correlational study on the relationship between nestling vocalizations and predation. Halupka (1998) found that meadow pipit (*Anthus pratensis*) broods that begged with calling when their nests were checked, and were thus presumed to have higher average begging levels overall, were no more likely to be depredated, and had similar survival times, to broods that begged less intensively. He further suggested that parental behavior, especially alarm calls, would normally alert nestlings to the presence of predators and reduce begging in their presence (Section III.A.1). He thus concluded that, in this case, begging calls did not carry a predation cost. One could equally conclude, however, that begging does have a predation cost, but the cost is mitigated by other factors, including parental behavior.

More direct evidence for a predation cost of begging calls comes from experiments using artificial nests with playbacks of nestling calls (Table 2). Such experimental tests began with Haskell (1994), who played western bluebird (*Sialia mexicana*) begging calls next to artificial nests placed either on the ground or in trees at a single study site, and found elevated predation rates at nests playing begging calls on the ground, but not in tree nests. In a follow-up experiment, playing begging calls at different rates at ground nests, he showed that artificial nests with higher call rates were more likely to be depredated. These experiments have been criticized for being unnatural in several ways that may have increased the likelihood of finding an effect (Haskell, 2002; Moreno-Rueda, 2007). Most notably, western bluebirds are cavity nesters with highly detectable and localizable calls (Section II.C.1) that would increase the likelihood of eavesdropping, especially when the calls were played from open nests placed on the ground. Furthermore, the calls were played constantly throughout the day, rather than more intermittently as might be found in natural nests, and nests would not benefit from parental defense. These departures from realism were intentional however, and adopted to increase the likelihood of finding an effect if one existed (Haskell, 1994). Another potential limitation was that the results might have been attributable to a few individual predators, because each experiment was conducted at a single study site.

A playback experiment that removed some limitations of Haskell's (1994) study nonetheless found similar results. Leech and Leonard (1997) conducted a similar experiment on tree swallows but used several study sites to ensure that predators were not the same individuals. They also played back nestling calls from ground and elevated locations, except here the elevated locations were nest boxes identical to those used at nearby study sites. In a further attempt to mimic the natural situation, they broadcast the calls from within the nest boxes, but placed the bait eggs (quail eggs) on a platform outside the nest to avoid confounding signal detection with the predator's ability to take the eggs. Finally, they played calls only in the morning and evening, rather than throughout the day. With all these modifications they, too, found that nestling calls increased the rate of predation, but here in both ground and elevated nests (Figure 1). Placing eggs outside the nestbox might have led to overestimating absolute predation rates, but begging calls clearly increased the risk of predation.

Table 2: Playback studies of the predation cost of begging calls, showing for each the comparison that was its main contribution to the literature, the main features of its experimental design, and its main result.

Common name	Scientific name	Main comparison[a]	Design				Effect on predation rate	Source
			Delivery (/min)	Exemplars, sites[b]	Nest (total n, n per treatment combination)[c]	Duration		
western bluebird	*Sialia mexicana*	Tree vs. ground	25 calls	1 tape, 1 site	90 total, 20-25/cell	12 h/d, for 5 d	Calling > silent control, but only at ground nests.	Haskell, 1994
western bluebird	*S. mexicana*	Low vs. high rate	13 calls (low), 25 calls (high)	1 tape, 1 site	50 total, 25/cell	12 h/d, for 5-6 d	High rate > low rate.	Haskell, 1994
black-throated blue warbler ovenbird	*Dendroica caerulescens* *Seirus aurocapilla*	Tree vs. ground species	2, 7-s bouts	3 tapes, 3 sites	360 nests, 30/cell	12 h/d, for 6 d	Tree sp. > ground sp., but only at ground nests.	Haskell, 1999
tree swallow	*Tachycineta bicolor*	Ground vs. raised	2, 30-s bouts	3 tapes, 18 sites	88 nests, 22/cell	6 h/d, for 1 d	Calling > background sounds at ground and raised nests	Leech and Leonard, 1997
indigo bunting brown-headed cowbird	*Passerina cyanea* *Molothrus ater*	Unparasitized vs. parasitized	1 call (bunting), 5 calls (cowbird)	1 tape, 1 site	45 nests, 15/cell	24 h/d, for 6 d	Parasitized > bunting > silence	Dearborn, 1999
bell miner	*Manorina melanophrys*	Call vs. white noise, With vs. w/o adults	0.5, 8-s bouts	5 tapes, 4 sites	168 nests 28/cell	12 h/d, for 5 d	Call or white noise > silence Call = white noise With = without parents	McDonald *et al.*, 2009

[a] The treatment comparison that distinguishes the study from others; most studies included other comparisons, e.g. call playback vs. silent control.

[b] Trial locations at least 450 m apart from others, as best as we could infer from the reported methods.

[c] Number of nests representing each combination of treatments (= each cell in a crosstabulation of treatments). E.g., call and silent treatments presented in both trees and on ground yield four possible treatment combinations (= cells), which in a balanced design with n=100 would yield 25 nests/cell. Nests per cell usually does not equal the total n divided by the treatments given in the "Main comparison" column, because most studies included additional comparisons.

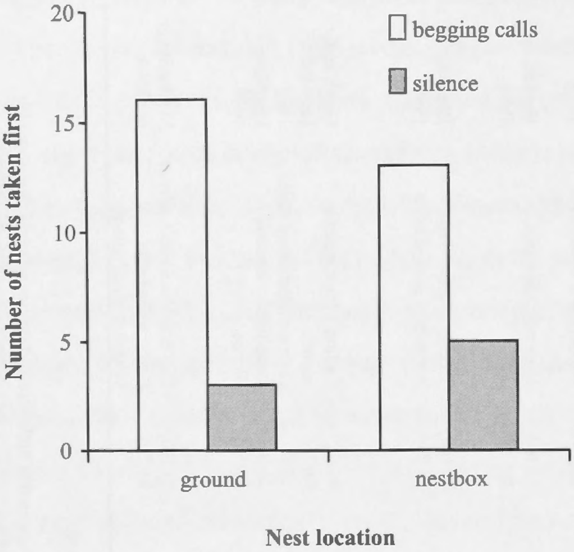

Figure 1. Begging calls attract predators. Number of artificial nests that were depredated first when accompanied by playback of tree swallow begging calls or silence. Nests were placed in pairs, one receiving playback and the other silent, either on the ground or raised outside nest boxes. Nests were fitted with timers so that the exact time of predation was known. (Data from Leech and Leonard, 1997.)

Dearborn (1999) emulated natural conditions still further by including both artificial and natural nests in the same study, to analyze the effects of interspecific brood parasitism on predation rates of parasitised indigo bunting (*Passerina cyanea*) nests. Songbird nests containing nestlings of the brood parasitic brown-headed cowbird (*Molothrus ater*) might be particularly subject to predation, because cowbird nestlings tend to give calls more loudly and at a higher rate than host nestlings, and because adults visit parasitized nests more frequently than unparisitized nests (Hannon *et al.*, 2009). Dearborn (1999) found higher predation at nests playing back cowbird calls compared to silent controls, with playback of indigo bunting nestlings alone receiving intermediate levels of predation. Reassuringly, predation rates at the nests with playback were similar to those at the natural nests they simulated, making it less likely that the playback results were attributable to unnatural characteristics of the nests or playbacks.

Recently, McDonald and colleagues (2009) improved still further on previous experiments, by choosing more natural playback locations, more realistic delivery of calls, more realistic diurnal timing, and better replication of playback stimuli. At four colonies of bell miners (*Manorina melanophrys*), begging calls were played back from speakers placed by used nests, which in turn were placed in species-typical nest locations, in transects starting within the colony and continuing beyond it. Playbacks were made from hundreds of exemplars of begging calls, and were compared with playbacks of white noise modified to have the same amplitude envelope as the begging calls, thus providing a comparison to test whether the frequency structure of the begging calls reduced the likelihood of predation.

Begging playbacks increased predation rates compared to the silent controls, but their effect was no different from the modified white noise playbacks. While McDonald and colleagues (2009) suggest this implies that begging calls are not structured to reduce predation risk (as discussed further in Section II.C), it is also possible that both begging calls and white noise have acoustic features, such as energy dispersed across a wide frequency range, that minimize predation risk, and so predation rates did not differ for that reason. Curiously, predation rates did not differ between nests in and out of the colony, despite adult bell miners being vigorous defenders of nests, clearly a result that requires further study.

Overall, these playback experiments are important because they show that begging calls can attract predators to nests, but they provide relatively little information on actual risk of predation at natural nests for several reasons. First, all the studies use playback at artificial or translocated nests, where predation rates may differ from those at natural nests (Burke *et al.*, 2004; Lindell *et al.*, 2004; Major and Kendal, 1996; Pärt and Wretenberg, 2002; Thompson and Burhans, 2004; Weidinger, 2001). Second, begging calls were played back more continuously than occurs in natural nests. Third, some of the studies lacked replication of playback sounds (Kroodsma, 1990; Kroodsma *et al.*, 2001). Finally, the absence of parents at experimental nests quite likely leads to an overestimate of the absolute costs of begging calls (Section III.A; Halupka, 1998; but see McDonald *et al.*, 2009). Indeed, these experiments are perhaps most useful in showing what the cost of calling would be, were it not reduced by the many anti-predator adaptations discussed throughout this review.

C. DESIGN TO MINIMIZE RISK

1. Signal Design and Risk of Predation: Design to Minimize Risk

If calling by nestlings does increase the risk of attracting predators, then we might expect to see features of call structure or delivery that have evolved to reduce that risk (with the caveat that, all things being equal, begging calls might be selected to be riskier than other vocalizations; Section II.A.1). What sort of design features we should expect depends on how predators use calls to find nests. This process can be broken down into several perceptual tasks: detection, localization, and recognition (Langemann and Klump, 2005).

Nestling calls increase predation risk only if they can be detected by predators. To detect a call, a predator simply has to distinguish its occurrence from the acoustic background. In general, detection improves with lower frequencies, which predators are better tuned to, higher amplitudes, which increase the signal-to-noise ratio, and longer durations and rates, which enhance temporal summation. Concentrating call energy into a narrow band of frequencies usually makes calls stand out from the background noise (Lohr *et al.*, 2003; Pohl *et al.*, 2009). However, spreading it out across a broader band through frequency modulation or other patterning can also make calls more obvious against noise that is simple in structure, such as the sound of a rushing stream. In more complex noise, such as a dawn chorus of singing birds, patterning within calls might instead make them blend into the background (Pohl *et al.*, 2009).

Localizing a call consists of determining its direction and distance. Direction is perceived by interaural differences in spectral composition and arrival time (Langemann and Klump, 2005). Thus direction is more readily perceived for broadband sounds, because the listener's head filters out higher frequencies more than lower ones, and for sounds with an abrupt onset, offset or temporal patterning, because they provide conspicuous markers of arrival times (Brown and May, 2005; Fay and Popper, 2005). Distance is perceived by the degradation and attenuation of the sound after it has passed through the environment; the farther the sound has traveled, the more it has degraded and the more energy it has lost, with higher frequencies showing such losses sooner (Naguib and Wiley, 2001). All these cues to localization are enhanced by broader band and more complex calls (Langemann and Klump, 2005).

The effects of attenuation and degradation are particularly important in affecting predation risk, because calls are safest if they do not reach the predator in the first place. Thus a nestling's first line of defense is to call quietly and at high frequencies, to reduce the transmission distance of the calls. The acoustic properties of the nest and its general location may help considerably to reduce transmission distance, at least in some directions. For example, nest cavity walls have been shown to block sound (Lampe *et al.*, 2004; Perera, 2008), nest cavity openings to direct calls (Mennill and Ratcliffe, 2004), and nest locations to mask calls (Fairhurst, 2006). These nest features might well be under selection to hide calls from predators, a promising topic for further research.

Recognition is the ability of a predator to classify the sound as coming from a nestling, as opposed to some other sound source. Begging calls might confound predators' attempts at recognition through crypsis, in which calls resemble background noise, or mimicry, in which calls resemble sound sources that are not profitable prey. For instance, American dipper (*Cinclus mexicanus*) nestlings produce hissing begging calls, which may make them cryptic next to the mountain streams where they occur (Fairhurst, 2006). Similarly, nestlings in some cavity nesting species, such as black-capped chickadees (*Poecile atricapillus*) also give hissing begging calls, but here the calls may mimic the sounds of a snake (Popp and Ficken, 1991; Section II.D).

In summary, there are several acoustic properties that might make calls hard for predators to detect, locate or recognize. Specifically, within the frequency range of begging calls, higher frequencies worsen detection and localization; narrower bandwidths, gradual onsets and offsets, and simpler structure worsen localization; and quieter, shorter sounds or less repetition worsen all aspects of call perception. Thus, predation should select for short, low-amplitude, high-pitched calls without sharp amplitude peaks. Selection on call bandwidth and complexity is harder to predict; simple, narrow band calls offer fewer cues to location, but might be easier to detect, depending on the background sounds.

Although an engineer could design a call that is difficult or impossible for a predator to detect, it could be impossible for nestlings to evolve such calls because if they changed their calls to avoid predation they would also lose features they need for communication. To the degree that parents and predators detect and recognize begging calls similarly, nestlings are in a direct bind between being heard and being overheard. In particular, virtually all of the call features that correlate with nestling hunger and age (Table 1) – lower frequency, greater bandwidth, and increased rate, duration, and amplitude – also increase the detectability of calls to predators. Indeed, it may be no coincidence that nestlings incur costs to signal hunger, as proposed by theoretical models of the evolution of reliable begging signals.

2. Signal Design and Risk of Predation: Evidence

Evidence that nestling calls have design features to reduce the risk of predation rests on a few interspecific comparative analyses and one experimental study. Redondo and Arias de Reyna (1998) noted that, contrary to predictions about cryptic design, most of the 24 species they examined had broadband begging calls (1-7 kHz). Nonetheless, the species that nest in the open, and whose young were thus easier for predators to locate and access (Fontaine *et al.*, 2007), produced calls with narrower frequency ranges and higher frequencies relative to their body size, both features which should make their calls less detectable and localizable (Section II.C.1). In contrast, Popp and Ficken (1991), examining a much larger and taxonomically broader sample of calls from 75 species, found a bewildering diversity in call bandwidth and structure, with no differences between cavity and open nesters in call duration, frequency range, or maximum or minimum frequency. In addition to having different results, these studies are inconclusive because they did not account for phylogenetic variation in call structure (Harvey and Pagel, 1991).

Only two studies have attempted to control for phylogeny when examining nestling call structure and predation risk, and both found that species at greater risk of predation had begging calls of higher frequency. Haskell (1999) reduced the effect of phylogeny by making comparisons within just one passerine family (wood-warblers, Parulidae), although four of the five tree-nesting species were more closely related than any pair of the five ground-nesting species tested (Lovette and Bermingham, 2002), so there were few evolutionarily independent contrasts (Harvey and Pagel, 1991). Nonetheless, all five ground-nesting species, which were assumed to be at greater risk of detection by predators, had higher frequency and, at older ages, less rapidly modulated calls than all five tree-nesting species. Briskie *et al.* (1999) controlled for phylogeny and also found that species with higher predation rates had quieter calls and higher frequencies. They used the method of independent contrasts to control for body size and known phylogeny across 24 species of diverse nesting ecology for which they had measured nest predation rates.

While Briskie and colleagues' (1999) study controlled for phylogeny, it does not differ from other correlative studies in that the relationships might be explained by confounding variables, especially considering how different the acoustics of nest cavities – which generally suffered lower predation rates – must be from those of open nests (Horn and Leonard, 2002; Ruxton, 2009). Thus some acoustic features that have been attributed to avoidance of predation might be caused by differences in nest-site acoustics. It is also surprising that the relationship between call features and predation rate held only within cavity nesting species, not within the open nesting species that were most prone to predation and thus under especially strong selection for concealment.

Haskell (2002), however, raised a fundamental criticism of all studies correlating nestling call structure with rates of predation. He pointed out that the key question is not whether call structure correlates with overall levels of predation, but whether the increase in conspicuousness brought on by calling results in an incremental increase in predation risk (Haskell, 1996; see also Martin and Briskie, 2009). In other words, it is irrelevant to count losses caused by predators that find nests in ways other than by overhearing nestling calls. Haskell (2002) attempted a meta-analysis using published data to compare predation rates on control nests to the additional predation rates introduced by playback, but there were only three published studies available at the time, and the result was inconclusive. His approach, however, could be used in future experiments that apply a consistent experimental protocol to several populations or species differing in their natural predation rates (see, for example, Ghalambor and Martin (2002) for such a test on adjustment of incubation feeding rate in response to predation). Until such tests are done, comparative evidence for antipredator design features of begging calls remain inconclusive.

Only one experiment has compared the effects of begging calls of different structure on the risk of predator attraction. Haskell (1999) compared predation rates on baited artificial nests from which the calls of ovenbirds (*Seiurus aurocapillus*) or black-throated blue warblers (*Dendroica caerulescens*) were broadcast, two of the species included in his comparative study (above). Ovenbirds nest on the ground and are more vulnerable to predators than black-throated blue warblers, which nest in trees. Consistent with this difference in risk, ovenbirds, like the other ground-nesting warblers included in his comparative study, have higher frequency calls that should be more difficult to detect. The playback experiment confirmed expectations based on call design. The calls of 8-day-old black-throated blue warbler nestlings played from the ground attracted more predators than the calls of 8-day old ovenbird nestlings. These results suggest that more vulnerable warblers indeed evolve more cryptic begging calls.

D. CALLING IN THE ABSENCE OF PARENTS

Perhaps surprisingly, nestlings of many species call when parents are absent from the nest, which could make them particularly vulnerable to predators. The costs of begging when parents are present can be reduced through adult behaviors such as approaching the nest cautiously to avoid detection (Section II.B.1), silencing noisy young with alarm calls (Section III.A), or inducing young to beg only at specific cues of parental arrival (Sections III.B, IV.A). Nestling vocalizations in the absence of parents, by contrast, are not afforded such protections, despite the fact that at times parent-absent calling can be quite conspicuous; some begging calls of nestling yellow-headed blackbirds (*Xanthocephalus xanthocephalus*) which are given both when parents are at the nest and when they are away, can be heard up to a kilometer from the nest (Price and Ydenberg, 1995)! Thus, it may be that the predation costs of nestling vocalizations occur when parents are not at the nest, rather than when they are present. Because parent-absent calling has received little attention in the literature, we first describe the types of calls nestlings may use and their occurrence, before moving on to consider their potential impacts on predation.

1. Types and Occurrence of Calls Given in the Absence of Parents

There are at least two types of calls given by young in the absence of parents, which probably have different causes and consequences for predation risk (Table 3). *Parent-absent begging* consists of long, broad frequency, relatively loud calls usually given to stimuli other than parental arrival at the nest (Budden and Wright, 2001b; Dor *et al.*, 2007; Leonard and Horn, 2001d). These calls are often also referred to in the literature as mistaken begging, begging errors, or secondary begging, and they seem to be

Table 3: Studies of parent-absent calling. Call type: B parent-absent begging; R repeat call (call type inferred when not specifically described). Call properties: refer to reported means, or estimated means from spectrograms. Relationship with: + call rate or intensity increases; - call rate or intensity decreases. Possible functions: ER error, e.g. response to inappropriate stimuli; RC remote communication; SN sibling negotiation. * call type or function not specifically mentioned by author, inferred from literature.

Common name	**Scientific name**	**Call type**	**Call properties**					**Relationship with**			**Possible functions**	**N**	**Source**
			Amp at 50 cm	**Peak Freq (kHz)**	**Freq Range (kHz)**	**Duration of single call (ms)**	**Rate**	**Hunger**	**Age**	**Other**			
rusty-breasted cuckoo	*Cacomantis sepulcralis*	R		7	3	100	1/s				RC	1	Grim, 2008
common cuckoo	*Cuculus canorus*	R		8	1		2/s	+			RC	10	Sicha *et al.*, 2007
blue tit	*Cyanistes caeruleus*	B				845ms/event	10/hr	+			ER	22	Dickens and Hartley, 2007
southern gray shrike	*Lanius meridionalis*	B						+	-		ER	9	Budden and Wright, 2001
brown-headed cowbird	*Molothrus ater*	B						+			ER	46	Rivers, 2009
Wilson's storm petrel	*Oceanites oceanicus*	R		5	2-3	30-200	1/s				RC*	5	Quillfeldt, 2002
house sparrow	*Passer domesticus*	B						+	-		ER	16	Dor *et al.*, 2007
great tit	*Parus major*	B							-		ER	15	Moreno-Rueda 2005
coal tit	*Periparus ater*	B							-		ER	44	Moreno-Rueda, 2005
white-browed scrubwren	*Sericornis frontalis*	B	44dB	5	6	200-800		+			ER	2 – 14	Maurer *et al.*, 2003; Magrath *et al.*, 2007
white-browed scrubwren	*S. frontalis*	R	31dB	7	1	50-150	1/s	+	+	+ to contact calls	RC, SN	2-14	Maurer *et al.*, 2003; Magrath *et al.*, 2007
spotless starling	*Sturnus unicolor*	R		6	2.8	160	1/s	+		+ when siblings +	RC, SN	9 - 16	Bulmer *et al.*, 2008
tree swallow	*Tachycineta bicolor*	B						+	+		ER	12 (2001); 27 (2005)	Leonard and Horn, 2001; Leonard *et al.*, 2005
barn owl	*Tyto alba*	R*				640	8-15/m	+		- when siblings +	SN	7-26 (2001); 74 (2009)	Roulin *et al.*, 2000; Roulin, 2001; Roulin *et al.*, 2009
yellow-headed blackbird	*Xanthocephalus xanthocephalus*	B						+	-		ER, SN	16	Price and Ydenberg, 1995
yellow-headed blackbird	*X. xanthocephalus*	R								+ when siblings +	RC	16	Price and Ydenberg, 1995

indistinguishable from the calls used to solicit food in the presence of parents (Magrath *et al.,* 2007). *Repeat calls* are given seemingly without prompt in the time periods between parental visits (Anderson *et al.*, 2010; Roulin *et al.*, 2000), typically at a rate of approximately one per second (Figure 2; Bulmer *et al.,* 2008; Grim, 2008a; Maurer *et al.,* 2003; Quillfeldt, 2002; Šicha *et al.,* 2007). They are commonly quieter, shorter, have a narrower frequency range than true begging calls, and are likely to be relatively difficult for predators to detect, at least from a distance (Section II.C.1; Bulmer *et al.,* 2008; Magrath *et al.,* 2007; Maurer *et al.,* 2003). Unfortunately, many authors refer to both types of calls as "parent-absent begging" which we believe obscures real differences in call causes and consequences. Furthermore, the acoustic features of calls given by nestlings in the presence and absence of parents are often not described, so we use the working definition that repeat calls are those given on a regular tempo in the absence of parents.

Nestling calling in the absence of parents appears to be relatively common in a wide variety of species. For example, parent-absent begging is common in tree swallows (Leonard and Horn, 2001d; Leonard *et al.*, 2005) and house sparrows (*Passer domesticus*; Dor *et al.*, 2007). Repeat calling also occurs in many taxa, including owls (Roulin *et al.,* 2000) cuckoos (Grim, 2008a; N. Langmore, pers. comm.; Šicha *et al.,* 2007), tube-nosed seabirds (Quillfeldt, 2002), and songbirds (Anderson *et al.*, 2010; Bulmer *et al.,* 2008; Grabowski, 1979; Maurer *et al.,* 2003; Price and Ydenberg, 1995). Among songbirds, noisy miners (*Manorina melanocephala*) and red wattlebirds (*Anthochaera carunculata*), both in the family Meliphagidae, have unusually conspicuous repeat calls audible from tens of metres away from the nest (personal observations). Repeat calling also occurs in woodpeckers, bee-eaters, herons, and raptors (Johnstone and Roulin, 2003; Roulin *et al.,* 2000). Yet despite their potential pervasiveness and clear potential to increase the risk of predator eavesdropping, the causes and potential functions of parent-absent vocalizations have been examined experimentally in only a few species, and fewer studies have addressed their potential consequences for predation.

The costs of calling in the absence of parents could be relatively high, but there is limited evidence to evaluate its impact on predation risk. Playback experiments show that predators can hear and be attracted to begging calls in the absence of parents

(Section II.B), and mistaken begging could be particularly costly if nestlings respond to cues produced by predators themselves (Section II.D.2.a). Further, when parents are absent they are not able to defend young from predators or silence them with alarm calls (Section III.A). Despite these factors, parent-absent calling might not necessarily increase predation risk. Repeat calls in particular are often cryptic (Maurer *et al.*, 2003), and some young can assess danger themselves and stop calling when they detect a predator nearby (Section IV.C), or they can be discerning about the cues of parental arrival to which they call (Section IV.A). Given the potential for calling in the absence of parents to place young at risk from predators, we need more field research to document its occurrence and assess its costs and benefits.

Thus far, the relationship of repeat calls to predation risk has only been investigated in white-browed scrubwrens, and evidence that they elevate predation risk is equivocal. Parents can silence nestlings giving repeat calls with alarms even when not directly at the nest, and thus may be able to decrease the risk of nestlings being overheard by hunting predators (Platzen and Magrath, 2004, 2005). Further, scrubwren repeat calls tend to be relatively quiet and have a narrow frequency range, and are likely to be more difficult for predators to detect than are true begging calls (Figure 2; Table 3; Maurer *et al.,* 2003). Additionally, nestlings are able to assess danger independently of their parents, and silence themselves in response to cues of danger (Section IV.C.). Despite this, playback of long bouts of repeat calls at the upper range of their natural amplitude (around 65 dB at 20 cm) at active scrubwren nests did attract more avian predators than the playback of amplified background noise, suggesting that even relatively soft vocalizations at the nest can increase the risk of predation (Haff and Magrath 2011).

2. Possible Functions of Calling in the Absence of Parents

Why nestlings vocalize in the absence of parents falls into three broad hypotheses; (a) nestling error; (b) sibling communication; and (c) “remote” communication with parents. The potential predation costs of calling in the absence of parents probably varies with each underlying cause of the behavior; error in begging is likely to increase predation risk, for example, while calls used in sibling communication or used to communicate with parents might reduce nest detectability, as we explain below.

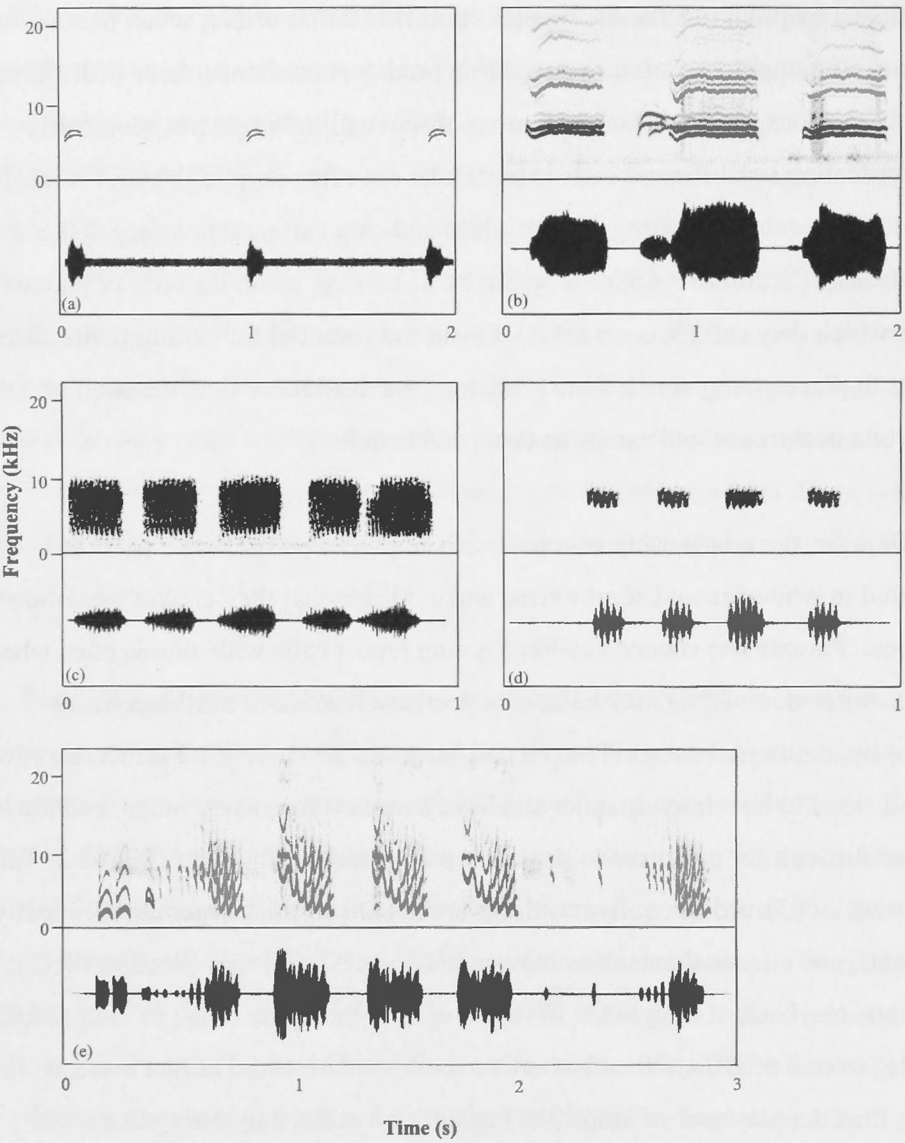

Figure 2. Examples of white-browed scrubwren calls used in parent-offspring communication. (a) "Peep" repeat call; (b) "whine", used in parent-present and parent-absent begging; (c) adult "buzz" or "ground" alarm, given in response to predators on the ground; (d) adult "aerial" alarm, given in response to flying predators; (e) example of one adult provisioning call, given to nestlings. Upper panels contain sonograms created in Raven 1.3 using settings: Blackman filter at 582 samples, and 3 dB filter bandwidth, 2.27 ms grid time, 21.5 Hz frequency grid, and 12 Hz of window scaling and 1s per line; lower panels show waveforms.

a. Begging errors and signal detection

Parent-absent begging frequently appears to be a mistaken response to cues other than adult arrival, and as such could greatly increase predation risk at the nest. Most typically, parent-absent begging calls are given in response to stimuli that are similar to cues of parents arriving at the nest, such as nest vibrations, passing shadows, adult activity outside the nest, or calls made by other bird species (Budden and Wright, 2001b; Dor *et al.,* 2007; Leonard and Horn, 2001; Magrath *et al.,* 2007). Nestlings sometimes also mistakenly beg to cues made by potential predators (Dearborn, 1998; Halupka, 1998; Khayutin, 1985; Leonard *et al.,* 2005; Moreno-Rueda, 2005; Schaller and Emlen, 1961). The most frequently proposed explanation of parent-absent begging is that it is simply an error on the part of nestlings, which must balance the need to compete for food with the risk of responding to the wrong stimulus. Indeed, mistaken begging is especially common when there is high incentive to respond quickly to adult arrival (Leonard and Horn 1996, 2001d), when nestlings have not yet developed the cognitive capacity to correctly detect cues of adult arrival (Clemmons 1995a), and when nestlings must make decisions about when to beg based on limited or unreliable information (Madden *et al*., 2005a). Errors in begging can clearly have a direct impact on predation risk, by increasing the likelihood of being overheard by predators that by coincidence are within earshot, and by begging to cues from searching predators and so helping them find the nest.

As predicted by signal detection theory, nestlings cannot increase their responsiveness to cues of adult arrival while simultaneously decreasing their frequency of response to inappropriate cues, since lowering the threshold for response to parents will increase mistaken begging (Figure 3a; Dor *et al.* 2007; Leonard *et al.* 2005; Wiley, 1994). The frequency of parent-absent begging in most species should therefore represent a trade-off between the costs of missing out on being fed and the risk of predation (Dickens and Hartley, 2007; Dor *et al.,* 2007; Moreno-Rueda, 2005). In fact, because nestlings that are the first to beg are often the first to be fed (Dearborn, 1998; Leonard and Horn, 1996; Smith and Montgomerie, 1991; Teather, 1992), there is a strong incentive to respond rapidly to subtle cues of adult arrival, and mistaken begging could therefore simply be a consequence of selection for a rapid begging response (Budden and Wright, 2001a; Leonard and Horn, 2001b; Roulin, 2001). Hunger also clearly affects the decision rules that nestlings use in weighing the costs of vocalizing to

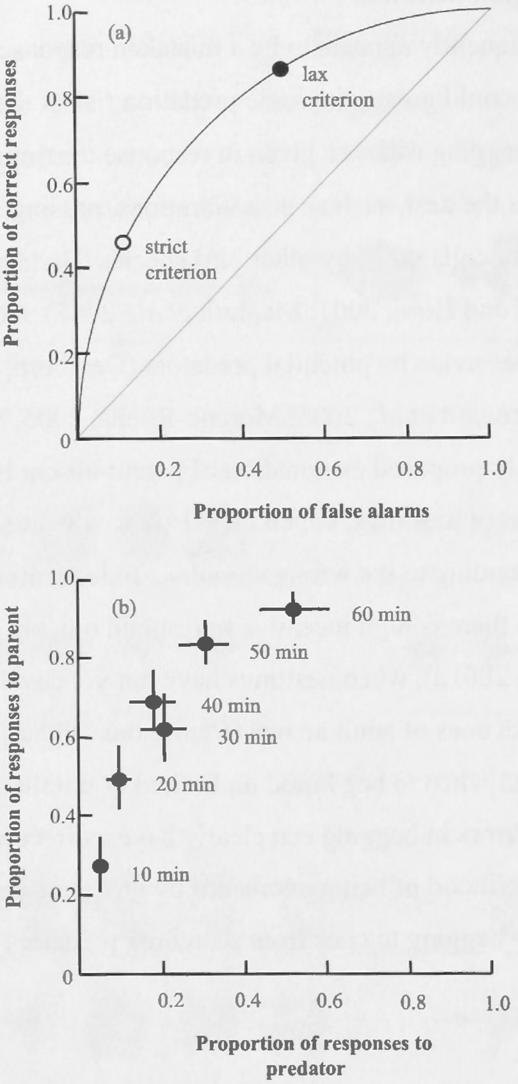

Figure 3. The trade-off between a nestling's responsiveness to cues of adult arrival and to inappropriate stimuli. (a) Schematic plot of the proportion of correct detections of an appropriate signal versus the proportion of incorrect responses (false alarms); black curve shows one possible relationship for a detectable signal; grey line shows the relationship for an undetectable signal (i.e. chance response); points illustrate that an increase in the receiver's responsiveness increases not only correct detections but also false alarms. (b) Response of nestling tree swallows to playback of the sounds made by parents or a predator, the common grackle, during a period of food deprivation; circles and lines represent mean ± SE positive responses out of five presentations that were given every 10 minutes. (Data from Leonard *et al.*, 2005.)

an ambiguous stimulus against the benefits of being fed, and the overall frequency of parent-absent begging increases with nestling short-term need (Table 3; Budden and Wright, 2001a; Dickens and Hartley, 2007; Leonard and Horn, 2001b; Maurer *et al.*, 2003; Rivers, 2009). Thus nestling need, combined with error in detection of adult arrival, may lead to increased detectability of nestlings when parents are not near the nest, and consequently an elevated risk of predation.

Tree swallows provide an example of the trade-offs between nestlings' abilities to simultaneously enhance detection of parental arrival and decrease the risk of predation. In this species there is a premium on rapid response to subtle cues of adult arrival, as the first nestling to respond is the most likely to be fed (Leonard and Horn, 1996). Nestlings respond rapidly to cues of adult arrival, and response time decreases as nestlings become hungrier (Leonard and Horn, 2001d; Leonard *et al.*, 2005). However, hungry nestlings also respond more frequently and more rapidly to inappropriate cues of adult arrival, such as sounds of a nest predator, the common grackle (*Quiscalus quiscula*) landing on the nest box (Figure 3b; Leonard *et al.*, 2005). Thus, as nestlings become increasingly responsive to cues of adult arrival, they also increase the likelihood of mistakenly responding to cues that may instead be made by a predator.

b. Communication among siblings

Calling in the absence of parents – perhaps primarily repeat calls – are used by some species to facilitate communication among siblings. The "sibling negotiation hypothesis" suggests that extended bouts of calling between parental visits are signals directed at siblings, and are used to negotiate over who is to receive the next meal (Johnstone and Roulin, 2003). Specifically, siblings communicate their motivation to compete through calling in the absence of parents, and use the vocalizations of their nest mates to assess how likely they are to win access to food at the next parental visit (Roulin *et al.,* 2009). Nestlings then adjust their calling level at feeding visits accordingly. Thus, sibling negotiation is an adaptive, "iterative" process, in which nestlings challenge each other over extended periods of time (Roulin *et al.,* 2000), and adjust their behavior until they arrive at an optimal equilibrium (Roulin *et al.,* 2009). Barn owl (*Tyto alba*) nestlings regularly call for long bouts between adult visits as a means of negotiation between siblings (Roulin, 2001). Calling increases with hunger, and less hungry nestlings call for shorter durations and retreat from physical competition more than hungry nestlings (Roulin *et al.,* 2000, 2009). Similarly, spotless starling (*Sturnus unicolor*) nestlings call regularly in long bouts not associated with a stimulus (Bulmuer *et al.,* 2008). Nestlings exposed to playbacks of repeat calls decreased their own competitive begging score (pushing, climbing and preening) during the next parental visit, suggesting that less needy nestlings decrease physical competition for food.

We see several ways in which sibling negotiation might affect predation risk. Clearly, extended bouts of calling by nestlings could increase the risk of predator eavesdropping, particularly if nestlings assess each other's need by increasing the amplitude or general intensity of their own calls in response to their siblings' calls (Bulmer *et al.,* 2008; Roulin, 2001b). Alternatively, if negotiation over who is to receive the next meal makes parental visits more efficient and less visually and acoustically conspicuous, then repeat calls could actually reduce the risk of nest detection by predators when parents are at the nest. A reduction in risk seems particularly likely if nestlings negotiate using repeat calls, rather than parent-absent begging, since "repeat calls" are usually less conspicuous (Section II.D.1).

c. Remote communication with parents

Young can use repeat calls to communicate their location or hunger level to parents, with varying effects on the risk of predation (Bulmer *et al.,* 2008; Maurer *et al.,* 2003; Price and Ydenberg, 1995). Signaling location could expose young to a high risk of predator eavesdropping, for example, while signaling hunger might not necessarily increase that risk, and could even reduce risk by helping to make parental visits to the nest more efficient.

Signaling location is potentially an important function of repeat calls for colonial nesting species and for young birds that have left the nest, but could also increase the risk that young will be detected by a predator. Repeat calls might assist colonially breeding adults find their offspring, particularly in species such as storm-petrels, which nest in burrows and only visit the nest at night (Quillfeldt, 2002). While colonially nesting seabirds often face relatively little risk from predators, the predation risk associated with repeat calls may be particularly important for fledgling songbirds, which are mobile, dispersed and often hidden in dense cover, and so must call to convey information about their location to foraging adults (Kunc *et al.,* 2009; Magrath *et al.,* 2006). Eavesdropping by predators at this stage may present a serious risk because fledglings can have loud calls to assist parents in finding and recognizing them (Beecher *et al.,* 1981a, 1981b).

Despite the possibility of eavesdropping by predators, repeat calls could reduce the overall risk of predation by remotely communicating nestling hunger to adults, thus allowing adults to assess nestling need from afar and minimize the number of visits to the nest. If repeat calls signal little hunger, adults could decrease the number of visits to the nest, while if repeat calls signal increasing hunger parents could increase rates or food loads to reduce nestling conspicuousness. There has been little study of this possibility, in contrast to evidence that begging calls do signal hunger to parents (Section II.A.2). Šicha *et al.* (2007) used a call playback experiment to test whether adult reed warblers (*Acrocephalus scirpaceus*) increase provisioning in response to the repeat calls of nestling common cuckoos (*Cuculus canorus*), but found no relationship between repeat call intensity and adult provisioning rate. The authors did not look at food load, however, and so it is possible that adults could have increased the amount of food they brought to nestlings without increasing their rate of visiting the nest, as might be expected in a high predation environment (Tarwater *et al*., 2009). The use of repeat calls by underfed fledglings to signal hunger is likely to be particularly costly, if hungrier nestlings call more conspicuously and are consequently easier for predators to detect (Magrath *et al*., 2006; Naef-Daenzer, 2001). If so, this could help explain the general pattern that underweight fledglings are more likely to die before reaching independence than their heavier counterparts (Magrath, 1991; Perrins, 1965).

Nestlings might be able to use repeat calls to communicate remotely with parents about hunger, or even danger itself, when predators are nearby. For example, because repeat calls can have acoustic properties that should make them difficult for predators to hear from a distance, they could allow nestlings to communicate with parents about hunger even in the presence of predators (Maurer *et al.,* 2003; Price and Ydenberg, 1995). Alternatively, nestling repeat calls could be a "watchman's song" (Wickler, 1985), signaling to parents that young have not detected any nearby disturbances, and that it is safe for adults to approach the nest. Neither of these hypotheses has been tested.

E. OTHER CALLS BY YOUNG

When danger is immediate, such as when a predator is at the nest, young can use several other acoustic signals that might help increase their chances of surviving the encounter. These types of signals can be directed at parents, at siblings, or at predators themselves, and fall into two broad categories: (a) distress calls, such as cries or screams, which could serve either as a "call for help" to their parents (Darwin, 1872), as a warning to siblings, or as a mechanism to startle predators into momentary retreat; and (b) defensive signals, such as acoustic mimicry of more threatening species, which could startle or frighten approaching predators but may well also be heard by parents. These defensive calls could therefore communicate directly with adults, or could reduce the need for defense, including alarm calls, by adults.

Nestlings across a broad range of taxa give screaming vocalizations when handled by a human or a predator (Roulin, 2001b). For example, tropicbird (*Phaethon sp.*) nestlings give "deafening" screams when handled, which makes one "glad to put them down" (Skutch, 1976). Most studies have suggested that nestling screams serve to attract parents (Benedict, 2007; Chaiken, 1992; Klump and Shalter, 1984; Redondo and Carranza, 1989). Parents attracted to the cries of their young can attempt to assist them by either distracting a predator, or by directly attacking it. For example, playback experiments on European starlings (*Sturnus vulgaris*) and magpies demonstrate that nestling screams attract parents, which are then likely to engage in aggressive defensive behaviors around the nest (Chaiken, 1992; Redondo and Carranza, 1989). Screams may also foil predators by frightening them, or by sending brood mates to cover (Roulin, 2001b). Roulin (2001b) suggested that nestling screaming can be so effective in deterring predation that it could mitigate the costs of conspicuous nestling begging. In support of this idea, a literature survey revealed that screaming was more frequently reported in species that had nestling begging calls with a broader frequency range, which is likely to make them more vulnerable to eavesdropping (Roulin, 2001b). A simpler interpretation of this pattern, however, is that nestlings that produce broadband vocalizations of any kind are more likely to be noticed and described as producing screams, as opposed to less subjectively startling sounds. Nonetheless, the possibility bears further study, because it would provide a clear example of how mitigating factors should be included in any account of the predation costs of vocalizations.

Nestlings of some species also produce defensive sounds and displays that probably serve to startle or repulse potential predators. For example, some pigeons and owls use bill clacking or snapping in conjunction with other defensive displays such as swaying, feather puffing, or noxious discharge of feces and preen gland substances to deter predators (Skutch, 1976). Other nestlings use calls and displays that seem to mimic threatening species. Nestling chickadees, titmice and tits (family Paridae) hiss and lunge when disturbed, for example, and nestling hoopoes (family Upupidae), woodhoopoes (family Phoeniculidae), and wood warblers (*Phylloscopus sibilatrix*) all hiss and display when approached by human observers (Apel and Weise, 1986; Sibley, 1955; Skutch, 1976). The behavior appears to mimic a snake and is startling even to observers prepared for the experience (Apel and Weise, 1986; Sibley, 1955). Similarly, burrowing owl (*Athene cunicularia*) nestlings use a buzzing call when threatened that is reported to mimic the tail shaking of a rattlesnake (Rowe *et al.*, 1986). Perhaps the most bizarre example of potential Batesian mimicry comes from northern flickers (*Colaptes auratus*), in which nestlings produce a buzzing when parents visit the nest, as well as when they are away, which has been likened to the sound produced by a hive of bees (Sibley, 1955). This "nestling buzz" is thought to deter potential nest predators such as squirrels (Wiebe and Moore, 2008). Thus far, the effectiveness of enemy mimicking or other defensive displays in nestlings has not been tested. Potentially, nestling defensive calls could affect predation risk indirectly, such as by allowing adults to use fewer alarm calls around the nest and thus reducing the risk of nest detection by predators (Section III.A). Alternatively, defenses such as the continuous buzzing of nestling flickers might be a "watchman's song", or another form of communication with parents that has evolved to be "cryptic", at least in the sense of not being recognizable as produced by a helpless nestling. Similarly, other apparently mimetic calls might communicate with parents as well as with predators. Further research using playback experiments is clearly necessary to directly test how such calls might affect predation risk and parent-offspring communication.

III. PARENTAL VOCALIZATIONS

Parents communicate with their offspring primarily about predators and food. Parental alarm calls potentially provide information to young about danger, which can silence young or otherwise make them less conspicuous to predators. However, as we shall see, not all parental alarm calls are directed to young, so it is necessary to carry out playback experiments to test what information is conveyed to offspring. Alarm calls might even place young at risk, as discussed in Section IV, by alerting predators that a nest is nearby. Parents also commonly give provisioning calls when they arrive at the nest to feed young, and they too could affect the risk that young are taken by predators, such as by increasing the risk of predator eavesdropping or by decreasing that risk by ensuring that young will beg only when it is appropriate to do so. Finally, we consider other types of parental calls that could affect the risk of offspring predation, including all-clear signals and calls used to lead young to safety.

A. ALARM CALLS

The calls made by young birds can betray their presence to predators (Section II.B), but parents might reduce this risk by giving alarm calls to warn nestlings to remain quiet or otherwise inconspicuous. Even if young are already quiet, they could betray their presence by being conspicuous in other ways, such as by movement, by being in visible positions in the nest, or through ungainly flight and other conspicuous behavior after fledging. It is important to know if parents can communicate with their young about danger, because they could thereby reduce the risk that their young will be detected or located by predators, and so affect our estimate of the costs of communication (Section II.A). Although parents do give alarm calls during breeding, they may function to communicate with other adults or predators rather than with their young (Caro, 2005; Klump and Shalter, 1984), so it is essential to test explicitly whether parents do communicate with young about danger.

It is important to know not only whether parents communicate with young about predators, but also what information they convey, because an individual's best response can depend on the type of predator or degree of danger (Caro, 2005; Evans, 1997; Zuberbühler, 2009). The issue of alarm call meaning and response has been studied in detail only for communication among adult vertebrates, but young should also respond appropriately to different alarm calls. The meaning of alarm calls has been most thoroughly studied in mammals, in which distinct alarm calls can convey information about different types of predators, for example in vervet and Diana monkeys (*Cercopithecus aethiops* and *C. diana*; Seyfarth *et al.*, 1980; Zuberbühler, 2000a,b,c). In contrast, sciurid rodents appear primarily to communicate about the degree of danger and therefore urgency of escape, rather than predator type (Blumstein, 2007; Furrer and

Manser, 2009), while meerkats (*Suricata suricatta*) communicate about both predator type and urgency (Manser *et al.*, 2002).

In birds, the most common alarm calls are usually classified as "mobbing" or "flee" alarm calls. Mobbing calls are given to terrestrial or perched predators not posing an immediate threat, and prompt others to approach and harass a predator, while flee (or "aerial") alarms are commonly given to hawks and other predatory birds, at least when in flight, and prompt others to freeze or flee for cover (Bradbury and Vehrencamp, 1998; Evans, 1997; Klump and Shalter, 1984). Either might also communicate with the predator, for example by informing the predator it has been seen and has lost the element of surprise (Zuberbühler, 2009). Both mobbing and aerial alarm calls can convey information about the degree of danger, related to the type of predator (Templeton *et al.*, 2005), its proximity (Leavesley and Magrath, 2005), or current behavior (Griesser, 2008).

It is necessary to consider the development and vulnerabilities of young to fully understand parental communication with offspring about danger. Young can change in their response to parental alarm calls as they age, either because of constraints or adaptation (Hollén and Radford, 2009). Altricial birds, in particular, suffer constraints imposed by sensory development, which mean that they can be unable to hear some alarm calls until they reach a specific age (Khayutin, 1985). At the same time, young can be vulnerable to different predators at different stages of development, with a dramatic change after they leave the relative safety of the nest. These changes in vulnerability might require adaptive changes in response to specific alarm calls (Magrath *et al.*, 2006). In this section, therefore, we consider the types and strength of evidence that parents communicate with young about danger, the information they convey, and the development of responses by young.

1. Parental Alarm Calls and Chick Behavior: Observational Evidence

Parents in many species give alarm calls when they have young, and alarm calling and other forms of defense usually increase during the nesting cycle (Caro, 2005; Klump and Shalter, 1984; Lima, 2009; Montgomerie and Weatherhead, 1988). In altricial birds, the intensity of calling and defense typically increases until fledging, and declines some time afterwards. This pattern is consistent with the brood becoming more valuable because the investment required to replace it increases (Montgomerie and Weatherhead, 1988). At the same time, older nestlings are likely to be more conspicuous to predators, and so the benefit of alarm calling and other forms of defense is likely also to increase simply because young are more vulnerable to detection by predators (Fasanella and Fernández, 2009; Harvey and Greenwood, 1978; Greig-Smith, 1980). In support of the idea that the timing of alarm calling is related to chick conspicuousness, reed warblers (*Acrocephalus scirpaceus*) start giving alarm calls to a human near the nest when their young are about 3 days old, the age at which nestlings start to call while begging (Davies *et al.*, 2004). Overall, therefore, greater alarm calling with brood age is consistent with adults communicating with increasingly conspicuous and vulnerable young (Section IV.B).

Observational studies suggest that some alarm calls communicate with young, and cause them to go silent or otherwise become less conspicuous. Furthermore, in several cases parents give more than one type of alarm call, with only one apparently used to silence young, while others are used to communicate with adults or predators. For example, rates of 'seep' alarms given by European robins (*Erithacus rubecula*) increased with the age and presumably conspicuousness of young, and fledglings stopped giving contact calls when their parents gave these alarms (East, 1981). In contrast, 'tic' alarms appeared to act as a distraction display to draw predators away from the nest. Similarly stonechat (*Saxicola torquata*) parents called at a higher rate to older nestlings and fledglings, with one alarm call type appearing to silence young and the other to distract predators (Greig-Smith, 1980). The American goldfinch (*Carduelis tristis*) also has two alarm calls, with 'sweeet' calls given throughout the year and apparently directed to other adults, and 'bearbee' calls given only in the breeding season and associated with begging nestlings becoming silent (Knight and Temple, 1986). Observational evidence therefore suggests that some types of parental alarm calls communicate with young, and cause them to become silent, while other alarm calls have different functions.

Adults might communicate about immediate danger and so prompt old nestlings to flee the nest and escape to cover (Skutch, 1976). For example, moustached warbler (*Acrocephalus melanopogon*) nestlings only jumped from the nest after the approach of a human if an adult gave an alarm call (Kleindorfer *et al.*, 1996). Similarly, a brood of nestling pinyon jays (*Gymnorhinus cyanocephalus*) abandoned their nest after a predator attacked, during which adult mobbing calls perhaps prompted the young to leave the nest (Marzluff, 1985). Parents of some species of birds give calls that appear to encourage young to leave the nest at the usual time of fledging (O'Connor, 1984; Raihani and Ridley, 2007a; Woods, 1993)~~,~~ and, although not related to imminent danger, can nonetheless lead young to safer locations (Raihani and Ridley, 2007b; Section III.C). Similarly, adults can give calls to gather precocial young and lead them to safety or food (Johnson *et al.*, 2008). In general, there are very few observations on parent-fledgling compared to parent-nestling communication.

2. Parental Alarm Calls and Chick Behavior: Experimental Evidence

Observations of parental alarm calling and the behavior of young are valuable in providing the context in which communication occurs, but it is essential to test ideas through experiment. Even if young are observed in the field going quiet after adults give alarm calls, this does not necessarily mean that these alarm calls communicate with young about danger. Nestlings might be responding directly to cues from the predator or observer (see Section IV.C), for example, or to other cues or signals from the calling parent or another adult.

Playback experiments demonstrate that parental alarm calls can communicate with young. We are aware of such experiments carried out on 21 species of birds, and in all but one species at least one type of alarm call caused young to go quiet or become less conspicuous in other ways, such as by stopping gaping or crouching and freezing (Table 4). These experiments cover a variety of species including altricial passerines, brood parasites, and semi-precocial and precocial species. In most cases, there is reasonable replication of subjects, although early studies had little or no replication of the playback exemplars, and are therefore pseudo-replicated (Kroodsma, 1990; Kroodsma *et al.*, 2001). This means that formally it is possible to draw conclusions only about the specific sound broadcast, not a class of sounds, such as "alarm calls". Nonetheless, the consistency of results across many studies and species, and the consistent responses of young within individual studies, suggests that further study would confirm conclusions on most species. Regardless of the consistency of findings, a

Table 4: Response of offspring to playback of adult alarm calls. The body of the table shows whether young responded with suppression or stopping moving, and whether the response depended on the type of conspecific alarm call, whether the alarm call was by a conspecific or heterospecific, or the age of the offspring. Empty cells imply the effect was not tested. Under species giving alarm calls, consp. means there there was a greater response to a conspecific compared to heterospecific alarm call, neither means that they responded to neither alarm, both means they responsed to both; brown-neaded cowbirds responded to red-winged blackbird alarm calls.

Common	Species	Group	Development	Methods	N: subjects (exemplars)	Suppression of calling or movement	Alarm call type	Species giving alarm calls	Age of young	Source
reed warbler	*Acrocephalus scirpaceus*	passerine	altricial	Lab	20 (20)	Yes		Yes (Consp.)		Davies et al. (2004)
red-winged blackbird	*Agelaius phoeniceus*	passerine	altricial	Field	9 (1)	Yes	Yes			Knight & Temple (1988)
				Lab	11 (3)	Yes		Yes (Consp.)		Madden et al. (2005a)
				Lab, Cross-foster	20 (3)	Yes		Yes (Consp.)		Madden et al. (2005b)
American goldfinch	*Carduelis tristis*	passerine	altricial	Field	2 (1)	Yes	Yes			Knight & Temple (1986)
yellow warbler	*Dendroica petechia*	passerine	altricial	Field	12 (2)	Yes	Yes			Gill & Sealy (2003)
robin	*Erithacus rubecula*	passerine	altricial	Lab	14 (14)	Yes		Yes (Consp.)		Davies et al. (2004)
				Lab, Cross-foster	12 (12)	Yes		Yes (Consp.)		Davies et al. (2004)
pied flycatcher	*Ficedula hypoleuca*	passerine	altricial	Field	6 (1)	Yes			Yes	Khayutin (1985)
				Field	11 (1)	Yes			Yes	Korneeva et al. (2006)
grey warbler	*Gerygone igata*	passerine	altricial	Lab	11 (11)	Yes		Yes (Consp.)	No	Anderson et al. (2010)
great tit	*Parus major*	passerine	altricial	Lab	5 (1)	Yes			Yes (cf 1981)	Ryden (1978a)
				Lab	5 (1)	Yes				Ryden (1978b)
				Lab	9 (1)	Yes				Ryden (1980)
				Lab	6 (1)	Yes			Yes (cf 1978a)	Ryden (1981)
Siberian jay	*Perisoreus infaustus*	passerine	altricial	Field	8 (1)	Yes				Griesser (2004)
redstart	*Phoenicurus phoenicurus*	passerine	altricial	PB?, Field	? (1?)	Yes			Yes	Khayutin (1985)
dunnock	*Prunella modularis*	passerine	altricial	Lab	15 (15)	Yes		Yes (Consp.)		Davies et al. (2004)
				Lab, Cross-foster	17 (17)	Yes		Yes (Consp.)		Davies et al. (2004)
stonechat	*Saxicola torquata*	passerine	altricial	Lab	6 (1)	Yes	Yes			Greig-Smith (1980)
eastern phoebe	*Sayornis phoebe*	passerine	altricial	Lab	10 (3)	No		No (Neither)		Madden et al. (2005a)
white-browed scrubwren	*Sericornis frontalis*	passerine	altricial	Field	10 (10)	Yes	Yes		Yes	Magrath et al. (2006)

Table 4: Response of offspring to playback of adult alarm calls. The body of the table shows whether young responded with suppression or stopping moving, and whether the response depended on the type of conspecific alarm call, whether the alarm call was by a conspecific or heterospecific, or the age of the offspring. Empty cells imply the effect was not tested. Under species giving alarm calls, consp. means there there was a greater response to a conspecific compared to heterospecific alarm call, neither means that they responded to neither alarm, both means they responsed to both; brown-neaded cowbirds responded to red-winged blackbird alarm calls.

Common	Species	Group	Development	Methods	N: subjects (exemplars)	Suppression of calling or movement	Alarm call type	Species giving alarm calls	Age of young	Source
				Lab	19 (19)	No	No (Neither)		No	Maurer et al. (2003)
				Field	11 (11)	Yes				Platzen & Magrath (2004)
				Field	13 (13)	Yes	Yes			Platzen & Magrath (2005)
brown-headed cowbird	*Molothrus ater*	passerine	altricial brood parasite	Lab	16 (3)	Yes		Yes (Blackbird)		Madden et al. (2005b)
common cuckoo (reed-warbler gens)	*Cuculus canorus*	non-passerine	altricial brood parasite	Lab	9 (9)	Yes		Yes (Consp.)		Davies et al. (2006)
				Lab, Cross-foster	7 (7)	Yes		Yes (Consp.)		Davies et al. (2006)
common cuckoo (redstart gens)	*Cuculus canorus*	non-passerine	altricial brood parasite	Lab	6 (6)	No		No (Neither)		Davies et al. (2006)
common cuckoo (unknown gens)	*Cuculus canorus*	non-passerine	altricial brood parasite	PB?, Field	? (1?)	Yes				Khayutin (1985)
laughing gull	*Larus atricilla*	non-passerine	semi-precocial	Lab	24 (1)	Yes				Impekoven (1970)
				Lab	Ex1: 18 (1); Ex2: 10 (1)	Yes	No (Both)			Impekoven (1975)
western grebe	*Aechmophorus occidentalis*	non-passerine	precocial	Field, Cross-foster	6 (1)	Yes		No (Both)		Buitron & Nuechterlein (1993)
mallard	*Anas platyrhynchos*	non-passerine	precocial	Lab	35 (1)	Yes				Evans & Gaioni (1990)
				Lab	63 (1)	Yes				Gottlieb (1979)
				Lab	30 (1) (660 individuals total)	Yes				Miller & Blaich (1986)
				Lab	180 (1)	Yes			Yes	Miller & Blaich (1987)
				Lab	60 (1)	Yes				Miller & Hicinbothom (1991)
				Lab	120 (1)	Yes				Miller (1980)
western sandpiper	*Calidris mauri*	non-passerine	precocial	Lab	27 (27)	Yes	Yes			Johnson et al. (2008)
eared grebe	*Podiceps nigricollis*	non-passerine	precocial	Field	10 (1)	Yes				Buitron & Nuechterlein (1993)
				Field, Cross-foster	1 (1)	Yes		Yes (Consp.)		Buitron & Nuechterlein (1993)

potential bias with the literature is that studies finding no effect of alarm calls might be less likely to be published. Therefore, although it is already possible to draw some broad conclusions about nestling response to parental alarm calls, it is still important to carry out more, fully replicated experiments to test the generality of published results.

White-browed scrubwren nestlings are typical of most species in responding with silence to parental alarm calls (Platzen and Magrath, 2004). Scrubwrens nest on or near the ground, and parental buzz or "ground alarm" calls are given to predators including snakes, lizards, mammals and birds perched or on the ground, which all pose a danger to young (Figure 1; Maurer *et al.*, 2003; Platzen and Magrath, 2005). A field playback experiment showed that these ground alarm calls silenced nestlings that had been giving "peep" repeat calls in the absence of parents, but only slightly delayed the onset of begging calls during a simulated parental visit 15 s later (Figure 4; Platzen and Magrath, 2004). Nestlings responded similarly at all ages tested (5, 8 and 11 days old; they fledge at 14 days). The results show that ground alarm calls silence young, and suggest that parental arrival acts as an "all clear" signal indicating that danger had passed. This study, another field playback experiment (Platzen and Magrath, 2005), and field recordings of nestling responses to alarm-calling adults (Haff, T. M. pers. obs), contradict the results of an earlier laboratory experiment on isolated nestlings that failed to find any suppression of calling to alarm playbacks (Maurer *et al.*, 2003).

Playback experiments confirm that young have very specific responses to alarm calls, distinguishing between conspecific and heterospecific calls, and among parental alarm calls. The young of some species are known to respond specifically to the playback of alarm calls of their own but not other species, showing that the response is not simply caused by any sound or any general acoustic properties shared by alarm calls. Begging reed warbler, dunnock (*Prunella modularis*) and robin chicks stopped gaping and calling in response to conspecific alarm calls but not to alarm calls of the other species (Davies *et al.*, 2004). Similarly, conspecific but not phoebe alarm calls caused red-winged blackbirds (*Agelaius phoeniceus)* to stop begging and crouch (Madden *et al.*, 2005a), and nestling grey warblers (*Gerygone igata*) begged more softly after conspecific compared to heterospecific alarm calls (Anderson *et al.*, 2010). Eared grebes (*Podiceps nigricollis)* responded by hiding in the parent's back feathers and becoming quiet after playback of a conspecific but not western grebe (*Aechmophorus occidentalis*) alarm call (Buitron and Nuechterlein, 1993). Playbacks also confirm that young distinguish among different parental alarm calls, as is suggested by field observations (above). Nestling American goldfinches crouched after playback of a 'bearbee' but not a 'sweet' call, which is consistent with field observations that 'bearbee' calls silence young whereas 'sweet' calls function to attract other adults (Knight and Temple, 1986). Similarly, playback of a 'whit' alarm suppressed begging by stonechat nestlings whereas a 'chack' alarm did not, also consistent with field observations (Greig-Smith, 1980). White-browed scrubwren nestlings adaptively discriminate between different parental alarm calls, becoming silent after playback of ground alarm calls (above), while ignoring playback of "aerial" alarm calls, which are given to predators in flight, and so only relevant to adults and fledglings (Figure 5, nestlings; Platzen and Magrath, 2005). Fledglings do respond to aerial alarm calls, as discussed in Section III.A.3.

Western sandpiper (*Calidris mauri*) chicks actively respond in different ways to two different alarm calls rather than, as in scrubwrens, merely responding selectively to relevant types of alarm calls while ignoring others. Young sandpipers reduced calling and moved away from a speaker playing adult "alarm" calls, whereas they went silent, crouched and froze to playback of "freeze" alarm calls (Johnson *et al.*, 2008). These differences are probably adaptive, as adults give "alarm" calls and approach predators that are on the ground some distance from chicks, apparently leading them away from the brood, whereas they give "freeze" calls to predators posing a more immediate danger, such as closer terrestrial predators or aerial predators in flight. Presumably "alarm" calls help distract predators and allow chicks to slip away unnoticed, whereas "freeze" calls prompt crypsis when movement is likely to betray their presence to the predator.

The young of only one of the 21 species studied, the eastern phoebe (*Sayornis phoebe*), showed no detectable response to playback of conspecific alarm calls, a result that might be related to specific features of nestling begging behavior (Madden *et al.*, 2005a). Playback of alarm calls had no statistically significant effect on gaping or calling, although there was a trend towards reduced calling after both conspecific and red-winged blackbird alarm calls compared to the song of a third species. The nestlings were 7 days old, an age at which many other altricial species respond to parental alarms. They also responded specifically by gaping and calling to the provisioning calls given by parents, showing that they did discriminate among adult calls. Madden and colleagues suggest that alarm calls are directed to adults and not young, and that alarm calling to young is relatively unimportant in a species that only begs in response to provisioning calls or the sight of the parent, and not in the absence of parents when young could be vulnerable to eavesdropping by predators (see Sections II.D, IV.A).

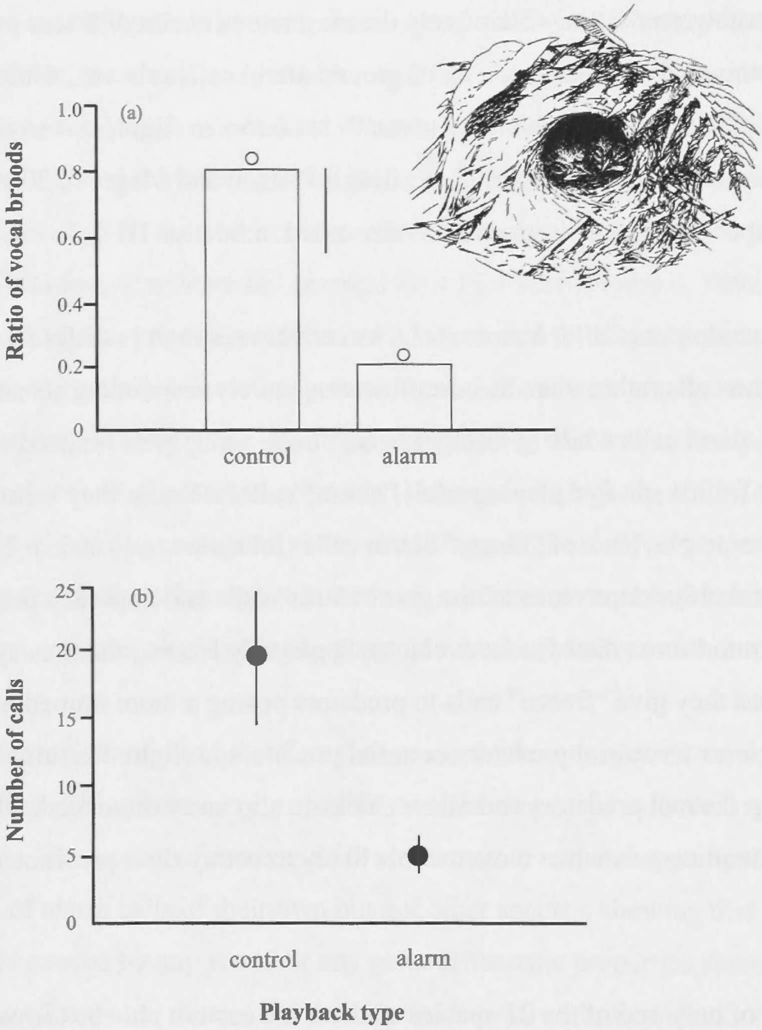

Figure 4. White-browed scrubwren nestling reaction to parental ground ("buzz") alarm calls. (a) Ratio of broods that continued to call in the 15 s after the alarm call playback; bars are means estimated from a mixed model; line represents LSD, black dots are means of observed data (N = 31 playbacks to 11 broods); (b) the number of calls given after the alarm call playback in those few cases where nestlings continued to call (N = 7 playbacks). (Redrawn from Platzen and Magrath, 2004, reprinted with permission of the authors; illustration of scrubwren nest by Peter Marsack, reprinted with permission.)

3. *Timing of Development of Responses to Alarm Calls*

There has been limited study of the development of alarm-calling behavior in birds. Hollén and Radford (2009) provide a broad review of the development of alarm calling behavior in mammals and birds, considering alarm call production, usage and response. Most studies on production and usage have been carried out on mammals, and here we focus on the development of responses by young birds to parental alarm calls.

The young of those precocial and semi-precocial birds tested respond to alarm calls immediately on hatching, whereas altricial nestlings become more responsive with age, in parallel with sensory development. Playbacks of adult alarm calls within a day of hatching cause gull, grebe and duck chicks to cease calling and freeze or hide (Buitron and Nuechterlein, 1993; Impekoven, 1975; Miller, 1980). Mallard (*Anas platyrhynchos*) embryos even respond to alarm playback, by stopping bill-clapping, in the days before hatching (Gottlieb, 1979). By contrast, pied flycatcher (*Ficedula hypoleuca*), redstart (*Phoenicurus phoenicurus*) and common cuckoo nestlings have been reported to show no defensive behavior to alarm calls or other stimuli until about the time their eyes open, at 5-6 days old (Khayutin, 1985). The lack of response by very young altricial nestlings is consistent with developmental constraints (Khayutin, 1985). For example, auditory sensitivity to higher acoustic frequencies increases until pied flycatchers are 10-11 days old, corresponding to the development of maximal response to playback of an adult alarm call (Korneeva *et al.*, 2006). However, there may be little selection for defensive behavior in very young nestlings because they are relatively inconspicuous and often brooded by parents, so the timing of development of sensory abilities could be a mechanism of adaptive change in response to alarm calls.

The possibility of adaptive timing of the development of response to alarm calls is supported by studies of both precocial and altricial species. For example, almost all mallard ducklings become silent and freeze after playback of maternal alarm calls within 24 h of hatching, but the response wanes after 48 h, and by 72 h only a minority freeze to alarm playback (Miller and Blaich, 1987). This transient response to maternal alarm calls is likely to be adaptive because the period of maximum response to alarm calls corresponds to the period when the female broods young on the nest on land, while the decline coincides with the time when she would have moved the ducklings to the relative safety of water (Miller and Blaich, 1987). Furthermore, ducklings a week old still responded to alarm calls with an increased heart rate (Evans and Gaioni, 1990), suggesting a lack of behavioral response was selected for and not simply the result of inattention. Among altricial species, great tits (*Parus major*) responded with silence to playback of a 'seet' alarm call when 14-18 days old, in the last few days before fledging, but did not do so when 10 days old (Rydén, 1978a, 1982). These alarm calls are given to hawks, and so are relevant to fledglings but usually not nestlings, so the late development of response again suggests adaptive timing.

As implied by Rydén's work on great tits, altricial birds provide an excellent model to test ideas about adaptive timing of behavioral development because they have an abrupt change at fledging that exposes them to new dangers. A key prediction about adaptive change is that birds with inaccessible or cryptic nests should respond to aerial alarm calls once they have fledged and become vulnerable to predators in flight. By contrast, if temporal changes merely reflect developmental constraints, there is no clear prediction about timing. Consistent with the prediction of adaptive timing, nestling scrubwrens started to respond with silence to aerial calls only a few days before fledging, and completely suppressed calling to these alarm calls as soon as they could be tested after fledging (Figure 5; Magrath *et al.*, 2006). The results suggest that the response to alarm calls is adapted to their current age rather than being an imperfect stage in the development of adult behavior. Overall, the differential response of scrubwren nestlings to ground and aerial alarm calls (above), and the change in response to aerial calls at fledging, both suggest specific adaptive responses to parental alarm calls to minimize the risk of predation.

4. Mechanism of Development

Cross-fostering and other studies show that offspring responses to parental alarm calls do not require learning, but are sometimes modified by experience. For example, robins and dunnocks raised by other species still respond to conspecific alarm calls, although more weakly than if they had been raised by their own species (Davies *et al.*, 2004). Similarly, red-winged blackbirds responded to conspecific but not eastern phoebe alarm calls regardless of whether they were raised by conspecifics or phoebes (Madden *et al.*, 2005a,b). Eared and western grebes cross-fostered before hatching by the other species responded to conspecific alarm calls, although western grebes also responded to eared grebe alarms (Buitron and Nuechterlein, 1993). Among semi-altricial species, previous auditory experience had little or no effect on the response of laughing gull (*Larus atricilla*) chicks to parental alarm calls (Impekoven, 1970, 1975), and 26 d old embryos of precocial mallard ducks stopped bill-clapping after playback of alarm calls even if they had no previous experience of the calls of parents or other embryos (Gottlieb, 1979).

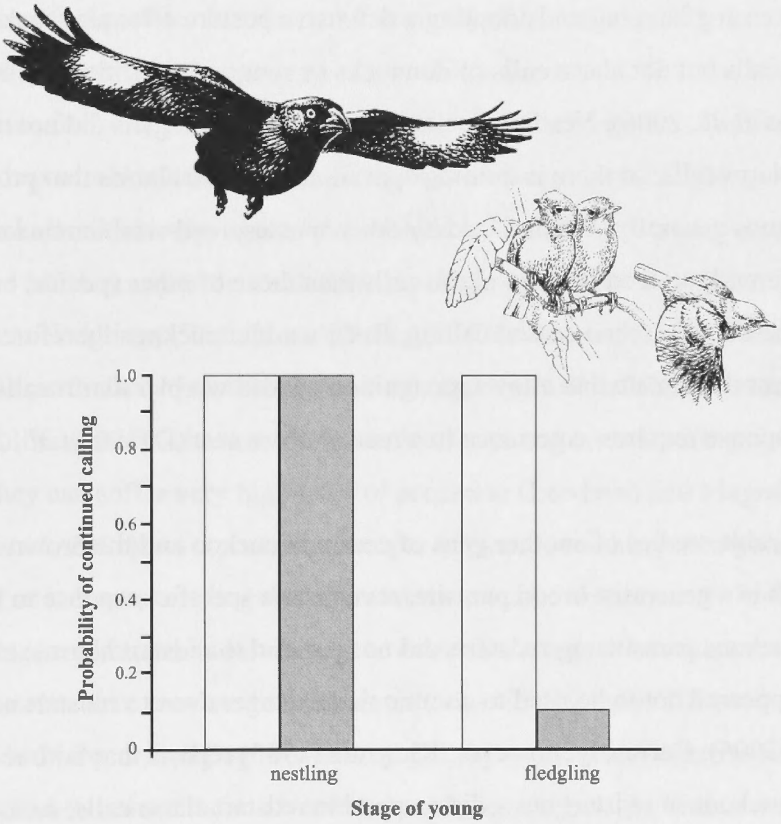

Figure 5. White-browed scrubwren nestling versus fledgling response to playback of control sounds (open bars) and parental aerial alarm calls (black bars); n=10 broods. (Redrawn from Magrath *et al.*, 2006, reprinted with permission of the authors; illustration of pied currawong and a brood of scrubwren fledglings by Peter Marsack, reprinted with permission.)

The response of brood parasites to host alarm calls provides a particularly interesting test of the importance of innate compared to learned responses. Brood parasites lay their eggs in the nest of other species, which subsequently raise their young (Davies, 2000), so there would seem to be strong selection to learn the communication signals of host species or to have an innate template that enables recognition without previous experience. Responding to alarm calls is likely to be particularly important, as brood parasites often beg conspicuously (Davies *et al.*, 2006; Madden *et al.*, 2005b).

At least one host race (gens) of common cuckoo has innate recognition of host alarm calls, but requires experience to behave adaptively. Nestlings of the common cuckoo gens specializing in parasitising reed warblers, and raised by reed warblers, responded by ceasing begging and adopting a defensive posture after playback of reed warbler alarm calls but not alarm calls of dunnocks or songs of chaffinches (*Fringilla coelebs*; Davies *et al.*, 2006). Nestling cuckoos from the redstart gens did not respond to reed-warbler alarm calls, so there is nothing special about these alarms that prompts silence in cuckoos generally. When raised by other species, reed-warbler cuckoos still responded differently to reed-warbler alarm calls than those of other species, but in this case they increased rather than ceased calling. Reed-warbler cuckoos therefore appear to hatch with a neural template that allows recognition of reed warbler alarm calls, but an appropriate response requires experience in a reed warbler nest (Davies *et al.*, 2006).

Comparable studies of another gens of common cuckoo and the brown-headed cowbird, which is a generalist brood parasite, revealed no specific response to host alarm calls. Cuckoos parasitising redstarts did not respond to redstart alarms, although these alarms appeared not to be used to communicate danger even to redstart nestlings (Davies *et al.*, 2006). Curiously, however, Khayutin (1985) reports that both redstart nestlings and cuckoos in redstart nests did respond to redstart alarm calls, so there may be geographic variation or different types of redstart alarm calls. By contrast, cowbirds responded to red-winged blackbird alarms regardless of whether they were raised by that species or eastern phoebes, which suggests an innate response to another icterid's alarm call, rather than adaptation to a specific host (Madden *et al.*, 2005b). It would be interesting to compare the acoustic structure of cowbird alarm calls with blackbird alarm calls, as this response by cowbird nestlings might represent early development of a response to conspecific alarm calls. Cowbird nestlings did not respond to phoebe alarms even when raised with phoebe young, suggesting they do not learn host alarm calls (Madden *et al.*, 2005b). Judging by the diversity of findings on brood parasites so far, it would be productive to study more specialist and generalist brood parasites, perhaps also including information on the parasite's own alarm-calling system.

5. Alarm Calls and Social Learning

Parental alarm calls might have a role in helping young learn to recognize predators, or parents might even use alarm calls specifically to teach young to recognize predators. Adult birds can learn to recognize predators or brood parasites, or even fear harmless models, by seeing or hearing other adults mobbing them, a process of associative social learning (Curio *et al.*, 1978a,b; Davies and Welbergen, 2009; Griffin, 2004; Vieth *et al.*, 1980). It seems plausible, therefore, that parental alarm calls could help young learn about predators, although we are not aware of any direct tests. Certainly the young of some species fledge with very limited ability to identify predators (Kullberg and Lind, 2002), and so would benefit from learning. It even seems possible that parents could give alarm calls to actively "teach" their young to identify predators just as pied babblers (*Turdiodes bicolor*) appear to teach their nestlings about "purr" calls that are then use to lead them as fledglings (Raihani and Ridley, 2007a). The benefits of active teaching are likely to be particularly great when there are high costs of individual learning (Thornton and McAuliffe, 2006), which seems plausible for young birds learning about predators, because they can suffer very high rates of predation (Leedman and Magrath, 2003; Naef-Daenzer *et al.*, 2001). As a possible example of parents teaching their young about predators, or at least providing the opportunity to learn, cooperatively breeding Siberian jay (*Perisoreus infaustus*) adults can give more alarm calls when there are offspring in the group rather than unrelated immigrants (Griesser, 2004a,b). The period of parental care after hatching or fledging provides ample opportunity for young to learn about predators, and so reduce their extreme vulnerability, suggesting further study would be fruitful.

B. PROVISIONING CALLS

Parents can affect the risk that young are taken by predators not only by silencing noisy offspring with alarm calls, but also by using calls that stimulate young to beg. These "provisioning" calls are generally given by parents when providing food to young, and are used in different species for a variety of purposes, including parent-nestling, parent-fledgling and adult-adult communication. Provisioning calls might affect predation risk to offspring in several ways. Specifically, they could help decrease predation risk by: (a) stimulating nestlings to beg, thus allowing for more efficient feeding visits and less parental time spent at the nest; (b) providing an "all-clear" signal for nestlings that it is safe to beg; or (c) facilitating learning in nestlings that may be important in helping to lower predation risk after fledging. Despite these potential benefits, provisioning calls could unintentionally increase predation risk by (d) attracting the attention of eavesdropping predators. In species that have complex food calls, such as scrubwrens, the calls probably affect predation risk in more than one of these ways.

In most species, provisioning calls incite nestlings to beg, and therefore can increase the efficiency of parental feeding visits by aiding in food transfer and decreasing the amount of time it takes to feed young (Buitron and Nuechterlein, 1993; Clemmons, 1995a; Leonard *et al.*, 1997; Madden *et al.*, 2005a). Indeed, parents tend to give more calls to very young nestlings, or to broods that are not begging when adults arrive at the nest, suggesting that parents use the calls at least in part to make nest visits more efficient (Bengtsson and Rydén, 1981; Clemmons, 1995b; Grieco, 2001; Khayutin, 1985; Kuhlmann, 1909; Leonard *et al.,* 1997; McDonald and Wright, 2008; Sieber, 1985). Prompting all young to beg immediately through provisioning calls could allow parents to compare nestling need and allocate food appropriately, thus maximizing the efficiency of feeding visits. Likewise, provisioning calls could also help parents coordinate feeding visits (Leonard *et al.*, 1997). Efficient visits to the nest can help to decrease predation risk by minimizing time and activity at the nest, and could also allow for fewer nest visits, all of which would help to decrease nest detectability (Section II.B.1).

Provisioning calls might decrease predation risk to nestlings by providing them with an unambiguous signal that parents have arrived with food and that it is safe to beg (Section IV.A; Madden *et al.,* 2005a, Magrath *et al.*, 2007). As discussed in Section IV.A, this could lead to a reduction in mistaken begging in the absence of parents and so reduce overall risk of eavesdropping by predators. If this is true, one would expect provisioning calls to be designed to contrast with other common sounds that the nestlings are likely to hear, to minimize mistaken begging.

Provisioning calls can also affect predation risk by facilitating social bonds or behaviors that are adaptive after young leave the nest. For example, adults of some species use the calls to promote individual recognition or social bonds after fledging (Beecher *et al.,* 1985; Leonard *et al.,* 1997; Lessells *et al.,* 1995; Sieber, 1985), which may be important in maintaining group cohesion and adult defense of fledglings. The most compelling evidence that provisioning calls can be important in reducing predation risk to fledglings comes from pied babblers (Raihani and Ridley, 2007a, 2008). Adult babblers use "purr" provisioning calls, primarily with older nestlings. During this nestling "training period", young learn to associate the call with a positive (food) reward, so that after fledging adults can use purr calls to lead fledglings, including away from potential predators (Section III.C).

Predators could potentially eavesdrop upon provisioning calls themselves and so increase the risk to young. In this case provisioning call structure could influence the probability of such eavesdropping. In most species, the calls are short, consist of only a few or a single element, and are relatively soft (Clemmons, 1995a; Khayutin, 1985; McDonald *et al.,* 2007; Riahani and Ridley, 2007a), features that probably minimize predation risk. One species of honeyeater has loud provisioning calls, but risks are perhaps reduced because they are aggressive birds breeding in cooperative colonies (McDonald and Wright, 2008). By contrast, white-browed scrubwrens are small, unaggressive birds whose nests are vulnerable to predators, yet their provisioning calls appear not to be cryptically designed. In this species, provisioning calls are long (5 to 645 ms), extremely complex (up to 160 different elements have been described from one population thus far), contain individual elements that can be either simple or complex in structure, and can be relatively loud (up to at least 70dB at 20cm; Figure 1; Platzen, 2004). The calls vary enormously both within and between individual adults. These acoustic features should make the calls easy for nearby predators to detect and locate, but the extreme variability may make it difficult for predators to learn to recognize that the call implies a brood of young. In fact, scrubwren provisioning calls contrast markedly with adult calls that have been demonstrated to increase the risk of nest predation, which are simple and stereotyped (e.g., the "chit" call of female red-winged blackbirds; Yasukawa, 1989). Predators may more easily develop an "auditory search image" for simple, stereotyped calls given near the nest than for calls that are complex and variable.

The variability of scrubwren provisioning calls might affect predation risk by making nestlings prone to mistaken begging to some other birds' vocalizations. The variability of provisioning calls means that at least some variants sound like the calls of other species (Section II.D). Indeed, scrubwren nestlings occasionally give begging calls to song of one sympatric species that is acoustically similar to some provisioning calls (Magrath *et al.,* 2007). Clearly, we require more work on the function of complex provisioning calls and their relationship to predation risk.

C. OTHER PARENTAL VOCALIZATIONS

In addition to provisioning calls (Section III.B) and alarm calls (Section III.A), several other adult vocalizations around the nest could affect predation risk. These include "all-clear" signals, contact calls used between adults, and "gather" calls used to rally precocial young and altricial fledglings.

Nestlings may reduce the risk of predation by monitoring "all-clear" signals given by parents, and so beg only when it is safe to do so. The benefits of monitoring calls that signal safety have long been proposed (Wickler, 1985), and have been demonstrated for species that forage together in groups (Bell *et al.,* 2009). Further, male songbirds of some species use their song as an "all-clear" signal that alerts females that it is safe to come off the nest without the risk of being observed by a predator (Lima, 2009; Wingelmaier *et al.,* 2007; Ziolkowski *et al.,* 1997). For example, female reed buntings (*Emberiza schoeniclus*) exit from incubation bouts significantly more than expected by chance when males are singing (Wingelmaier *et al.,* 2007). Similar patterns have been found in house wrens (*Troglodytes aedon*) great tits and red-winged blackbirds (Burton and Yasukawa, 2001; Lind *et al.,* 1996; Ziolkowski *et al.,* 1997). Nestlings may also potentially use male song as an all-clear signal about when it is safe to beg, although neither the response of nestlings to male song nor male response to nestling vocalizations has yet been assessed in species whose adults use song as an all-clear signal.

In a similar way, nestlings could potentially monitor current predation risk using the calls made by adults travelling to and from the nest. Many species use "contact" calls near the nest to communicate information to their mates about feeding visits, nest attendance, or to maintain pair bonds (Leonard *et al.,* 1997; McDonald *et al.,* 2007; McDonald and Wright, 2008; Yasukawa, 1989). For example, scrubwren adults give "chip" and "buzz" contact calls while approaching their nests (Higgins and Peter, 2002). While the primary purpose of these calls seems to be to communicate with other adults rather than with nestlings, nestlings do monitor "chips", and increase their rate of repeat calls as calling adults approach the nest, potentially using the calls either as an "all clear" signal that it is safe to vocalize, or as advanced warning of a feeding visit (Maurer *et al.,* 2003; Horn *et al.,* in prep). Predators might also be able to use contact calls to home in on active nests, however, as parents increase the rate of chip calls as they approach the nest. Perhaps in response to this risk, parents call significantly less as they approach the nest in the five minutes after a predator has been sighted nearby (Horn *et al.,* in prep).

"Gather" calls are used by adults of both precocial chicks and altricial fledglings to call young together, potentially leading them away from danger or reuniting family groups that have been scattered after a disturbance. For example, parent western sandpipers give "gather" calls that attract chicks (Johnson *et al.,* 2008). Potentially, the calls are used to draw chicks away from relatively distant predators that are not likely to detect the movement of young. Calls with a similar function may also be used in altricial species to gather or lead fledglings away from predators. For example, pied babbler nestlings are taught to associate positive rewards with a call that is later used to lead fledglings around the territory, including away from danger (Section III.C; Riahani and Ridley, 2007a).

IV. ACOUSTIC INTERACTIONS BETWEEN PARENTS AND YOUNG

Adults can use alarms and other calls to help mediate the trade-offs nestlings face between being heard by their parents and being overheard by predators, but exactly how predation risk is minimized ultimately comes down to how nestlings and adults interact. Within the bounds of potential conflict over resource allocation between parents and their young (Section II.A.), such cooperative interactions may be selected for because both parties ultimately benefit from a successful breeding attempt. In general, acoustic interactions between parents and their offspring fall into three categories: (1) offspring can follow general rules for when it is safe to beg, and either beg preferentially to adult provisioning calls ("switching on"), or stop vocalizing in response to adult alarms ("switching off"); (2) parents could make adaptive decisions about whether or not to give alarm calls based on current nestling behavior; or (3) nestlings can monitor their environment independently of their parents, and consequently adult decisions about when to vocalize could be in part based on this capacity. We consider each of these possibilities in turn.

A. “SWITCH ON” OR “SWITCH OFF” STRATEGY

Nestlings may modulate their vulnerability to eavesdropping predators by either “switching on” or “switching off” begging depending on parental calls (Madden *et al.,* 2005a). Some species follow a strategy of remaining quiet unless switched on by a parental provisioning call (Section III.B); others beg to many subtle, potentially ambiguous cues of parental arrival, but switch off to alarm calls warning of danger (Section III.A). Those species that remain silent unless a parent gives a provisioning call have no need to heed alarm calls, so species might rely primarily on one strategy or the other. For example, Madden and colleagues (2005a) found that eastern phoebes and red-winged blackbirds followed different begging strategies. Phoebe nestlings begged to playback of provisioning calls, but did not stop begging after playback of adult alarm calls. By contrast, playback of adult provisioning calls to blackbird nestlings did not induce a stronger begging response than simple mechanical vibration of the nest substrate, but nestlings did fall silent to adult alarm calls. Adult phoebe alarms appear designed to warn mates to avoid approaching the nest in the presence of predators, while parent blackbirds frequently give alarm calls even when no other adult is near the nest. Overall, blackbird nestlings beg easily to ambiguous stimuli, but switch off to parental alarm calls warning them of danger, while phoebe nestlings do not beg unless prompted by adults, and so response to parental alarm calls are unnecessary.

The different rules used by blackbirds and phoebes to minimize the chance of being eavesdropped upon by predators might be due to differences in the two species’ nesting ecologies (Madden *et al.,* 2005a). Phoebes build mud nests on firm, protected substrates, such as cliff overhangs or buildings, while blackbirds build nests of woven vegetation in reeds and other non-rigid plants (Weeks, 1994; Yasukawa and Searcy, 1995). Detection of adult arrival by cues such as mechanical vibration of the nest substrate can be difficult for species that nest on rigid surfaces, and consequently nestlings would profit from remaining silent until gaining reliable cues of adult arrival, such as provisioning calls or direct sight of an adult. Given that they do not beg to unreliable cues, there is no selection to respond to adult alarm calls. For species that nest on softer substrates, mechanical vibrations may be the first cue of parental arrival. Nestlings should therefore beg promptly to any similar stimuli, particularly if the first nestling to beg is the most likely to be fed (Leonard and Horn, 1996; Teather, 1992). Indiscriminate begging could make nestlings vulnerable to eavesdropping predators, however, and so young should be selected to respond promptly to adult alarm calls. How widespread these strategies are across species with different nesting ecologies has not yet been tested, but should be expected in a variety of taxa across a broad ecological spectrum.

Species that nest on both firm and flexible substrates should profit from both switching on to provisioning calls and switching off to adult alarms. Such a dual strategy is consistent with the ecological predictions of Madden *et al.* (2005a) because nests placed on the ground or in rigid vegetation provide minimal vibrational cues of parental arrival, while nests placed in flexible vegetation should provide such cues. So far white-browed scrubwrens are the only species that has been documented to both switch on to parental provisioning calls and switch off to adult alarms (Haff and Magrath, 2010; Platzen and Magrath, 2004, 2005; Magrath *et al.,* 2007), although grey warbler young also switch on to adult provisioning calls and reduce begging call amplitude, but not call rate, in response to playback of adult alarm calls (Anderson *et al.*, 2010). We expect that more species should profit from following such a dual strategy. This is because there is likely to be a continuum of cues that nestlings use to detect parental arrival, and strong selection for rapid response to subtle cues of arrival, regardless of nest site. Species that beg too freely are likely to be vulnerable when no parents are near the nest, however, and so there is also likely to be selection for response to alarm calls, or selection for independent detection of cues made by predators themselves (Section IV.C). Similarly, species like scrubwrens that have regular, unprompted "repeat calls" (Section II.D) are likely to be selected to switch off such calls after adult alarm calls, and to independently assess danger, regardless of the nest site and adult provisioning calls.

Food availability and risk of predation are also likely to influence the evolution of switch on or switch off begging strategies in nestlings (Magrath *et al.*, 2007). If food is limited, young should be "quick on the trigger", and respond quickly to subtle cues of adult arrival. In environments where food is not limited, young can be discriminating in response to cues of adult arrival, and follow a switch on rule. Similarly, if there is a high risk of predation, selection should favor nestlings that switch off in response to adult alarm calls, or that only respond to strong cues of parental arrival, whereas if predation is rare, there will be little selection for responding to alarm calls.

Selection for less discriminating begging seems to be common where short-term shortages of food are common and there is little predation (Dor *et al.,* 2007; Leonard and Horn, 1996, 2001a; Leonard *et al.,* 2005; Price and Ydenberg, 1995). In nestling tree swallows, for example, the risk of predation is relatively low, and nestlings that are the first to beg are the most likely to be fed (Leonard and Horn, 1996). Nestlings therefore face strong selection to respond rapidly to any cue of adult arrival, and as a consequence frequently beg to inappropriate cues, including sounds made by potential nest predators (Section II.D; Leonard and Horn, 2001a; Leonard *et al.,* 2005). When predation is common, nestlings can be “adaptively pessimistic” in response to ambiguous cues of parental arrival, and have a more discriminating begging threshold (Haff and Magrath, 2010). In white-browed scrubwrens, which have high rates of nest predation (Platzen and Magrath, 2004), the costs for nestlings of becoming dinner appear to be greater than the benefits of competing for another meal. Nestling scrubwrens delay the onset of begging to adult provisioning calls following playback of alarm calls (Platzen and Magrath, 2004), and interpret some ambiguous cues of adult arrival as potentially dangerous by switching off repeat calling independently of their parents (Section IV.C; Haff and Magrath, 2010). More experimental studies that examine the role of food limitation and predation risk in a variety of habitats will help us to understand more fully the evolution and flexibility of nestling begging strategies.

B. STRATEGIC PARENTAL RESPONSE TO NESTLING VOCALIZATIONS

Adults of many species face strong trade-offs in deciding whether or not to give alarm calls near the nest in the presence of a predator, and their decision to do so may in turn be affected by the vocal behavior of their offspring (Andersson *et al.,* 1980; Burger *et al.,* 1989; Fasanella and Fernandez, 2009; Harvey and Greenwood, 1978; Montgomerie and Weatherhead, 1988; Redondo, 1989). Although parental alarm calls can increase the chance of nest survivorship (Section III.A; Grieg-Smith,1980; Knight and Temple, 1986; Section III.A), calling near the nest can also attract enemies (Grim, 2008a; Krama and Krams, 2005; Smith *et al.,* 1984; Yasukawa, 1989), or even provide them with information about nest location (Montgomerie and Weatherhead, 1988). Whether or not to call may therefore be affected by the likelihood that a predator will detect nestlings. Both parents and offspring would profit if adults called to warn young only when there is a high risk of being overheard, such as when nestlings are vocalizing loudly.

There is some experimental evidence that adaptive changes in response to nest enemies are driven at least in part by the vulnerability of nest contents. Gill and Sealy (1996) found that during the laying stage parent yellow warblers (*Dendoica petechia*) reacted strongly to a model brood parasite, a brown-headed cowbird, and only weakly to a model of a generalist avian predator, a common grackle. By contrast, during the nestling stage parents ignored the cowbird model, which posed no threat to nestlings, but mobbed the grackle model intensely. While the authors proposed that the brood value hypothesis (Section II.A) could explain the change in adult reaction to the grackle model, the adaptive reduction in response to the cowbird model during the nestling period suggests that parents also make decisions about nest defense based on the vulnerability of nest contents. The change in response to the grackle model might therefore also be explained by adult response to nestling vocalizations, if adult alarm calls are used to silence noisy young. Unfortunately, the authors did not test how nestling yellow warblers responded to adult alarm calls, or whether or not adults monitored nestling activity level.

The best, but still indirect, evidence that adults might increase their propensity to alarm call when nestlings are more vocal comes from American goldfinch (Knight and Temple, 1986). Nestlings went silent to playback of an adult alarm call, and observations suggested that adults gave alarm calls when nestlings were active. The authors then tested the idea that parent goldfinches call more when nestlings are more active by cross-fostering nestings of different ages, and therefore different activity levels, between nests. Parents given older nestlings increased their number of alarm calls, while parents given younger nestlings decreased calling, suggesting that adult alarm calling is influenced by the behavior of their young. Unfortunately, the results of this study are difficult to interpret, not just because of playback design (Section III.A), but also because changes in adult behavior after cross-fostering of young could be due to adults reassessing the value of their young. Clearly future studies should test ideas about parental response to nestlings by manipulating brood noisiness without changing brood age or value. Only in this way can we fully understand the potential of parent-offspring communication to reduce the risk of nest predation.

C. DIRECT ASSESSMENT OF DANGER BY YOUNG AND PARENTAL RESPONSE

Responding independently to predators may be an important way that nestlings can affect predation risk, particularly in situations when no adults are nearby to warn of impending danger. Such behavior could decrease the risk of begging to inappropriate cues, including those made by approaching predators, particularly in species that switch on begging relatively easily (Section IV.A). Further, independent assessment of danger by nestlings could reduce the costs of parent-absent vocalizations (Section II.D), and so may also affect how adults respond to danger near the nest (Section IV.B).

Very young animals of a variety of taxa can independently assess risk and respond appropriately (Caldwell *et al.*, 2010; Chivers *et al.*, 2001; Laurila *et al.*, 2002; Magrath *et al.*, 2007; Schaller and Emlen, 1961; Sih and Moore, 1993; Relyea, 2003; Warkentin, 2005). For example, the larvae and even embryos of some amphibians can respond to chemical cues of predators and alter their optimal hatch date accordingly (Chivers *et al.*, 2001; Sih and Moore, 1993). Further, embryo red-eyed treefrogs (*Agalychnis callidryas*) hatch early and escape to safety in response to vibrations that mimic a snake approaching the egg-mass (Caldwell *et al.*, 2010; Warkentin, 2005). In birds, some researchers have reported a defensive reaction in response to vibrational or visual cues. Older nestling common grackles, for example, crouch in response to both non-parental visual cues and mechanical vibration of the nest (Schaller and Emlen, 1961). In fact, a crouching response and presumed concomitant reduction in calling to inappropriate stimuli – in most cases, observers at the nest – has been reported in nestlings in a variety of species (summarized in Schaller and Emlen, 1961; see also Kleindorfer *et al.*, 1996). Unfortunately, the potential for simultaneous adult alarm calls to induce a defensive response in nestlings confounds interpretation of these observations of nestling behavior.

Acoustic cues of approaching danger may be particularly relevant for younger nestlings that do not have a fully developed sense of vision (Clemmons, 1995b; Leonard *et al.*, 1997), as well as for nestlings that have a limited field of view due to constraints caused by nest structure. Response to sounds may also allow more opportunity for nestlings to react in time to avoid predation, as acoustic cues may be detected while a predator is not yet directly at the nest.

We know of only two studies that have tested the response of nestling birds to acoustic cues of a predator, both on white-browed scrubwrens. In the first study, nestlings stopped repeat calling after playback of the sound of their major avian predator, the pied currawong (*Strepera graculina*) walking on leaf litter (Magrath *et al.*, 2007). The effect was striking, and comparable to that of alarm calls: nestlings remained silent for over 2 minutes in some cases, after only 3 seconds of playback. The experiment did not, however, reveal what acoustic features of a currawong walking warned of danger. Unlike other sounds played back during the same experiment (adult calls or heterospecific bird calls), which were all voiced and tonal, the sound of the predator walking was atonal, with a broad frequency range and irregular amplitude peaks that correspond to a quick succession of three or four footsteps (Figure 6a).

A second study investigated the specific cues that nestlings use to assess danger (Haff and Magrath, 2010). The sound of a predator walking in leaf litter might simply be novel, for example, and so nestlings might stop calling in response to novel sounds in general. Alternatively, nestlings might go silent to atonal broadband sounds, or they might respond specifically to an erratic pattern of footsteps. To investigate these alternatives, nestlings were presented with (a) the sound of a predator walking, as well as with three novel computer-generated sounds designed to test whether nestlings suppress calling to novelty alone, to broadband sounds in general, or to the erratic pattern of footsteps. Specifically, the computer generated sounds presented to nestlings were: (b) a tonal playback consisting of short tones strung together in an erratic pattern similar to a predator walking; (c) a 'smooth', atonal broadband playback consisting of a broadband white noise that gradually increased and then decreased in amplitude; and (d) an 'erratic' atonal broadband sound consisting of white noise arranged into a pattern similar to the predator walking playback (Figure 6). Nestlings suppressed calling similarly in response to both broadband playbacks, but not at all to the novel tonal playback (Figure 7). No playback suppressed nestling calling as strongly as the sound of an actual predator walking. Thus, nestlings can be finely tuned to acoustic cues of danger that indicate specific risk near the nest. This capacity could greatly reduce the costs of nestling vocalizations, particularly when parents are absent. Combined with a switch off strategy of responding with silence to adult alarms, independent assessment of danger by nestlings could provide young with some measure of protection from eavesdropping predators almost all of the time.

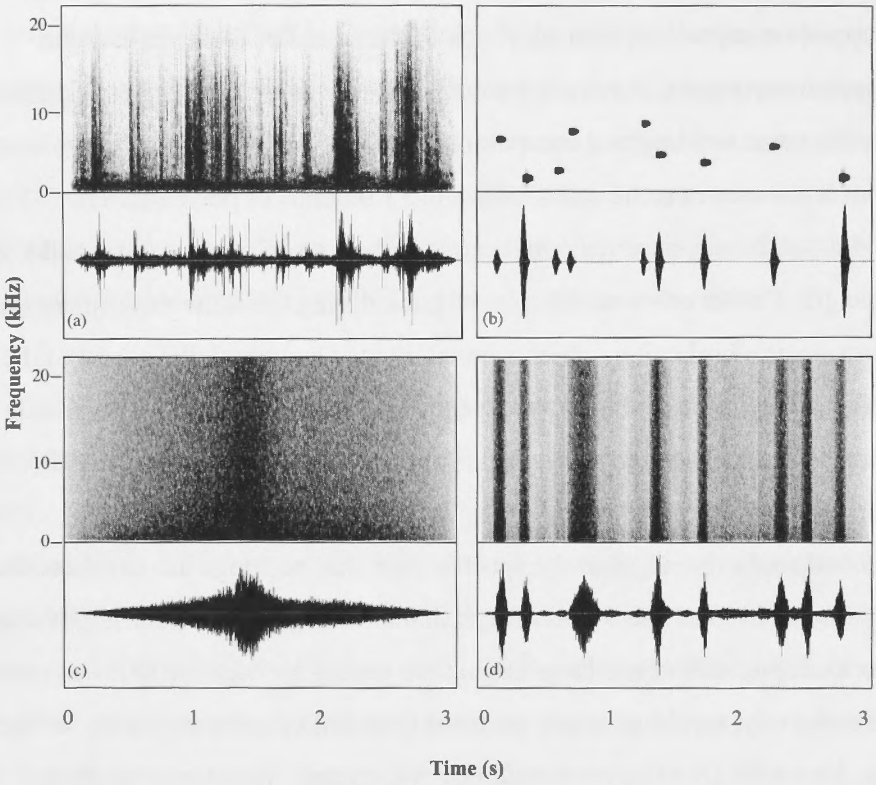

Figure 6. Examples of playbacks to individual broods of white-browed scrubwren nestlings testing independent assessment of acoustic cues of danger. (a) Pied currawong walking on leaf litter; (b) computer-generated tonal sound; (c) computer-generated smooth broadband sound; and (d) computer-generated erratic broadband sound. Upper panels contain sonograms created in Raven 1.3 using settings described in fig. A.1; lower panels show waveforms. (Taken from Haff and Magrath, 2010, figure 1, with permission from Elsevier and the authors.)

The ability of nestlings to independently assess danger is likely to affect adult behaviour, with consequent implications for predation risk. For example, adults may choose not to alarm call near the nest if young are likely to have already detected a predator, particularly if the predator has not yet discovered the nest. Adults might even listen for repeat calls to assess whether nestlings have detected danger. Furthermore, adults might forage farther away from the nest, in more profitable locations, if nestlings can respond independently to cues from nearby predators. As well as direct benefit to the adults, foraging in better locations could enable delivery larger food loads and fewer

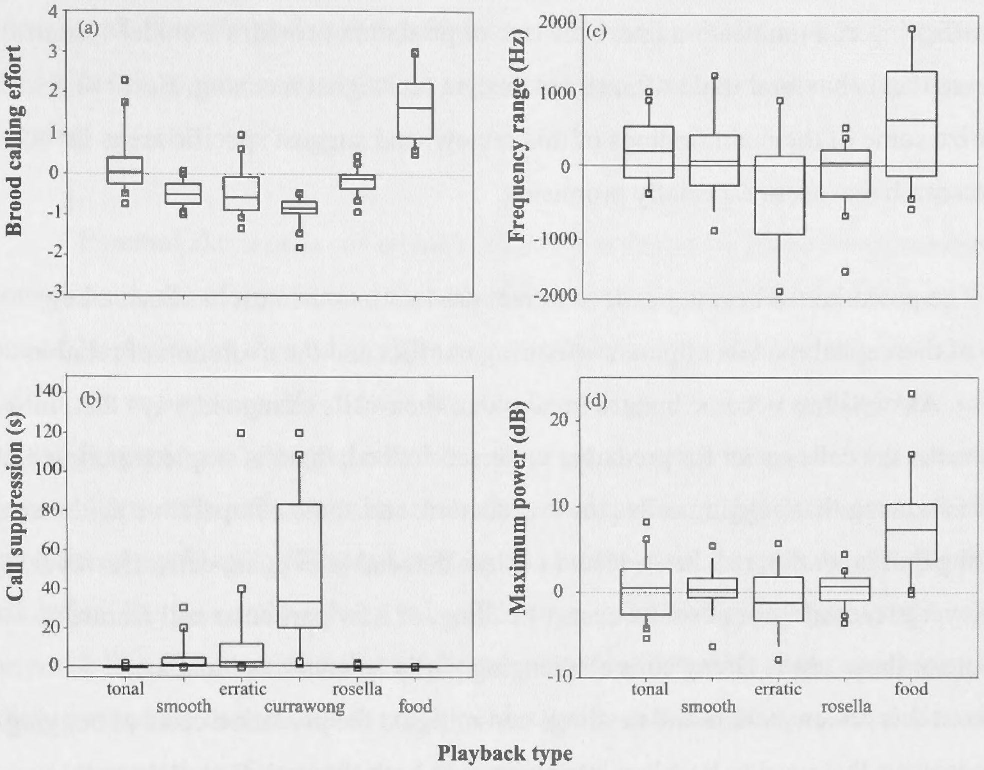

Figure 7. Nestling white-browed scrubwren reaction to playbacks of natural and computer-generated sounds; all measurements represent differences in nestling calling in the 10 s before versus the 10 s after the playback, with the exception of call latency. (a) Brood calling effort, the first component extracted from a PCA of number of calls and total duration of calling; (b) duration of call suppression (s); (c) mean frequency range (Hz); (d) mean maximum amplitude (dB). The playbacks were “tonal”, novel tonal computer-generated playbacks; “smooth”, smooth broadband computer-generated playbacks; “erratic”, erratic broadband computer-generated playbacks; “currawong”, natural recordings of pied currawongs walking on leaf litter; “rosella”, bell contact call of crimson rosellas, *Platycercus elegans*, harmless parrots; and “food”, parental provisioning calls. (c) and (d) do not include the “currawong” playback because too few broods called in the 10s after the playback to analyze changes in call frequency and amplitude. Box plots show the inter-quartile range and median, whiskers represent the 10th and 90th percentiles, and other symbols show outliers. (Taken from Haff and Magrath, 2010, figure 3, with permission from Elsevier and the authors.)

visits to the nest, so reducing nest conspicuousness. These possibilities have not been tested in any animal, as far as we are aware.

V. CONCLUSIONS AND FUTURE DIRECTIONS

Parent-offspring communication under the risk of predation provides a model system for research on behavioral trade-offs, signal design, and signal meaning. Here we summarize some of the main findings of this review, and suggest specific areas for future research that seem especially promising.

The potential for begging calls to attract predators to the nest has been a key feature of theoretical models of parent-offspring conflict and the evolution of reliable signaling. As nestlings become hungrier and older, their calls change in ways that, in theory, make the calls easier for predators to detect. Indeed, there is ample experimental evidence showing that begging calls attract predators, and some comparative evidence suggesting that predation risk has selected for less detectable begging calls. However, we have yet to measure the absolute costs of calling, or how particular call features contribute to those costs. Doing so is challenging partly because, as illustrated throughout this review, adults and nestlings can mitigate the predation costs of begging in various ways that need to be taken into account in both theoretical models and empirical research. Future work would do well to emulate Martin and colleagues' (2000b) ingenious measurements of the effect of adult activity on nest predation, for example, to better measure those costs and to relate them to interspecific variation in call features. They should also more directly examine exactly how predators use acoustic cues to detect and track down nests.

Parent-absent vocalizations occur when parents are not present to mitigate predation risk, and so the calls could potentially incur much of the cost of nestling calling. Despite this, the functions and predation costs of parent-absent calling remain largely uninvestigated. There appear to be two different types of calls given in the absence of parents: mistaken begging and repeat calls. Mistaken begging occurs when nestlings respond to inappropriate cues of adult arrival, while repeat calls are given on a regular tempo without immediate prompts and are more cryptic acoustically than begging calls. Both call types provide avenues for future research. Mistaken begging offers opportunities to apply signal detection theory to behavioral trade-offs, in this case the trade-off between maximizing at the chance of being fed while minimizing the risk of being overheard. Repeat calling poses a host of new questions. Are nestlings signaling to each other or to their parents, and with what rewards, and what costs? So far, the possibility that nestlings might signal to parents well beyond the nest remains unexplored. If nestlings do use repeat calls for this purpose, it would challenge many long-standing assumptions about the costs and benefits of parental visits and nesting begging.

Parental alarm calls can silence offspring or otherwise make them become less conspicuous, therefore reducing the risk of eavesdropping by predators. Indeed, all but one of 21 playbacks show that offspring respond to at least one type of parental alarm call; in the one species that did not respond, alarm calls seem directed solely to other adults. Furthermore, young usually have very specific responses, such as responding only to alarm calls indicating a threat to the brood, and responding to conspecific but not heterospecific calls. The reed-warbler race of the common cuckoo provides the exception that proves the rule by being the only example of young having an innate response to a heterospecific alarm call, that of its host. Parents might also communicate about immediate danger and so prompt older young to leave the nest, but there has been no experimental confirmation.

In those few species tested, precocial and semi-precocial species respond to alarm calls at hatching, whereas altricial species become more responsive with age. In both cases responses do not require learning, but can be refined with experience. Such changes in response with age probably reflect both sensory development and adaptive changes in behaviour with age. There is little known about the timing of development of responses to alarm calls, even though the abrupt change in vulnerability to predators that comes with fledging offers a natural experiment for testing adaptive predictions. For example, of two species tested, young start responding to aerial alarm calls only late in the nestling period, just before fledging when they become exposed to flying predators. Another issue deserving research is the possibility that parents might use alarm calls to help nestlings learn about predators, perhaps even to an extent one might call teaching.

Provisioning calls, given by parents arriving at the nest with food, could decrease the risk of nest predation by helping to reduce mistaken begging, as well as by increasing the efficiency of food transfer and minimizing the amount of time adults spend at the nest. Further, provisioning calls can be used to lead young after they have fledged, thus assisting fledglings avoid and possibly learn about predators. The potential for predators to eavesdrop on provisioning calls, and the function of complex provisioning calls such as those found in scrubwrens, have not been explored. Provisioning calls, even if used only early in the nestling stage, are also a particularly promising system for studying the ontogeny of the food-versus-risk trade-off faced by nestlings.

The ability of adults and their offspring to respond dynamically each others' vocalizations could help reduce the risk posed by eavesdropping predators. Nestlings can react to adult calls in order to minimize predation risk by going silent to adult alarm calls, begging to adult provisioning calls, or by doing both. Whether and how adults respond to nestling vocalizations under the risk of predation remains poorly tested, despite the vulnerability of noisy young to eavesdropping predators and the potential ability of adults to silence their offspring through alarm calls. Individual decisions by adults of when to alarm and when to remain silent might be influenced by the ability of nestlings to assess danger independently of their parents, an ability only recently discovered in scrubwrens and deserving further investigation. Certainly nestlings must rely heavily on their parents for information about the world beyond the nest, but they might not be as constrained by their poor perception as often supposed; scrubwren nestlings, for example, make surprisingly fine distinctions between acoustic cues of a nearby predator compared to other similar sounds. Indeed, it is the combination of rapid changes in perceptual abilities and vulnerability over the nestling period, all against a background of conflicts of interest over information exchange (Kilner and Hinde, 2008), that make parent-offspring communication under predation such a rich area for future work.

ACKNOWLEDGMENTS

RDM would like to thank the many people who have been involved in the research on acoustic communication, and particularly the students with whom it has been great fun to work, including Dean Ansell, Tom Bennett, Anastasia Dalziell, Pam Fallow, Janet Gardner, Michelle Hall, Mae Hingee, Adam Leavesley, Ashley Leedman, Golo Maurer, Trevor Murray, Ben Pitcher, Dirk Platzen and my co-author Tonya Haff. The work has been funded by the grants from the Australian Research and Australian National University. TMH would like to thank Alex Dorland and Adam Searcy for their outstanding help in the field. MLL and AGH would like to thank the Coldwell, Hines, and Minor families who have generously allowed research on their land and the numerous students and colleagues who have collaborated on various begging projects over the years. Work by MLL and AGH is funded through a NSERC Discovery Grant to MLL.

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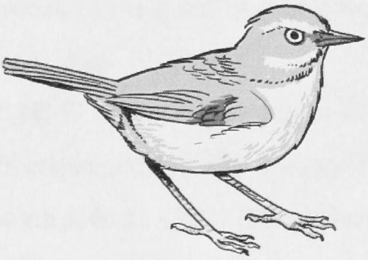
APPENDIX B

Literature cited: chapters 1 - 6



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