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Evolutionary interactions of brood parasites and their hosts

Recognition, communication and breeding biology

A thesis presented in partial fulfilment of the requirements for the degree of

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Frontispiece



Photo by Tomáš Grim

Abstract

Obligate brood parasites lay their eggs in nests of other species, relying on these host parents to care for their offspring. This phenomenon has been a curiosity amongst researchers since its first description and has become a model study system for testing such ideas as coevolution and species recognition. This thesis examines a few of the many questions that arise from this breeding system. The New Zealand Grey Warbler (*Gerygone igata*) and its brood parasite, the Shining Cuckoo (*Chrysococcyx lucidus*) are used as the main study species, although research on the eviction behaviour of Common Cuckoos (*Cuculus canorus*) has also been conducted. First, the current state of knowledge and recent discoveries regarding nestling rejection abilities of hosts is reviewed in chapter one. Second, a comparative study of New Zealand passerine begging calls has been conducted to test for begging call similarity between a brood parasite and its host, as well as developing a new technique for detecting the mode of coevolution that may be occurring in the parasite – host relationship. Parent-offspring communication in Grey Warblers is also examined to test for both parental and nestlings. Parents use both alarm calls to warn offspring of potential danger, and also parental feeding calls to elicit a begging response from nestlings. By contrast, nestlings are able to signal both age and short term levels of need to parents through the acoustic structure of the begging call. The evolutionary costs and benefits of egg eviction behaviour in the Common Cuckoo are also tested. An experimental approach showed that egg eviction had a growth cost, but this cost was temporary and restricted to during and immediately after the egg eviction phase. A pattern of compensatory growth was observed after the eviction period, so that during the later nestling stages there was no difference in mass,

and no difference in fledging age. Finally, variation in the Grey Warbler breeding biology and Shining Cuckoo parasitism rates are examined through both time and across latitudes. This research has shown a counterintuitive pattern of breeding phenology across latitudes. These patterns have implications for Shining Cuckoos both in terms of timing of available nests and host selection.

Keywords: Begging call, breeding phenology, brood parasitism, coevolution, Common Cuckoo, eviction, Grey Warbler, parent-offspring communication, Shining Cuckoo.

Preface

This study focuses on the evolution and maintenance of key traits that are involved in brood parasitism. Most of the research was conducted within New Zealand on the Grey Warbler (*Gerygone igata*) and its brood parasite, the Shining Cuckoo (*Chrysococcyx lucidus*), although one of the chapters uses the Common Cuckoo (*Cuculus canorus*) and its host the Great Reed Warbler (*Acrocephalus arundinaceus*). Although brood parasitism is the common theme of this thesis, each chapter (chapters 1 – 6) has been modified from manuscripts that have been written as scientific papers, and can therefore be viewed as independent studies. Due to the thesis being in this format, some repetition amongst chapters inevitably occurs. References, acknowledgements and appendices are therefore at the end of each chapter. Supervisors Mark Hauber and Dianne Brunton are co-authors of most manuscripts, as stated at the start of each chapter, and have been important with assistance in experimental design, writing the thesis and advice on statistical analysis procedures. Input from other co-authors is stated specifically below. Chapter one has previously been published as a research focus paper within the journal *Trends in Ecology and Evolution*, of which Mark Hauber is a co-author. This introduces some of the key ideas involved with recognition of brood parasite offspring by host species. Chapter two is in press with the *Biological Journal of the Linnean Society*, and uses comparative and bioinformatic procedures as a new technique of detecting co-evolution within brood parasites. Assistance with the bioinformatic analyses was provided by Howard Ross. Chapter three has been submitted to the journal *Animal Behaviour* and uses an experimental approach to investigate the parent-offspring communication used by the Grey Warbler. Chapter four is research that has been

conducted in Hungary on the Common Cuckoo testing the cost of egg eviction behaviour to cuckoo nestlings' growth rates. For this research, Csaba Moskát and Miklós Bán assisted with fieldwork in Hungary, Tomáš Grim assisted with data analysis and Phillip Cassey provided funding. This research has been submitted to the journal *American Naturalist*. Chapter five investigates the honest information content of begging calls of the Grey Warbler and is being submitted to the journal *Ethology*. Chapter six uses four different data sets on the breeding biology of the Grey Warbler to investigate the changes in breeding phenology with latitude and through time and the ways that this can affect the Shining Cuckoo. Brian Gill and Jim Briskie are both co-authors on this research, as they have provided data on Grey Warbler breeding biology from Kaikoura.

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When, I completed my Masters thesis, I started off the acknowledgements with a few statistics. Once again, this feels appropriate. At that time, my masters thesis had taken up 822 days, or 8.7% of my life. By contrast, my PhD thesis has taken up (approximately) 1620 days, or 15.04% of my life thus far. Obviously, anyone that has experience such an undertaking knows that it is not possible to spend so much time trying to complete a task, without the help of many people. These people are mentioned below, all of whom I am greatly indebted to for their assistance and support during this time.

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The second chapter of this thesis investigates the begging call similarity of the Grey Warbler and Shining Cuckoo through the use of a comparative framework. In order to do this kind of research, I required begging calls of all New Zealand passerines, which was certainly not an easy task. Many dedicated volunteers, researchers and conservation staff assisted with locating nests of various species from throughout the country. So I am very grateful for the assistance of Alana Alexander, Gavin Anderson, Shauna Baillie, Marleen Baling, Jake Bapty, Manuela Barry, James Briskie, Emily Brugge, Taneal Cope, Mark Delany, Graeme Elliot, Barbara Evans, Morag Fordham, Brian Gill, Tomas Grim, Charlotte Hardy, Malcolm Harrison, Weihong Ji, Stacey Hill, Todd Landers, Barry Lawrence, Nora Leuschner, Tim Lovegrove, Eric Marsden, Luis Ortiz Catedral, Kevin Parker, Jo Peace, Marion Rhodes, Peter Samas, Hazel Speed, Rose Thorogood, Megan Willans (and field assistants) and Sarah Withers.

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Table of contents

FRONTISPIECE	II
ABSTRACT.....	III
PREFACE	V
ACKNOWLEDGEMENTS	VII
TABLE OF CONTENTS	XII
LIST OF FIGURES	XV
LIST OF TABLES	XVIII
LIST OF SUPPLEMENTARY MATERIALS.....	XX
1 A RECOGNITION-FREE MECHANISM FOR RELIABLE REJECTION OF BROOD PARASITES.....	1
1.1 ABSTRACT	2
1.2 INTRODUCTION	3
1.3 DARWINIAN ALGORITHMS TO REJECT PARASITES	3
1.4 NESTLING DISCRIMINATION WITHOUT RECOGNITION	4
1.5 IMPLICATIONS FOR HOST–PARASITE COEVOLUTIONARY PROCESSES.....	9
1.6 CONCLUSION	11
1.7 ACKNOWLEDGEMENTS	12
1.8 REFERENCES.....	12
2 BEGGING CALL MATCHING BETWEEN A SPECIALIST BROOD PARASITE AND ITS HOST: A COMPARATIVE APPROACH TO DETECT CO-EVOLUTION.	14
2.1 ABSTRACT	15
2.2 INTRODUCTION	16
2.3 MATERIAL AND METHODS	19
2.3.1 <i>Begging call recordings</i>	19
2.3.2 <i>Phylogeny of New Zealand passerines</i>	21
2.3.3 <i>Data Analysis</i>	21
2.4 RESULTS	24
2.4.1 <i>Host-parasite begging call similarity</i>	24
2.4.2 <i>Similarity between begging call and phylogenetic trees</i>	25
2.4.3 <i>The effect of parasite and host on the phylogenetic signal of the begging call similarity tree</i>	27
2.5 DISCUSSION.....	29
2.6 ACKNOWLEDGEMENTS.....	33
2.7 REFERENCES	34
2.8 SUPPLEMENTARY MATERIAL.....	40
3 SPECIES-SPECIFIC MODULATION AND ONTOGENETIC SHIFT OF THE RESPONSES OF GREY WARBLER (<i>GERYGONE IGATA</i>) NESTLINGS TO PARENTAL FEEDING AND ALARM CALLS	45
3.1 ABSTRACT	46
3.2 INTRODUCTION.....	48

3.3	METHODS.....	53
3.3.1	<i>Study Species and Site</i>	53
3.3.2	<i>Collection of acoustic stimuli</i>	58
3.3.3	<i>Preparation of playback sequences</i>	59
3.3.4	<i>Conducting the playbacks</i>	59
3.3.5	<i>Statistical Analysis</i>	61
3.3.6	<i>Ethical note</i>	63
3.4	RESULTS.....	64
3.4.1	<i>Begging Solicitation Calls</i>	64
3.4.2	<i>Alarm call playbacks</i>	67
3.5	DISCUSSION.....	71
3.6	ACKNOWLEDGEMENTS.....	76
3.7	REFERENCES.....	77
4	EGG EVICTION IMPOSES A RECOVERABLE COST OF VIRULENCE IN CHICKS OF THE COMMON CUCKOO.....	83
	ABSTRACT.....	84
4.1	INTRODUCTION.....	85
4.2	METHODS.....	89
4.2.1	<i>Field Procedures</i>	89
4.2.2	<i>Sample Sizes</i>	90
4.2.3	<i>Data Analyses</i>	91
4.3	RESULTS.....	93
4.4	DISCUSSION.....	97
4.5	ACKNOWLEDGEMENTS.....	101
	LITERATURE CITED.....	102
5	HONEST INFORMATION CONTENT OF NESTLING BEGGING CALLS IN THE GREY WARBLER.....	107
5.1	ABSTRACT.....	108
5.2	INTRODUCTION.....	109
5.3	METHODS.....	111
5.3.1	<i>Study Site and Species</i>	111
5.3.2	<i>Playback experiment</i>	112
5.3.3	<i>Statistical methods</i>	115
5.4	RESULTS.....	116
5.4.1	<i>Call rate</i>	116
5.4.2	<i>Call structure</i>	116
5.5	DISCUSSION.....	122
5.6	ACKNOWLEDGEMENTS.....	125
5.7	REFERENCES.....	126
6	COUNTERINTUITIVE PATTERNS OF BREEDING PHENOLOGY VARIATION WITH LATITUDE IN THE GREY WARBLER (<i>GERYGONE IGATA</i>) AND IMPLICATIONS FOR ITS BROOD PARASITE, THE SHINING CUCKOO (<i>CHRYSOCOCCYX LUCIDUS</i>).	131
6.1	ABSTRACT.....	132
6.2	INTRODUCTION.....	133
6.3	METHODS.....	137
6.3.1	<i>Historical nesting records</i>	137
6.3.2	<i>Study Sites and Species</i>	137
6.4	DATA ANALYSIS.....	140
6.5	RESULTS.....	141
6.5.1	<i>Clutch Size</i>	141
6.5.2	<i>Frequency of broods and timing of breeding</i>	144
6.5.3	<i>Brood parasitism rates</i>	145
6.5.4	<i>Adult Mass</i>	145
6.5.5	<i>Nestling Growth</i>	145
6.6	DISCUSSION.....	151
6.7	ACKNOWLEDGEMENTS.....	156
6.8	REFERENCES.....	157

7	CONCLUSIONS AND FUTURE DIRECTIONS	163
7.1	BROOD PARASITISM RESEARCH	164
7.2	PARENT-OFFSPRING COMMUNICATION	166
7.3	CONSERVATION	168
7.4	REFERENCES.....	170
8	APPENDICES	176
8.1	CHAPTER 1: PUBLISHED VERSION	176
8.2	CHAPTER 2: PUBLISHED VERSION	180

List of Figures

- Figure 1. A typical brood of reed warbler chicks (depicted) demands much parental care. Broods of one or four reed warblers or a single common cuckoo chick that remain in the nest beyond the typical nestling period of the host, face abandonment by parents (Grim, 2007, Grim *et al.*, 2003). Reproduced with permission from T. Grim. 6
- Figure 2: Dendrograms of begging call similarities created by cluster analysis based on acoustic features. Three New Zealand native species sets were used; a) all passerines and out groups, b) passerines and c) oscines. The host and brood parasite species are highlighted in bold. 26
- Figure 3: The stimuli used in the playback experiment. The two main types of adult conspecific vocalizations that are used for parent-offspring communication, a) begging solicitation call and b) parental alarm call and c) the heterospecific begging solicitation call and d) alarm call, and the e) heterospecific song used as a control. 57
- Figure 4: Mean discrimination scores (± 1 standard error) of the begging response for nestlings when presented with each of the five different acoustic stimuli. The five stimuli are fantail alarm call (HA), fantail song (C), grey warbler alarm call (CA), grey warbler begging solicitation call (CB), and the welcome swallow begging solicitation call (HB). Age groups were combined due to no significant difference. 65
- Figure 5: Alterations in calling rate of 12 (■) and 16 (□) days grey warbler nestlings for a) begging solicitation calls and b) alarm calls. 68
-

Figure 6: Alterations in the a) frequency, b) duration and c) amplitude of nestling begging calls of 12 (■) and 16 (□) day old grey warbler nestlings in response to the three different begging solicitation calls.....	69
Figure 7: Alterations in the a) frequency, b) duration and c) amplitude of nestling begging calls of 12 (■) and 16 (□) day old grey warbler nestlings in response to the three different alarm stimuli.	70
Figure 8: Hatchling common cuckoos in the process of evicting host chicks and eggs [inset] from great reed warbler nests. Photo credit: C. Moskát and M. Honza (inset photo).....	88
Figure 9: Growth of common cuckoo chicks in great reed warbler nests with host eggs left that had to be evicted by cuckoo chicks (black circles: control/evictor group) or where host eggs were removed (open circles: experimental/non-evictor treatment) for a) mass, b) tarsus, c) gape length, d) gape width, e) gape area. Values are means ± SE....	96
Figure 10: The two typical types of vocalisations given by Grey Warbler nestlings; a) a longer begging call following the parental feeding call and b) the shorter non-begging call.....	118
Figure 11: The relationship between the time since nestlings heard their parental feeding call and a) frequency ($r = -0.34, p < 0.001$), b) frequency range ($r = -0.06, p = 0.06$), c) duration ($r = -0.27, p < 0.001$) and d) amplitude ($r = -0.14, p < 0.001$) of nestling vocalisations. Lowess smoothing is used to give lines of best fit for all graphs.	119
Figure 12: Mean (± SE) begging call rate (number of begging calls per second given after parental feeding call) given by Grey Warbler nestlings across three food deprivation periods (i.e. hunger levels) at 12 () and 16 () days.	120

Figure 13: Mean (\pm SE) of (a) amplitude, (b) centre frequency, (c) frequency range, and (d) duration of begging calls for Grey Warbler nestlings across three food deprivation periods (i.e. hunger levels) at 12 (■) and 16 (□) days.	121
Figure 14: Average Grey Warbler clutch sizes (eggs) from the two sites in New Zealand, Tawharanui and Kaikoura. Kaikoura is shown as two separate columns for the two studies conducted at the same site. Bars are means \pm standard error.	142
Figure 15: The effect of latitude on clutch size for Grey Warblers throughout the range of New Zealand. Data is from OSNZ nest records.	142
Figure 16: The relationship between lay date (5 th of September = Day 1) and clutch size for a) Kaikoura study 2, b) Tawharanui, and c) OSNZ nest record data (25 th of June = Day 1).	143
Figure 17: Seasonal patterns of egg laying in the Grey Warbler in a) Tawharanui and b) Kaikoura study 1(1976-1979), c) Kaikoura study 2 (2001-2007), d) OSNZ records. The number of eggs laid are grouped into weekly intervals.	148
Figure 18: Differences in adult Grey Warbler mass between Kaikoura and Tawharanui. Adults were caught by mist netting birds from May to July at each site. Bars are means \pm standard error.	149
Figure 19: Growth rates of a) mass and b) tarsus of nestlings at Tawharanui (○) and Kaikoura (●). Lines of best fit are logistic curves for mass and a third degree polynomial fit for tarsus (see Methods for equations). Lines of best fit are denoted as solid lines for Kaikoura and dashed lines for Tawharanui data.	150

List of Tables

Table 1. Suggested mechanisms of brood abandonment in evicting brood parasites.....	5
Table 2: Empirical probability that two designated taxa form a species pair on a tree of random topology, or when the leaves are randomised on the observed topology of begging call similarity. In each case, 10^4 randomizations were performed.	28
Table 3: The congruence of the topology of the call similarity cluster diagram with respect to the phylogeny. The underlying null distribution of each metric was obtained by randomizing the topology of the cluster diagram and then comparing it with the known phylogeny. The “randomness” of the observed cluster diagram is indicated by the percentile at which it fell on the null distribution. Low percentiles are indicative of non-randomness. In each case, 10^6 randomizations were performed.	28
Table 4: Differences in growth parameters between experimental (chicks raised alone, host eggs removed) and control (host eggs left and evicted) cuckoo chicks in great reed warbler nests. Data from <i>a priori</i> defined phases of development were analyzed separately. Growth was estimated as deviations from growth patterns of control chicks randomly sampled in the study population (see Methods). Effect size (mean \pm SE) is the difference between the growth parameter of experimental and control groups (i.e., positive effect = greater growth of experimental chicks). Sample sizes for respective periods are given as number of nests/chicks and measurements and df refers to denominator degrees of freedom from GLMM models controlling for chick identity and age.....	95

Table 5: The effect of the number of eggs evicted by cuckoo nestlings on growth parameters within the control group (nestlings that evicted eggs). Sample sizes for respective periods are given as number of nests/chicks (N) and measurements (n), and df refers to denominator degrees of freedom from the LMM model controlling for chick identity and age.....	97
Table 6: A summary of the factors that are known to affect various breeding parameters for birds and the change caused by each effect.	136

List of Supplementary Materials

Suppl. 1: Locations and samples sizes for the begging call recordings made for each species.....	40
Suppl. 2: Phylogeny of the 20 New Zealand species used in comparative analysis of begging calls.	42
Suppl. 3: Example spectrograms of the begging calls of a) shining cuckoo and three New Zealand passerine species: b) grey warbler, c) bellbird and d) whitehead.....	43
Suppl. 4: Example spectrograms of the begging calls of a) shining cuckoo and three New Zealand passerine species: b) grey warbler, c) bellbird and d) whitehead.....	44
Suppl. 5: Sample sizes for the number of cuckoos at each age class within each experimental group.	106

1 A recognition-free mechanism for reliable rejection of brood parasites



Common Cuckoo (*Cuculus canorus*) in the late stages of the nestling period (Photo: Michael Anderson)

This chapter is modified from the manuscript:

Anderson, M. G. & Hauber, M. E. (2007) A recognition-free mechanism for reliable rejection of brood parasites. *Trends in Ecology & Evolution*, **22**, 283-286.

1.1 Abstract

Hosts often discard eggs of avian brood parasites, whereas parasitic chicks are typically accepted. This can be explained theoretically by fitness losses associated with adults learning to recognize parasitic young and mistakenly rejecting their own young. A new experimental study confirms that rejection of parasitic chicks, without relying on memory to discriminate between foreign and own young, is a feasible and potentially cost-free mechanism used by reed warblers to reject common cuckoo chicks. By abandoning broods that are in the nest longer than is typical for their own young, parents can reliably reject parasite nestlings and reduce fitness losses owing to having to care for demanding parasitic young. Discrimination without recognition has important implications for the realized trajectories of host–parasite coevolutionary arms races.

1.2 Introduction

Social parasites exploit the foraging and breeding efforts of their hosts. Obligate brood parasitic birds, for instance, lay their eggs in the nests of other species and reduce the reproductive output of hosts that care for unrelated young. Despite fitness losses, hosts of some brood parasites, including *Molothrus* cowbirds, accept distinctive foreign eggs and chicks in their nest. By contrast, victims of *Clamator* and *Cuculus* cuckoos often reject parasitic eggs, despite the typically close visual match between foreign and host eggs (Davies, 2000). The mimicry of host chick phenotypes is rare among the different avian brood parasite lineages (McLean & Waas, 1987), yet discrimination of parasite and host chicks by foster parents is even more infrequent (Grim *et al.*, 2003, Langmore *et al.*, 2003). How can foster parents in the few species where hosts do reject parasitic young, discriminate between their own and foreign chicks? In a recent experimental study, Grim (2007) demonstrates that rejection of common cuckoo *Cuculus canorus* chicks by host reed warbler *Acrocephalus scirpaceus* parents is based on intrinsic differences in the duration of parental care required by broods of host versus parasite young.

1.3 Darwinian algorithms to reject parasites

The diversity of strategies by which avian brood parasites overcome host defences has offered one of the best opportunities for studying coevolution through observation and experimentation (Davies, 2000). The cognitive processes used by hosts to defend

against mimetic parasite eggs involve recognition through the assessment of the match between a learned template of own eggs and the phenotype of the potential parasite egg (Rothstein, 1975). By contrast, theoretical models demonstrate that, even in the absence of costly neural structures associated with memory formation and storage, chick discrimination through learning might be maladaptive. This is because the cost of discrimination errors would be too high for both evicting and non-evicting cuckoo (Lotem, 1993) and cowbird (Lawes & Marthews, 2003) chicks. Specifically, misimprinting on a parasitic young during the first nesting attempt by a host would lead to mistaken rejection of its own chicks in all subsequent broods.

In line with this theory, there are few reported examples of brood parasite discrimination at the nestling stage, although this might instead reflect less research effort in this area (Grim, 2006). However, the experience of the hosts with raising young and, thus, learning about offspring, might not be required to identify parasites (Langmore et al., 2003). For example, just as memory might not be required to locate and benefit from caching seeds (Smulders & Dhondt, 1997), the rejection of brood parasites might not require the recognition of foreign nestlings (Grim et al., 2003).

1.4 Nestling discrimination without recognition

Grim (2007) illustrates how a custom-designed cross-fostering experiment can test between different proximate cues that are used by host parents. Initial observations revealed (Grim et al., 2003) that some common cuckoo chicks were abandoned during the advanced stages of the nestling period by reed warbler hosts. The recognition of nestlings based on phenotype alone (e.g. appearance or vocalizations) was unlikely as

other experimental work already showed that reed warblers readily accept and feed heterospecific nestlings (Davies et al., 1998). Three possible explanations for nestling rejection remained feasible: (i) the parental-fatigue hypothesis; (ii) the time-limit hypothesis; and (iii) the single-chick hypothesis (Box 1).

Through a series of experiments, Grim and helpers created ‘shortened’ nests in which younger broods were swapped with older broods and ‘prolonged’ nests in which older broods were replaced with younger broods. Switching warbler chicks of different ages generated broods that received significantly extended or shortened parental care periods compared to what is typical for non-parasitized reed warbler broods (Figure 1). In addition, broods of four versus single warbler chicks were also generated, thereby creating variation in the overall amounts of care required for each brood within both shortened and prolonged treatments. Two types of nest served as controls: handling-only and cross-fostering of same age broods. The variations in the duration and the amount of parental care received then enabled the author to disentangle the three possible recognition-free mechanisms (Table 1).

Table 1. Suggested mechanisms of brood abandonment in evicting brood parasites

Hypothesis	Age at abandonment ^a	Parasite mimicry expected	Reason for abandonment at given brood age
Recognition-based mechanism			
1. Begging call mimicry	4–5 days	Yes	Age when chicks begin to vocalize
Recognition-free mechanisms			
2. Parental fatigue	8 days	No	Age when the cumulative amount of provisioning by parent exceeds that required by brood of host
3. Time limit	12 days	No	Nestling period exceeds that of healthy host chicks
4. Single chick	1–3 days	No	Extent of maximum hatching asynchrony in host broods

^aA hypothetical host with a nestling period of 11 days.



Figure 1. A typical brood of reed warbler chicks (depicted) demands much parental care. Broods of one or four reed warblers or a single common cuckoo chick that remain in the nest beyond the typical nestling period of the host, face abandonment by parents (Grim, 2007, Grim *et al.*, 2003). Reproduced with permission from T. Grim.

The results on nest desertion rates were clear cut with regards to crucial predictions of the alternatives (Table 1). In support of the time-limit hypothesis, nest desertion only occurred in prolonged nests. A finding of similar rejection rates of single and four-chick broods was contrary to both the parental fatigue hypothesis and the single-chick hypothesis. Furthermore, the single-chick hypothesis was also rejected because no desertions occurred in single versus four-chick nests within either the shortened or the control treatments.

Desertions occurred in prolonged nests at a rate of 22% which closely reflected the observed desertion rate (15.8%) of nests naturally parasitized by cuckoos at the same

study area (Grim et al., 2003). This implies that similar proximate mechanisms for nest desertion might be utilized by natural and experimental foster parents. However, the average nestling age at which chicks died was lower for experimental broods with warbler chicks (Grim, 2007) than for sympatric, natural broods with cuckoo chicks (Grim et al., 2003).

Box 1. Mechanisms of nestling rejection

For host parents to be able to reject brood parasite nestlings, some form of proximate cue is required to discriminate foreign chicks from their own nestlings. These can take the form of recognition based (1) or recognition-free (2–4) mechanisms of discrimination.

1. Begging-call mimicry

Nestlings give begging calls when being fed by parents. These calls can vary between species and offer a cue that host parents can use to discriminate brood parasite nestlings. Brood parasites are able to counteradapt by mimicking the begging calls of their host (Langmore et al., 2003). Nestlings that do not show an acceptable level of vocal mimicry should be rejected near the age at which host chicks typically start to vocalize.

2. Parental-fatigue hypothesis

Parents might desert nestlings that require too much care to avoid excessive loss of future reproductive potential. This can occur if parasite nestlings require more food than does a brood of host nestlings. Parents might be physiologically unable to provide for the larger parasite nestling and so might either abandon when their exhaustion levels are

too high or use the total amount of care required by young to discriminate between their own and foreign chicks. The desertion of parasite nestlings should occur once food provisioning levels are greater than the normal range observed for parents at unparasitized nest.

3. Time-limit hypothesis

Parasite nestlings fledge after a considerably longer period of time than do the offspring of their hosts, owing to the larger size of the parasites and the physiological constraints placed on their growth. Host parents can use this duration cue as a method to discriminate brood parasites from their own young (Grim, 2007). Nestling rejection should therefore occur once the duration of parental care exceeds that required for host nestlings.

4. Single-chick hypothesis

Many brood parasite nestlings evict their nest mates, leaving a sole parasite chick for foster parents to feed. Brood loss could be used as a cue by parents to assess the risk for (partial) predation or to identify the nestling that they are feeding as a parasite. According to this scenario, broods with single nestlings should be disproportionately rejected. Nestling desertion should occur within the first few days of hatching, once a nestling is found to be alone in the nest after accounting for natural levels of hatching asynchrony.

1.5 Implications for host–parasite coevolutionary processes

Previous models of parasite rejection mechanisms led researchers to conclude that it would be maladaptive to learn to recognize nestlings for cuckoo hosts because of costly errors of accepting parasitic young and rejecting own young (Lotem, 1993). However, under this novel mechanism of discrimination without recognition, rejection errors are not made because nest abandonment occurs solely after the typical length of the host nestling period. In support of such a cost-free mechanism, Grim found no evidence at this research site for rejection errors where broods of reed warbler young were abandoned by parents (Grim, 2007, Grim *et al.*, 2003). Nonetheless, discrimination without recognition is not a strictly cost-free rejection mechanism. This is because, in 78% of the cases, parents did fledge chicks from prolonged nests, thereby accepting the cost of longer parental care provided for experimentally ‘parasitized’ nests. Second, parents might not always reliably abandon parasitized broods in host species whose typical nestling period overlaps in duration with that of the nestling periods of the parasitic species (Kleven *et al.*, 1999).

Theoretical scenarios of coevolutionary arms races have also typically evoked escalating cycles between antiparasite defences by hosts and counteradaptations by parasites (Davies, 2000, Langmore *et al.*, 2003). When foreign eggs are rejected because they look different, egg mimicry evolves (Davies, 2000). In turn, when nestlings are rejected because their begging displays look or sound different, mimicry of begging behaviours evolve (Langmore *et al.*, 2003). However, it appears that there is little defence against having a nestling period that is too long compared to that of the reed warbler, as common cuckoo chicks tend to have similar nestling periods regardless

of host species size (Kleven et al., 1999). The absence of additional reduction in the duration of parasite nestling periods might represent the endpoint for any future coevolutionary process within this particular host–parasite system.

Alternatively, brood abandonment by reed warblers might represent a trait that evolved independently of cuckoo parasitism as a life-history tradeoff between current and future parental investment. If longer nestling periods are predictive of lower success of the current brood, owing to disease or weather-related slowing of growth, then parents might abandon current broods and attempt to breed later. Determining whether the abandonment by reed warblers of prolonged broods is a specific anti-parasite response will require conducting Grim’s experiments in genetically isolated populations of reed warblers that have never been exposed to brood parasitism, or in a series of a sister taxa of host and non-host species.

Recognition-free discrimination of brood parasites raises additional research questions and possibilities in coevolution and cognition. This mechanism not only shows that nestling discrimination is possible for evicting parasites raised alone, but also confirms that discrimination might not require prior learning or parental experience by hosts (Langmore et al., 2003). What then are the phenotypic and cognitive tricks used by single cuckoo chicks that cause naturally parasitized nests to be abandoned after a longer period of care than what is seen for experimentally prolonged broods of warbler chicks? And why did chicks in the shortened treatment consistently remain in the nest longer to receive more parental care than did control and prolonged host broods?

Differences in the duration of parental care across treatments might be due to differences in the proximate, solicitation stimuli given by nestlings. The endogenous cues used by host parents to determine the appropriate duration of nestling care are also

unknown. If the duration of parental care is under hormonal control (Silverin, 1980) in reed warblers, it might be pertinent to test for hormonal titer differences between chick rejecters and acceptors. Most importantly, the causes of sensory and endocrine differences when responding to prolonged parental care would also need to be explored because, to date, we lack direct evidence about the genetic control of parasite-rejection mechanisms in any avian hosts (Martin-Galvez et al., 2006), even though heritability and, thus, evolvability, of rejection decisions are pivotal assumptions of coevolutionary theory.

1.6 Conclusion

Our knowledge of the evolutionary diversity and frequency of nestling discrimination abilities by host parents has increased considerably over recent years. New findings add to this knowledge and offer several additional lines of research into the cognitive and physiological basis of recognition systems. They also suggest that the rules of nestling discrimination are varied and quite different from those of egg discrimination (Lotem, 1993), inviting more research into the genetic, developmental, physiological and perceptual bases of host–parasite chick discrimination. These results will, in turn, be incorporated into evolutionary models of host–parasite systems and shape our understanding of the complexity of the arising coevolutionary processes.

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2 Begging call matching between a specialist brood parasite and its host: A comparative approach to detect co-evolution.



Shining Cuckoo, *Chrysococcyx lucidus* (Photo by Michael Anderson)

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2.1 ABSTRACT

Studies of avian brood parasite systems have typically investigated the mimicry of host eggs by specialist parasites. Yet, several examples of similarity between host and parasite chick appearance or begging calls suggest that the escalation of host-parasite arms races may also lead to visual or vocal mimicry at the nestling stage. Despite this, there have been no large scale comparative studies of begging calls to test whether the similarity of host and parasite is greater than predicted by chance or phylogenetic distance within a geographically distinct species assemblage. Using a survey of the begging calls of all native forest passerines in New Zealand we show that the begging call of the host-specialist shining cuckoo (*Chrysococcyx lucidus*) is most similar to that of its grey warbler (*Gerygone igata*) host compared to any of the other species, and this is unlikely to have occurred by chance. Randomization tests revealed that the incorporation of the shining cuckoo's begging calls into our species-set consistently reduced the phylogenetic signal within cluster trees based on begging call similarity. In contrast, the removal of the grey warbler calls did not reduce the phylogenetic signal in the begging call similarity trees. These two results support a scenario in which coevolution of begging calls has not taken place; the begging call of the host retains its phylogenetic signal, while that of the parasite has changed to match that of its host.

Additional Keywords: comparative methods - nestling rejection — recognition systems.

2.2 INTRODUCTION

Coevolution is a reciprocal process whereby an alteration in a trait of one species causes a change in a second species, leading to a further response in the first species (Futuyma, 1998, Janzen, 1980). In a linear form of coevolution, two species reciprocally evolve in response to each other in what has frequently been termed an evolutionary arms race (Dawkins & Krebs, 1979, Futuyma, 1998). The relationship between avian hosts and their brood parasites offers some of the best examples of this type of coevolution (Rothstein & Robinson, 1998). A potentially useful way of detecting the coevolution is to apply a comparative method to detect deviation from the phylogenetic position of both host and parasite taxa with respect to their specific trait-sets. Here we apply randomization tests to a comparative dataset for this aim.

Previous phylogenetic methods to explicitly test for host-parasite co-evolution (Banks *et al.*, 2006, Johnson *et al.*, 2001) showed that speciation events of the parasite reflect those of the host, resulting in parallel phylogenies of host and parasite taxa (Paterson & Banks, 2001). However, these methods have typically tested host-parasite systems with only pairs of species of hosts and their respective species-specific parasites. We adapted this approach specifically to avian brood parasites where the parasite has multiple hosts available but only exploits one host species (Payne, 2005a). If traits of brood parasites are coevolving with traits in their host (Davies, 2000, Davies & Brooke, 1989, Langmore *et al.*, 2003), then trait similarity trees of taxa that include actual and potential hosts as well as their parasites, would indicate how similar parasites actually are to hosts. Grim (2005) suggested numerous alternative explanations to trait similarity that are not due to coevolved mimicry (e.g. random matching, crypsis in the shared

environment). Several of these can be tested by the use of phylogenetic methods, including: 1) phylogenetic constraints (i.e. being closely related), 2) random matching (i.e. similarity due to chance, not co-evolution), and 3) non-random matching (i.e. due to similar selection pressures on both host and parasite).

In this study, we tested for coevolution of begging call signals in New Zealand between a specialist native brood parasite, the shining cuckoo (*Chrysococcyx lucidus*), and its host the grey warbler (*Gerygone igata*) (Gill, 1983, Gill, 1998). Previous work suggests begging call mimicry in this system based on the pairwise acoustic similarity of host and parasite nestlings (McLean & Waas, 1987). We specifically evaluated whether this is a result of a coevolutionary process; with begging call mimicry evolving in the parasite and begging call discrimination evolving in the host. In this scenario, the parasite would evolve a similar begging call to the host, due to the host rejection of vocally dissimilar nestlings (Grim, 2006, Langmore *et al.*, 2003). In response, the host would be expected to alter its begging call, increasing its ability to discriminate parasites. This process would repeat as a coevolutionary arms race, leading to the loss of any phylogenetic signal (i.e. tendency for closely related species to resemble each other), in begging calls of both host and parasite.

To test this coevolutionary scenario, we first generated a similarity tree of begging calls using cluster analysis methods with native passerines in New Zealand to quantify the acoustic distance between host and parasite. We then used this tree to evaluate the chance that these species would be the most closely matching taxa based on randomization procedures. Second, we applied phylogenetic tree comparison techniques to evaluate the extent of the phylogenetic signal in the interspecific acoustic similarity

patterns. Finally, we examined the effects that the inclusion or exclusion of either the parasite or its host had on the phylogenetic signal in the acoustic similarity tree to evaluate if coevolution occurred.

We predicted one of three outcomes; that the host and parasite similarity would 1) not be greater than predicted by chance, 2) have matching traits, but the host trait was not altered in response, and 3) have matching traits, which were both altered from their original evolutionary position through an arms race. In the first and second cases, no coevolution occurred, whereas the third scenario would suggest that coevolution occurred in the form of chase-away selection (Hauber & Kilner, 2007), where the trait deviated from what would be expected from phylogenetic history (Fisher, 1930, Gavrillets & Hastings, 1998, Servedio & Lande, 2003). This strategy would benefit the host, as altering the structure of nestling begging calls would potentially improve discrimination. Alternatively, under the second scenario host parents respond by increasing their threshold of discrimination for begging calls, progressively selecting for similar sounding parasite nestlings. However, 2) and 3) are also consistent with the scenario that either host and parasite traits evolved in parallel owing to a shared ecological variable, such as mortality caused by acoustically oriented predators, during ontogeny (i.e. host and parasite chicks both grow up in host nests) (Grim, 2005) while 2) is also consistent with the possibility that parasites evolutionary response involves learning to match host begging calls (Langmore *et al.*, 2008, Madden & Davies, 2006).

2.3 MATERIAL AND METHODS

2.3.1 Begging call recordings

Begging calls were recorded from nestlings of native New Zealand passerines, including all forest species that are found on the North and South Islands. In total, there are 20 such extant species in New Zealand, of which 2 were not sampled as they are only located on the Chatham Islands (black robin, *Petroica traverse*; Chatham Island warbler, *Gerygone albofrontata*) and we were not permitted to gain access to nestlings. We were also unable to record the remaining native New Zealand passerine (fernbird, *Bowdleria punctata*) due to difficulty locating nests. The other 17 species were recorded from locations throughout the country (see Suppl. 1). The begging calls of three non-passerine species were also used in the analysis: 1) the shining cuckoo, 2) orange-fronted parakeet (*Cyanoramphus malherbi*) and 3) the New Zealand kingfisher (*Halcyon sancta*). The shining cuckoo was added to test the similarity of its begging call to its host, the grey warbler. The shining cuckoo is widespread in New Zealand, so all species recorded have the potential for sympatry (Robertson *et al.*, 2007), with the exception of the alpine rock wren. The two other species were used as opportunistic outgroups for the analysis.

Begging calls were recorded from broods under natural situations during parental feeding visits, by setting up a microphone as close as possible to the nest without causing disturbance (usually 20-30cm). The nest was subsequently observed from a distance (typically 10-15m) to ensure that normal parental behaviours resumed. We controlled for nestling development by attempting to record nestlings on the day that primary feathers emerged from the sheaths (Briskie *et al.*, 1999), as determined by

either direct inspection or the age of nestlings. However, some instances required nestlings to be recorded opportunistically. If age could not be determined, nestlings from the mid to late stages of development that were responding vocally to parental nest visitations were recorded. Calls were then recorded for up to 90 minutes to ensure that several feeding bouts occurred. Nestling begging calls were recorded with a Sennheiser ME 66 microphone or a Panasonic RP-VC201 stereo tie-clip microphone, depending on nest accessibility, onto a Sony MZ-NH700 Hi-MD Minidisc with a sampling rate of 44.1kHz. Recordings were subsequently examined in Raven 1.3 (Charif *et al.*, 2007). Sound recordings were digitised and visualised as spectrograms (Hann, window size 5.33 mS, 3 dB bandwidth of 270 Hz, frequency grid DFT size 256 samples and 188 Hz) for analysis (see Suppl. 3 for examples).

For each species, attempts were made to record at least three nests, however this was not always possible (see Suppl. 1 for sample sizes). Only one shining cuckoo nestling was recorded during the nestling stage, so the begging calls of two fledglings were also used. To ensure that the fledgling begging calls did not alter the results, the cluster analysis (see following data analysis section) was conducted separately for both nestling and fledgling stages. The overall tree topology was identical for both analyses, and this topology did not change when the two age groups were combined. Only begging calls given by nestlings when parents were at the nest were used, thus avoiding parent-absent vocalisations (Šicha *et al.*, 2007). From each nest 10 individual begging calls were used that did not overlap with begging calls of siblings.

Begging calls were analyzed using Sound Analysis Pro (Tchernichovski *et al.*, 2000) and relevant sound parameters were measured for each begging call. These measures

were 1) mean frequency modulation (FM), 2) mean amplitude modulation (AM), 3) mean entropy (ENT), 4) mean frequency (FREQ) and 5) call duration (DUR) (see Suppl. 4 for explanations of parameters, and Tchernichovski *et al.* (2000), for further definitions of measurements).

2.3.2 Phylogeny of New Zealand passerines

An unweighted phylogeny of New Zealand passerines was compiled from published molecular phylogenetic relationships (Barker *et al.*, 2004; Driskell *et al.*, 2007; Keast, 1977; Miller & Lambert, 2006; Sibley & Ahlquist, 1987). Where analyses of the species in question were unavailable, their position was generally able to be resolved by the position of higher taxonomic levels. The only unresolved group was for the family Pachycephalidae (genus *Mohoua*). The three endemic species of this genus, are considered to be closely related (Keast, 1977, Sibley & Ahlquist, 1987) and were thus put as a polytomy (Suppl. 2).

2.3.3 Data Analysis

2.3.3.1 Generation of phylogenetic species sets and begging call similarity trees

Phylogenetic trees of three sets of taxa were used in the analysis: 1) all 17 recorded New Zealand passerines, the shining cuckoo and two non-passerines as outgroups (20 species), 2) all recorded New Zealand passerines and the shining cuckoo (18 species) and 3) all recorded New Zealand oscines and the shining cuckoo (16 species). The final tree was added because of the possibility that the New Zealand wrens (Acanthisittidae)

begging calls may be anomalous amongst New Zealand's passerines, as wrens are an ancient preoscine passerine lineage (Barker, 2004).

Hierarchical cluster analyses were used to reveal the structure of begging calls amongst New Zealand passerines by using of the five sound variables that were extracted from the begging calls. Cluster analyses at the species level were conducted in Statistica v.6.0 (Statsoft, 2001) for the three sets of species (as above) using average linkage (unweighted pair-group average) as the fusion strategy and Euclidean distances as the distance metric (McGarigal *et al.*, 2000). The dendrograms produced were used as the trees for randomization analyses of tree topology and phylogenetic signal.

2.3.3.2 Probability of parasite and host being sister taxa

The results of the begging call cluster analyses consistently found that the shining cuckoo and the grey warbler were a sister pair (see Results). To test the statistical probability of this occurring by chance, we conducted two randomization procedures using the program PAUP v.4 (Swofford, 2002). First, we estimated the probability of two designated taxa forming a sister pair on a randomized tree by creating trees of random topology, with a constant number of species and calculating how frequently the species pair clustered together. We repeated the randomization procedure using 10,000 iterations; increasing the number of iterations by a factor of 10 had no qualitative effect on the results.

Second, we estimated the probability that the two designated taxa occur as a species pair on the observed topology by chance. This procedure used the existing tree created from

the cluster analysis and randomizing the position of the species on the tree (10,000 iterations). Both of these randomization procedures were conducted on the nestling begging call tree for each of the three taxonomic groups.

2.3.3.3 Similarity between begging call and phylogenetic trees

To test the effect of phylogeny on the structure of begging calls of New Zealand passerines, the topologies of the phylogenetic trees were compared to the begging call trees using two tree-comparison metrics: 1) the symmetric difference or “partition” metric (SD) and 2) agreement subtree (d) metrics (largest common pruned trees) (Goddard *et al.*, 1994, Penny & Hendy, 1985) using the program PAUP v.4 (Swofford, 2002). Both metrics have a value of zero when the topologies being compared are identical.

For each metric, its sampling distribution under the null hypothesis that begging call similarity was random with respect to phylogeny was determined empirically. First, the topology of the acoustic similarity cluster diagram was randomized. Then its similarity to the topology of the phylogeny was estimated using the two metrics. This procedure was repeated 1 million times to produce a frequency distribution of the topology comparison metric under the random hypothesis. Then the observed similarity cluster diagram was compared to the phylogeny by computing the metric. The empirical probability of the observed value of the metric was estimated as the percentile of the corresponding value in the frequency distribution. If there is close agreement in the topologies of the two trees, the observed metric will fall at a low percentile of the null

distribution. However, if the two trees have effectively random topologies with respect to one another then the observed metric will be expected to occur at a higher percentile.

These tree comparison metrics were calculated for the three different sets of trees. For each of the three species sets, the analysis was performed three times: (1) with the shining cuckoo present, (2) with the shining cuckoo absent, and (3) with both the shining cuckoo and grey warbler absent. Therefore, nine tree comparison metrics were calculated (Table 3). By comparing begging call similarity and phylogenetic trees without the shining cuckoo we tested whether begging call similarity is the result of shared evolutionary history or relatedness. This first test of a phylogenetic signal is useful, as it was then used to test what effect the addition/removal of 1) the parasite (second analysis) and 2) parasite and its host (third analysis) has on the phylogenetic signal. Any effect on the phylogenetic signal can be an indication of the evolutionary and/or co-evolutionary processes that have occurred between parasite and host.

2.4 RESULTS

2.4.1 Host-parasite begging call similarity

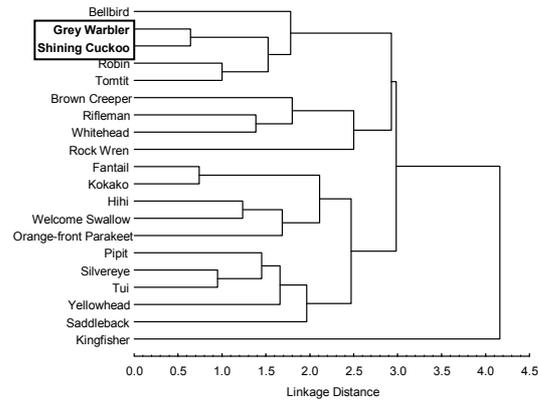
The begging call of the shining cuckoo and the grey warbler consistently grouped together as sister taxa in the cluster analyses, in all three taxonomic data sets (Figure 2). Both of the randomization tests indicated that the probability of this occurring by chance was 2 – 5% (see Table 2).

2.4.2 Similarity between begging call and phylogenetic trees

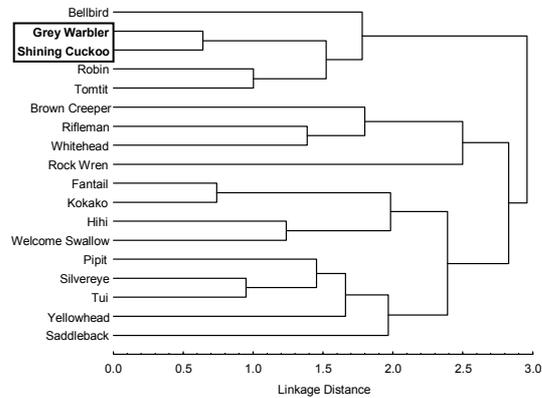
The cluster analysis dendrograms of begging call similarity were compared with the phylogeny of the corresponding species to test if begging call similarity results from evolutionary proximity or relatedness. We tested this by quantifying the similarity between trees when the shining cuckoo was included or excluded from the species set. We predicted that the presence of the shining cuckoo would reduce the phylogenetic signal of begging calls. The observed value of the symmetric difference metric fell between the 16th and 18th percentile of the distribution of this metric on randomized cluster diagrams (Table 3). There was little change in the signal by varying the number of taxa included in the phylogeny.

In contrast, when the agreement subtree metric was used (Table 3), the percentile at which the metric fell decreased as we increased the number of species in the analysis (16 species, 13.1%; 18 species, 4.1%; 20 species 1.1%). This suggests that the agreement subtree metric was more sensitive to changes in tree topology and that the phylogenetic signal in begging call similarity was present; a feature that was enhanced with increased taxon sampling.

a)



b)



c)

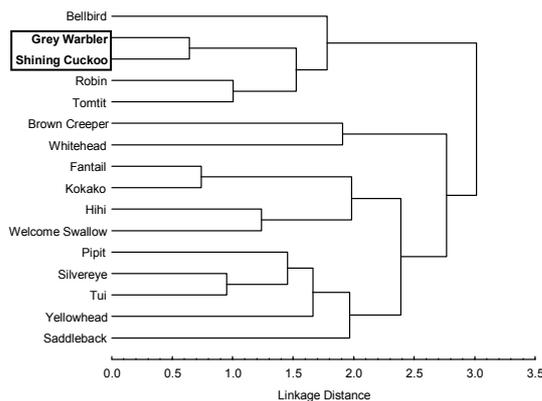


Figure 2: Dendrograms of begging call similarities created by cluster analysis based on acoustic features. Three New Zealand native species sets were used; a) all passerines and out groups, b) passerines and c) oscines. The host and brood parasite species are highlighted in bold.

2.4.3 The effect of parasite and host on the phylogenetic signal of the begging call similarity tree

We tested how the strength of the phylogenetic signal in the begging call dendrogram was affected by both the host and the parasite by assessing the effect of their addition and removal from the tree comparisons. First, we asked whether the addition of the shining cuckoo makes the begging call similarity diagram more random-like by virtue of its placement. We detected no change in the percentiles at which the symmetric difference metric fell when we added the shining cuckoo (Table 3).

In contrast, for each case involving the agreement subtree metric, the presence of the shining cuckoo increased the percentiles at which the observed diagram fell sharply, indicating a more random cluster diagram topology and, thus, less phylogenetic signal. Accordingly, the placement of the shining cuckoo was consistently different to that expected given its phylogenetic position. (Table 3, Figure 2).

Conversely, the presence/absence of the grey warbler, but not the shining cuckoo, had minimal effect on the symmetric difference metric, but a more marked effect on the subtree agreement metric (Table 3, Figure 2). Specifically, for the latter metric, in two of the three data sets the inclusion of the grey warbler increased the phylogenetic signal in the begging call cluster diagram (Table 3, Figure 2).

Table 2: Empirical probability that two designated taxa form a species pair on a tree of random topology, or when the leaves are randomised on the observed topology of begging call similarity. In each case, 10^4 randomizations were performed.

	Trees randomized	Species randomized
16 species	0.036	0.049
18 species	0.031	0.036
20 species	0.027	0.033

Table 3: The congruence of the topology of the call similarity cluster diagram with respect to the phylogeny. The underlying null distribution of each metric was obtained by randomizing the topology of the cluster diagram and then comparing it with the known phylogeny. The “randomness” of the observed cluster diagram is indicated by the percentile at which it fell on the null distribution. Low percentiles are indicative of non-randomness. In each case, 10^6 randomizations were performed.

Taxonomic Group	Symmetric Difference Metric			Subtree Agreement Metric		
	With parasite	Without parasite	Without parasite or host	With parasite	Without parasite	Without parasite or host
NZ Oscines	15.2%	16.4%	1.8%	78.7%	13.1%	7.5%
NZ Passerines	16.1%	17.0%	18.1%	7.0%	4.1%	7.9%
NZ Passerines and outgroups	16.7%	17.6%	18.5%	16.1%	1.1%	6.9%

2.5 DISCUSSION

Several studies have invoked mimicry as the evolutionary explanation of the similarity between the begging call of nestling brood parasites and their hosts (Davies *et al.*, 1998, Langmore *et al.*, 2003, Langmore *et al.*, 2008). However, in studies of focal pairs of host-parasite taxa it can remain unclear how similar the taxon-specific begging calls are with respect to a diverse suite of available or potential hosts. We have shown here that the begging calls of a specialist avian brood parasite and its host are more similar to each other compared to all other available hosts and that this level of similarity was unlikely to have occurred by chance.

Several previous studies demonstrated that avian acoustic signals, both songs and flight calls have phylogenetic signals (McCracken & Sheldon, 1997, Päckert *et al.*, 2003). Our tree comparison methods also showed that the acoustic structure of the begging calls of New Zealand forest birds retained a considerable phylogenetic signal. It is known that the frequencies of bird songs are influenced by habitat (Seddon, 2005, Slabbekoorn & Smith, 2002) and may change through time due to cultural evolution (Jenkins, 1978, MacDougall-Shackleton & MacDougall-Shackleton, 2001). The retention of a phylogenetic signal requires that the ecological conditions that are necessary for the behaviour to occur remain constant through phylogenetic history (Paterson *et al.*, 1995). Begging calls may be a useful trait in this respect, as they are less influenced by sexual selection or cultural evolution, compared to adult vocalisations. Nevertheless, begging calls are also extensively shaped by ecological factors, including predation (Briskie *et al.*, 1999, Haskell, 1994), relatedness (Boncoraglio & Saino, 2008, Briskie *et al.*, 1994) and learning by nestlings (Langmore *et al.*, 2008; Madden & Davies, 2006).

The use of comparative methods in the study of avian host-parasite coevolution has been limited. For example, most studies of egg mimicry have typically compared parasite egg appearance directly to host egg appearance in a species-pair design (Cherry *et al.*, 2007a, Davies & Brooke, 1989, Langmore *et al.*, 2005, Soler *et al.*, 2003, Starling *et al.*, 2006). In addition, Soler and Moller (1996) and Hauber (2003) used comparative analyses on the egg appearances and the clutch sizes, respectively, of potential or actual hosts to test for the effects of evolutionary history with an egg-mimic cuckoo, *Cuculus canorus* and the generalist brown-headed cowbird, *Molothrus ater*. Payne (2005b) used a comparative framework to test the possibility of coevolution between *Vidua* parasites and their hosts by looking at the nestling mouth markings and colouration compared within the old world finches (Hauber & Kilner, 2007). Krüger and Davies (2002) and Mermoz and Ornelas (2004) used comparative methods to detect interspecific brood parasitism, specific life history and morphological adaptations within parasite lineages of cuckoos and cowbirds. However, none of these prior analyses used quantitative comparative methods to evaluate the phylogenetic signals of host traits with respect to the evolutionary history of parasitism. Our comparative approach shows how similar parasite traits actually are to traits of hosts, which is important for invoking mimicry as an explanation for similarity (Grim, 2005).

An ideal context to use this technique in future work is where the brood parasite is known to be mimetic, in the trait that is being tested, of several host species. For example, egg mimicry in the European cuckoo or the pallid cuckoo, where distinct gentes are known (Davies, 2000, Gibbs *et al.*, 2000, Starling *et al.*, 2006). Each gens should match its own host in the mimetic trait more closely than the match by other

gentes, or any of the other available hosts (Langmore *et al.*, 2005). Alternatively, the coevolving trait in the host may not be the begging call itself but the ability to recognize and discriminate between their own and foreign begging calls (Hauber & Sherman, 2001). Finally, the shining cuckoo uses other host species in Australia (Payne, 2005a), and may have evolved strategies to evade the host defences of Australian species, while the grey warbler may lack such host defences. Further comparative research into the begging call of the shining cuckoo in both Australia and New Zealand should help to elucidate the degree of similarity and explanations for the presence or absence of coevolution with different host species.

The present study has shown that an avian brood parasite is more similar to its host species than any of the other available hosts. We have shown through the use of a comparative method combined with randomization techniques that coevolution through reciprocal changes in the begging call is not present within this brood parasite system. Instead, the parasite has closely matched the begging call of its host, but the host has not altered its begging call in response, a pattern suggesting a process of sequential evolution. It also remains a possibility that coevolution has occurred in the host perceptual system of call recognition rather than in the host begging call. However, it is unclear whether the matching of host calls by the parasite is an evolved inflexible display or if it is the cuckoo's ability that has evolved to learn and match the most effective begging signal to solicit parental care from foster parents (i.e. by matching host begging calls; (Langmore *et al.*, 2008). Future studies of mimicry should consider how closely matched avian brood parasites actually are to their hosts, by comparing brood parasites to more species than just the host and another non-host for instance. This may increase knowledge of such ideas as the threshold that is required for parasite

rejection to occur in the host (Reeve, 1989) and the perceptual mechanisms used for host selection by the parasite (Cherry *et al.*, 2007b).

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2.8 Supplementary Material

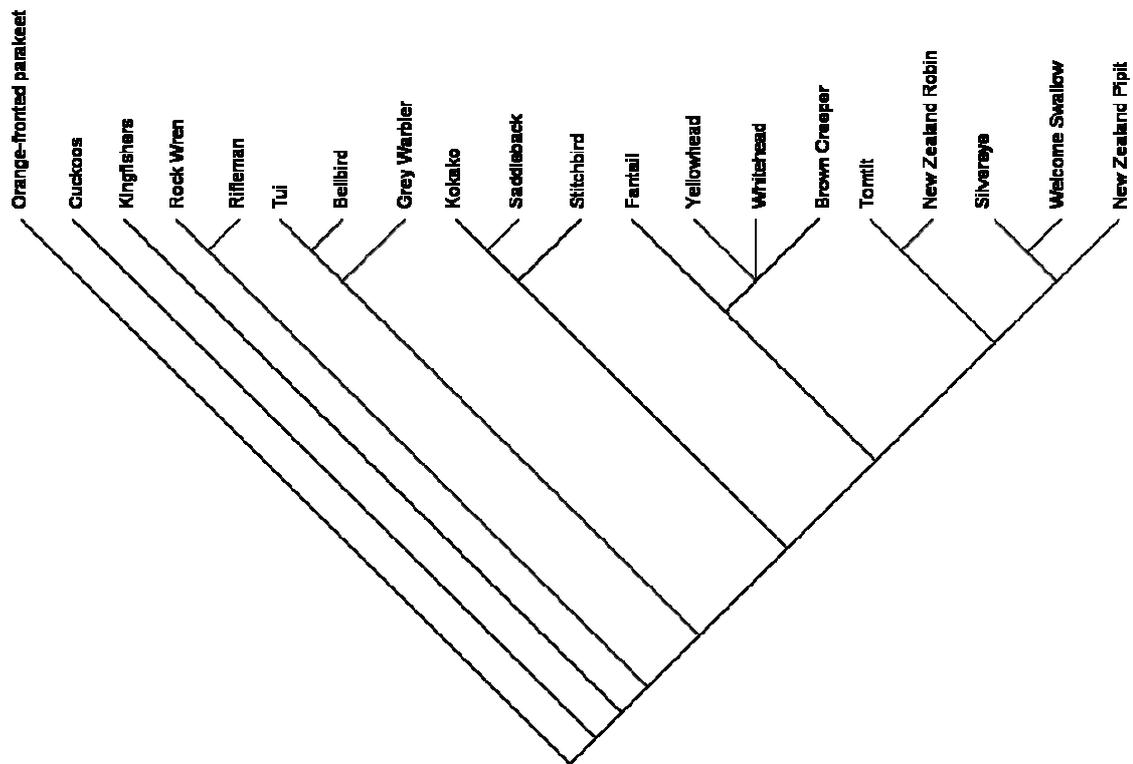
Suppl. 1: Locations and sample sizes for the begging call recordings made for each species.

Species	Species Name	Location	Nestling age (fledging age)	No. of nests
Rock Wren	<i>Xenicus gilviventres</i>	Murchison Mountains	20 (24)*	1
Rifleman	<i>Acanthisitta chloris</i>	Dart Valley	~18 (24)	1
		Little Barrier Island	? (24)	1
Tui	<i>Prothemadera</i>	Tawharanui Regional Park	~16 (21)	1
	<i>novaeeseelandiae</i>			
		Tiritiri Matangi Island	~12 (21)	1
Bellbird	<i>Anthornis melanura</i>	Tiritiri Matangi Island	~6 (14)	1
Grey Warbler	<i>Gerygone igata</i>	Tawharanui Regional Park	12-17 (17)	10
Kokako	<i>Callaeas cinerea</i>	Tiritiri Matangi Island	~20 (31)	2
		Hunua Regional Park	~15 (31)	1
Saddleback	<i>Philesturnus carunculatus</i>	Tiritiri Matangi Island	~18 (26)	1
Hihi (stitchbird)	<i>Notiomystis cincta</i>	Little Barrier Island	? (28-34)	2
Fantail	<i>Rhipidura fuliginosa</i>	Tawharanui Regional Park	6-9 (13)	3
Yellowhead	<i>Mohoua ochrocephala</i>	Dart Valley	~12-18 (22)	3

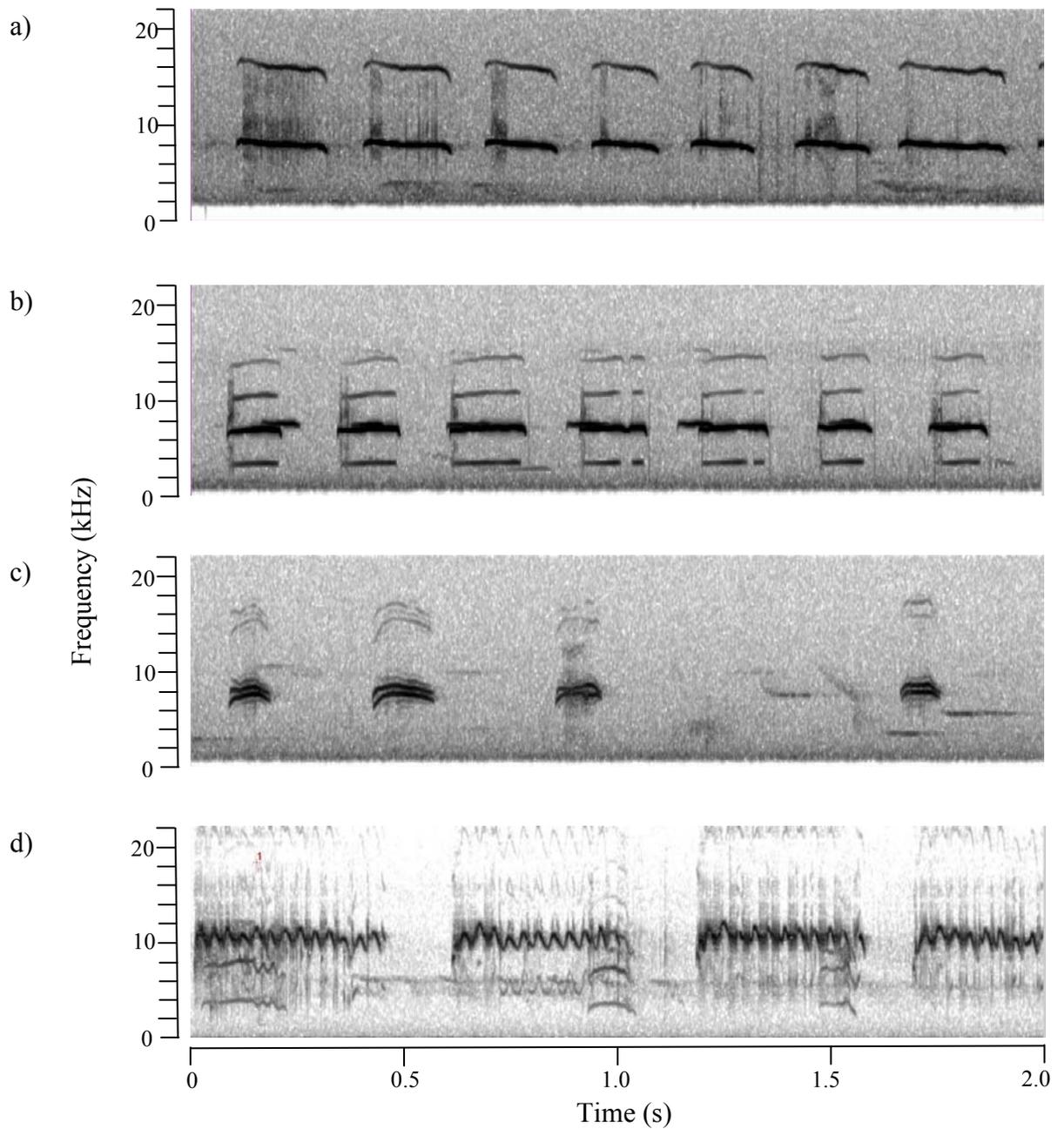
Whitehead	<i>Mohoua albigilla</i>	Tiritiri Matangi Island	(36°36'S, 174°53'E)	~10-14 (17)	2
Brown Creeper	<i>Mohoua novaeseelandiae</i>	Kowhai Bush	(42°22'S, 173°36'E)	? (20)	1
Tomtit	<i>Petroica macrocephala</i>	Hunua Ranges	(37°01'S, 175°09'E)	12 (18)	1
New Zealand Robin	<i>Petroica australis</i>	Tiritiri Matangi Island	(36°36'S, 174°53'E)	11& 19 (21)	2
Silvereye	<i>Zosterops lateralis</i>	Tawharanui Regional Park	(36°22'S, 174°50'E)	~5-8 (10)	3
Welcome Swallow	<i>Hirundo tahitica</i>	Tawharanui Regional Park	(36°22'S, 174°50'E)	10-16 (21)	3
New Zealand Pipit	<i>Anthus novaeseelandiae</i>	Tawharanui Regional Park	(36°22'S, 174°50'E)	10 (14-16)	1
Shining Cuckoo	<i>Chrysococcyx lucidus</i>	Wenderholm Regional Park	(36°32'S, 174°42'E)	18 (19)	1
Orange-fronted parakeet	<i>Chrysococcyx lucidus</i>	Tawharanui Regional Park	(36°22'S, 174°50'E)	Fledglings	2
New Zealand Kingfisher	<i>Cyanoramphus malherbi</i>	Maud Island	(41°01'S, 173°52'E)	30 (35-40) [#]	1
	<i>Halcyon sancta</i>	Muriwai	(36°49'S, 174°26'E)	? (26-27)	1

*Fledging ages taken from Heather and Robertson (2005)

[#]Pers. Comm.. Luis Ortiz Catedral



Suppl. 2: The molecular phylogeny of the 20 New Zealand species used in the comparative analysis of begging calls.



Suppl. 3: Example spectrograms of the begging calls of a) shining cuckoo and three New Zealand passerine species: b) grey warbler, c) bellbird and d) whitehead.

Suppl. 4: Definitions of the sound measurements used in the analysis of begging calls.

Sound Parameter	Units	Definition
Frequency modulation	degrees	The mean slope of frequency contours
Amplitude modulation	1/ms	Changes in amplitude across the sound
Wiener entropy		A measure of randomness on a scale of 0–1; white noise has an entropy value of 1, and complete order, for example a pure tone, has an entropy value of 0
Mean frequency	kHz	A smooth estimate of the centre of derivative power
Duration	Ms	call length

3 Species-specific modulation and ontogenetic shift of the responses of grey warbler (*Gerygone igata*) nestlings to parental feeding and alarm calls



Grey Warbler nestling (Photo: Michael Anderson)

This chapter is modified from the manuscript:

Anderson, M. G., Brunton, D. H. and Hauber, M. E. Species-specific modulation and ontogenetic shift of the responses of grey warbler (*Gerygone igata*) nestlings to parental feeding and alarm calls. (submitted to *Animal Behaviour*)

3.1 Abstract

Vocal communication between parents and offspring, including parental feeding solicitations and begging calls of young, can increase the risk of predation through acoustic cues, attracting predators searching for prey. In turn, parents can use a “switch off” signal (alarm call) to stop progeny from vocalising. Such calls predictably alter nestling behaviour by suppressing their vocalizations or inhibiting movement, making chicks and the nest less detectable to predators. Alternatively, a “switch on” signal (feeding or solicitation call) may be used to initiate a begging display in young by parents. Whether these cues are species-specific has not yet been tested, as similar cues may be used amongst avian species. These findings may also offer insight into cognitive development and the earliest developmental uses of referential communication, potentially demonstrating the youngest ages of understanding language. We tested the species-specificity and the behavioural and acoustic consequences of the responses of individual grey warbler (*Gerygone igata*) nestlings to both parental feeding and alarm calls at 12 and 16 days old (nestling period: 17 days) in a sound-isolation chamber. Differences in begging call acoustic structure were detected across age groups that were likely due to ontogenetic effects. However, it was found that nestlings consistently reduce the amplitude of the begging call in response to alarm calls, regardless of the developmental stage. We also found that nestlings in both age groups responded by gaping only to conspecific, and not heterospecific, begging solicitation calls or other acoustic stimuli. Following alarm calls, nestlings did not cease begging, but altered the structure of the begging call, most notably reducing amplitude. This suggests that these changes reduce the detectability of calling nestlings. These patterns are consistent with a trade-off in chicks’ signal-specific responses to parental

calls, which optimizes the probability of being fed during parental nest visits whilst also reducing predator detection.

Keywords: alarm call, begging, *Gerygone igata*, grey warbler, begging solicitation call, parent-offspring communication, vocal communication.

3.2 Introduction

Vocalizations of nestling birds typically solicit food from provisioning parents by signalling need (Kilner et al. 1999), but can also be given when parents are absent (Budden and Wright 2001; Leonard and Horn 2001b; Dor et al. 2007). Nestlings raise their begging rate and amplitude to communicate greater hunger levels to increase provisioning by parents (Leonard and Horn 2001a; Hauber and Ramsey 2003) or to compete more successfully with siblings (Dearborn 1998; Lichtenstein and Sealy 1998; Leonard et al. 2000; Roulin et al. 2000; Hauber et al. 2001; Leonard and Horn 2001b; Roulin 2002). However, these signals can be exploited by predators that eavesdrop on begging calls to locate nests, with nests containing louder, more conspicuous nestlings increasing the risk of predation (Haskell 1994; Leech and Leonard 1997; Briskie et al. 1999; Dearborn 1999). These two selection pressures, signals of need and predators that eavesdrop, can act in opposing directions, causing an evolutionary paradox. Alternatively, a predation cost of begging may reinforce the honesty of begging calls. Several explanations have been proposed to resolve this problem: nestlings can either 1) only beg when parents provide a begging solicitation call (Leonard et al. 1997a; Madden et al. 2005a; Raihani and Ridley 2007), 2) cease begging when parents give an alarm call (Platzen and Magrath 2004; Madden et al. 2005a; Platzen and Magrath 2005; Magrath et al. 2007).

One constraint that nestlings encounter is determining the correct time to beg. This requires the ability to discriminate between cues given by parents arriving at the nest (i.e. nest movement, shadows cast by arriving parent) and false cues (i.e., wind, clouds; called false alarms by (Dor et al. 2007)). In many species of birds, the parents give calls

as they arrive at the nest or when feeding nestlings (Clemmons 1995b; Leonard et al. 1997a; Madden et al. 2005a; Magrath et al. 2007; Raihani and Ridley 2007). These feeding calls, or begging solicitation calls, may be a cue that young nestlings can perceive, as it is typically given just after hatching and then used less frequently as nestlings develop (Bengtsson and Ryden 1981; Clemmons 1995b). This ontogenetic shift is likely to be due to nestlings' abilities to learn other cues, often produced when parents arrive at the nest and thus reducing the need for begging solicitation calls to solicit a begging response from nestlings. Begging solicitation calls also have the added benefit of reducing inappropriate begging due to false cues, as begging can be energetically costly (Leech and Leonard 1996; Kilner 2001; Rodriguez-Girones et al. 2001; Chappell and Bachman 2002).

Begging solicitation calls may also act as a strategy to reduce detection by predators, by indicating that it is safe to beg, effectively acting as a "switch on" cue (Madden et al. 2005a). By only responding to begging solicitation calls, nestlings are able to greatly reduce the chance of predation, as parents are unlikely to arrive at the nest when predators are present (Platzen and Magrath 2004; Madden et al. 2005a; Platzen and Magrath 2005). However, several factors can act to decrease the threshold of chick responsiveness. Nestlings also face the selection pressure of benefiting from being the first in the nest to respond when parents arrive, as it increases the chance of being fed at the particular visit (Roulin 2001a; Porkert and Pinka 2006). In addition, as hunger levels increase, the threshold may be reduced, again to increase the chance of being fed over siblings (Dickens and Hartley 2007). Finally, lower relatedness of chicks in broods with high extra-pair parentage reduces the kin-selected benefits of ensuring the safety of the whole brood at some cost to the individual chick who begs less, implying increased

begging intensity for species with lower within brood relatedness (Briskie et al. 1994; Hauber and Ramsey 2003; Boncoraglio and Saino 2008).

A second strategy that can be used to reduce nestling predation is the use of parental alarm calls. Alarm calls are an effective means of eliciting an appropriate response (silence, crouching in the nest) in nestlings of several species (Davies et al. 2004; Platzen and Magrath 2004; Madden et al. 2005a). Some species of brood parasite nestlings have been able to tap into this parent-offspring communication system, with the ability to recognise host parents alarm calls and thereby responding appropriately. Davies et al. (2006) showed that this response was specific to nestlings of the reed warbler host-races of cuckoos, indicating that the response is not an innate sensory bias amongst cuckoo chicks and that the alarm calls of new hosts were not learned when chicks were transferred to other species nests. This maximizes survival of brood parasite nestlings in the nest of their hosts by reducing predation, despite the uncertainty of host species identity for the young of generalist brood parasites (Madden et al. 2005b; Davies et al. 2006). This differs from the “switch on” strategy in that nestlings are able to vocalise while parents are not at the nest, allowing them to compete with siblings (Roulin et al. 2000; Roulin 2001a), while also maintaining readiness for when parents return and maximizing their chance of being fed (Dor et al. 2007).

Yet, another strategy that nestlings may employ to avoid detection by predators is to independently assess the risk of predation. This requires nestlings to be able to respond appropriately to cues that may be given by predators when near the nest. Magrath et al. (2007) was the first study to experimentally test the response of nestlings to cues given

by known predators. It was found that white-browed scrubwren (*Sericornis frontalis*) nestlings are not only able to use “switch on” and “switch off” cues given by parents, but that they are also able to recognize the sound of their predators footsteps and respond appropriately with silence. It makes evolutionary sense for nestlings to possess the ability to independently assess potential risk, as parents are not always near the nest to warn nestlings of predation. It is likely that this strategy is employed by many other species, with the prevalence and accuracy being mediated by the habitat-specific variation in predation pressure. Another factor that may mediate the use of alarm calls and the acoustic structure of begging calls is the use of ‘screaming’ by nestlings to deter predators (Roulin 2001b). Nestlings that use this strategy typically have louder begging calls than those that do not, suggesting that this strategy evolved as an anti-predator strategy in species that have conspicuous begging calls.

In our study, we used a playback experiment to test the response of grey warbler (*Gerygone igata*) nestlings to parental vocalizations, to test whether a “switch on” and/or a “switch off” mechanism is employed, and if chicks respond specifically to their cues given by their own species. Few studies have examined if nestlings respond directly to either alarm (Maurer et al. 2003; Platzen and Magrath 2004; Madden et al. 2005a) or begging solicitation calls (Leonard et al. 1997a; Maurer et al. 2003; Madden et al. 2005a; Magrath et al. 2007) by use of experimental playbacks, and none that we know of have tested if these cues are species-specific or if the acoustic properties of these calls are shared amongst species. These two alternatives also offer the possibility of testing habitat-specific vocal signals of communication. The playback experiment was designed to test the response of nestlings to various classes of acoustic stimuli. This was to quantify several aspects of nestling begging behaviour to determine if 1) chicks

only gave a begging response to begging solicitation calls, 2) this response was species specific, 3) nestling vocalizations were modulated after hearing parental alarm calls and 4) there was an ontogenetic shift in nestling responses. To do this we used a sound chamber set up, where nestlings were transported from the nest and tested individually, removing any other potential cues that may stimulate a begging response (e.g. light, siblings). We then tested the response of nestlings to conspecific begging solicitation calls and several other acoustic stimuli (heterospecific begging solicitation calls and heterospecific songs) as controls. We chose heterospecific stimuli to serve as biological controls to test if nestlings showed a begging response to any acoustic stimuli. We also quantified each nestling's responses to parental alarm calls, by first playing a begging solicitation call then followed by an alarm call to see if individuals modified their responses. Finally, we evaluated the potential patterns of ontogenetic change in nestlings' responses to parental calls, by comparing different chicks' behaviours at two ages prior to fledgling. We predicted that conspecific solicitation calls should cause chicks to gape and alter the begging rate and acoustic properties of the begging call. If begging solicitation calls share acoustic properties amongst species, then the response should be the same for con- and heterospecific begging solicitation calls. Alternatively, if the response is species-specific, these changes should be consistently different from both control stimuli. For the separate test of the switch off signal, we monitored the responses of individual grey warblers that were solicited to beg using a begging solicitation call but which were then played a parental alarm call. To assess species specificity, we also played heterospecific alarm calls and controls following grey warbler begging solicitation calls. We predicted that chicks should cease begging following the alarm call, or alternatively give a scream response (Roulin 2001b).

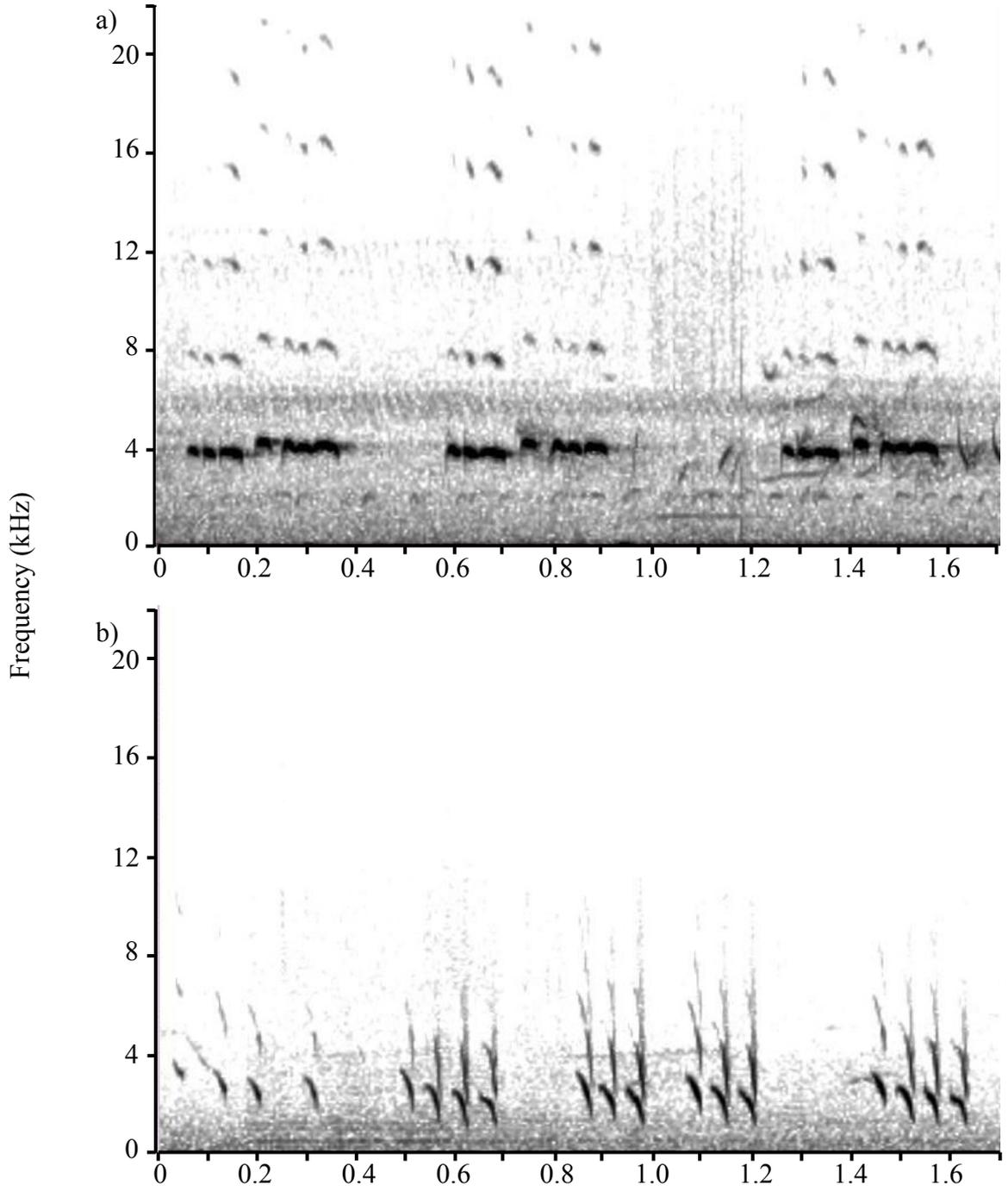
3.3 METHODS

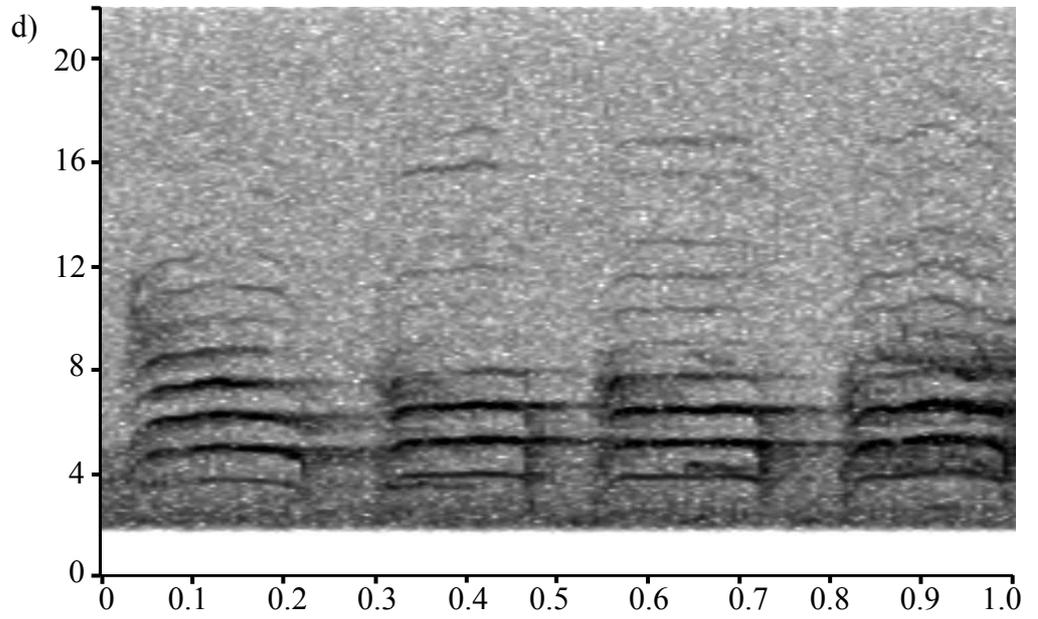
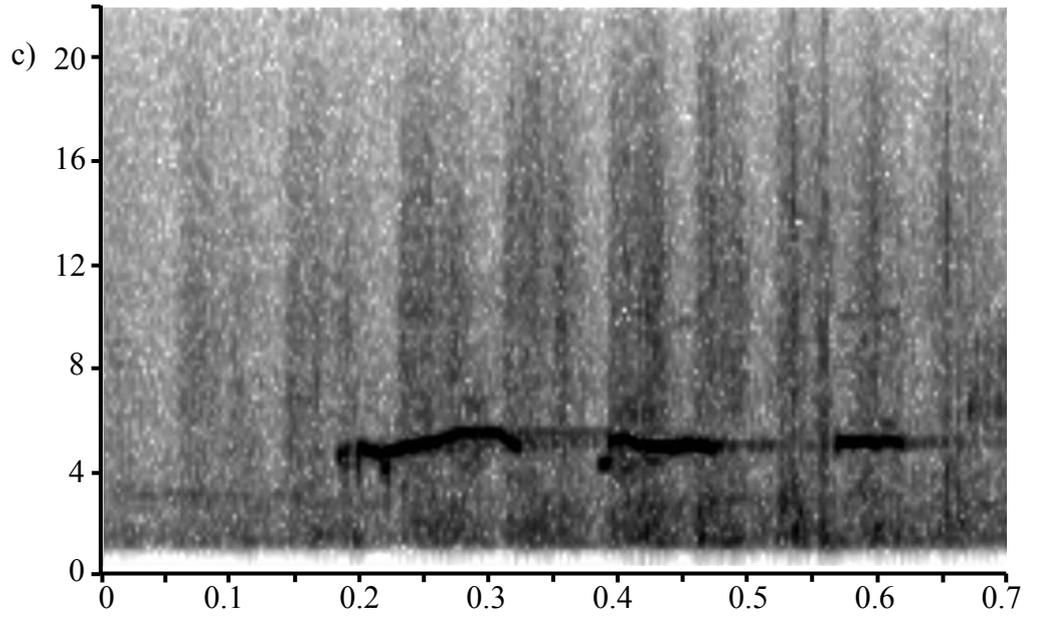
3.3.1 Study Species and Site

The grey warbler is an endemic New Zealand passerine in the family Acanthizidae (Heather and Robertson 1997). Grey warblers build enclosed, pensile nests at heights of 1-10 m, with an average of 3.5 m (Gill 1982). Pairs are formed prior to the breeding season and are highly territorial, with some territories being maintained year-round. During the breeding season, pairs usually have one or two clutches of 3-4 eggs (Gill 1982; M.G.A., unpub. data). The nestling period is 17-18 days, at which time offspring fledge and remain dependant on parents for a further 28-35 days (Gill 1982). This research was conducted at Tawharanui Regional Park (36°22' S, 174°50' N), located 52 km north of Auckland.

Grey warbler nestlings have two types of vocalizations; 1) a short, non-begging vocalisation, when parents are absent from the nest and 2) a longer begging vocalisation that is given when parents feed nestlings. Both vocalizations are high pitched (7.5-9 kHz) and vary with age (McLean and Waas 1987; M.G.A., unpub. data). The rate that non-begging calls are given varies with age, but can occur as often as 5 calls per second for a brood of chicks during the final stages of the nestling period (M.G.A., unpub. data). Nestlings start to vocalise at about four days of age, but are difficult to elicit a begging response from out of the nest until 8-10 days (M.G.A., unpub. data). Nestlings of 12 and 16 days from different broods were used for this experiment, to test for developmental differences in responses to stimuli.

Parents give two types of calls that are of apparent importance for nestlings. Alarm calls (Figure 3a) are given when potential predators (e.g. shining cuckoo, *Chrysococcyx lucidus* (Briskie 2007); morepork, *Ninox novaeseelandiae*; pukeko *Porphyrio porphyrio*; and humans *Homo sapiens*) are detected in the vicinity of the nest. These calls tend to be a series of repeated trill calls. Parents also give parental feeding calls, or begging solicitation calls (Figure 3b), when arriving at the nest with food for nestlings. These calls tend to be a series of short ‘chip’ calls that can be given during the entire feeding event and can be given either before or after arrival at the nest (Michael Anderson, *unpub. data*)





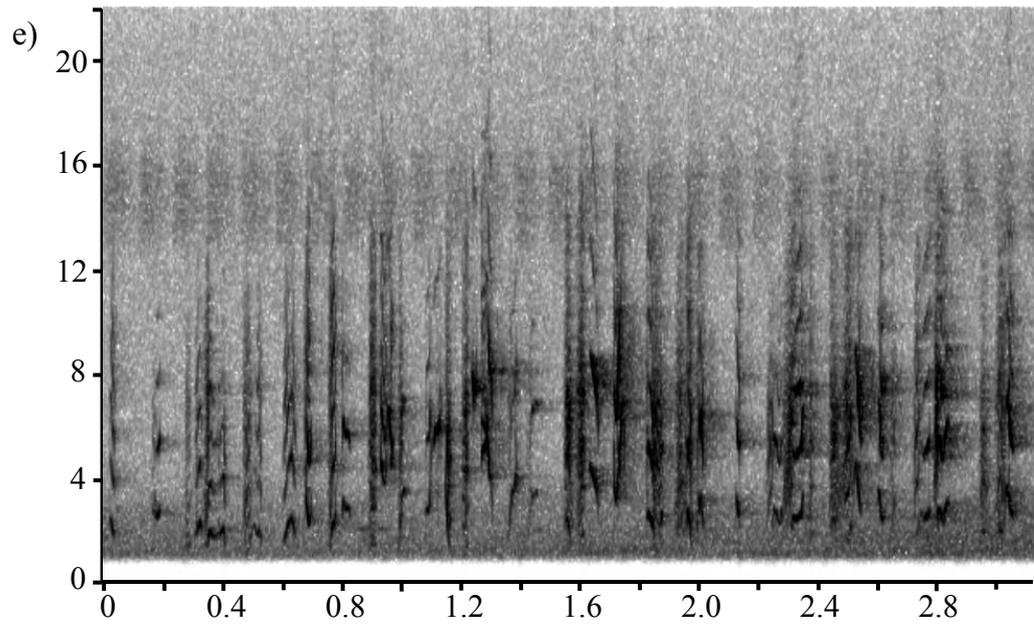


Figure 3: The stimuli used in the playback experiment. The two main types of adult conspecific vocalizations that are used for parent-offspring communication, a) begging solicitation call and b) parental alarm call and c) the heterospecific begging solicitation call and d) alarm call, and the e) heterospecific song used as a control.

3.3.2 Collection of acoustic stimuli

Five types of acoustic stimuli used for the playback experiments were recorded prior to these experiments at the study location. Grey Warbler begging solicitation calls and alarm calls were recorded during the early nestling stages before they are able to vocalise (1-4 days after hatching; $n = 11$ nests, one call of each type was used from each nest). Only the calls of the nestlings' own parents were used in the playback sequences to avoid any possible problems of either pseudoreplication (Kroodsma 1989) or parent-offspring recognition (Rowley 1980; Leonard et al. 1997b). We chose heterospecific stimuli to serve as biological controls to test if nestlings showed a begging response to any acoustic stimuli. These were the vocalizations of sympatric oscines: the Fantail (*Rhipidura fuliginosa*) song (FS) and alarm call (FA) and the Welcome Swallow (*Hirundo tahitica*) begging solicitation call (WB). Both of these species are commonly found at the study site. Heterospecific vocalisations of Fantail alarm calls and songs were recorded within local territories ($n = 2$) during the breeding season. Welcome swallow begging solicitation calls were recorded at a single nest site ($n = 1$ nest) located within the study area. All acoustic stimuli were recorded with a Sennheiser ME 66 microphone onto a HiMD Minidisc as 44.1kHz, 16bit .wav files. Recordings from nests were made by attaching the microphone approximately 20-30cm below the nest, and recording for 90 minutes. Recordings were subsequently examined in Raven 1.2.1 (Charif et al. 2004) then edited and amplified to achieve standardized call length (4 s) and peak amplitude (20 kU).

3.3.3 Preparation of playback sequences

A paired playback regime was constructed to test the response of nestlings to begging solicitation calls (B) and alarm calls (A). The playback sequences consisted of a conspecific stimulus, a heterospecific stimulus of the same vocalisations type, and a heterospecific control sound (song: C), separated by long silent periods (60s) to reduce carry over effects. For the test of the switch-on hypothesis, we used a comparison of chick responses monitoring behaviours of individual grey warbler chicks following begging solicitation calls (CB), heterospecific begging solicitation calls (HB), and heterospecific controls (C).

This combined aim resulted in the construction of the following 5 playback sequences: 1) C only, 2) HB only, 3) CB followed by HA, 4) CB followed by C and 5) CB followed by CA. This meant that nestlings were presented with the CB stimulus three times and all other stimuli once (5 stimuli types per nestling; Figure 3). The order that these sequences were presented to nestlings were random. The sound recordings were analysed separately for alarm call and begging solicitation call stimuli. The first 4 s after the begging call solicitation calls were analysed for sequences 1, 2 and 3. The first 4 s after the second stimulus for 3, 4 and 5 were analysed for the nestling response to alarm calls.

3.3.4 Conducting the playbacks

The playback experiment was conducted on individual nestlings that were removed from the nest and exposed to the playback sequences in a sound-isolation chamber near

the nest site. Each nestling was fed until satiation, with WombarooTM insectivore rearing mix, to standardise hunger levels (Kilner et al. 1999; Lichtenstein 2001; Madden et al. 2005a, b). Nestlings were placed in the chamber, following feeding, within 10 minutes of removal from the nest. Experiments were conducted away from nest sites so parents did not continue to alarm call. At least one nestling was left in the nest so that normal parental feeding behaviours resumed. Pocket hand-warmers (KathmanduTM) were used to keep nestlings warm within the sound chamber. This provided a constant level of warmth throughout the experiment. Nestlings were stimulated to beg by playing them begging solicitation calls. Alternative methods of inducing begging were trialled, such as tapping the bill and tapping on the box (Kilner and Davies 1999; Madden et al. 2005a, b), but no begging response was given by nestlings. Nestlings were thus held inside the sound-isolation chamber for 30 minutes after feeding to satiation before the playback sequences were conducted. Under natural situations, parents visit nests approximately once every 8 minutes (Michael Anderson, unpub. data), so this period would ensure that nestlings were hungry.

The playback sequences were played to nestlings from a CD player connected to a pair of Sony SRS-A5S speakers placed inside the sound-isolation chamber. The amplitude of all playback trials was set at a constant level that was realistic for what nestlings would experience at the nest (as measured from nest recordings: alarm calls, 60-70dB; begging solicitation calls, 50-60 dB). Video and sound recordings of nestlings were made throughout each trial to record the responses of nestlings to playback sequences. An infra-red (8 LED) pinhole camera was set up inside the chamber above the nestlings, which was connected to a Sony DCR-TRV 480E camcorder. Sound recordings were made with a Panasonic RP-VC201 stereo tie-clip microphone

(frequency response 100 Hz to 20 kHz), connected to a Sony MZ-NH700 Hi-MD Minidisc. Prior to each trial the amplitude was calibrated by playing a constant tone with an electric metronome (Sabine Metrotune MT9000) at the same distance from the microphone as the nestling, while simultaneously recording the amplitude with a Digitech QM-1589 sound level meter next to the microphone. This measurement was then used to later calibrate the amplitude of the nestling begging calls. All sound recordings were digitally transferred to Raven 1.2 and spectrograms (Hann, window size 5.33 mS, 3 dB bandwidth of 270 Hz, frequency grid DFT size 256 samples and 188 Hz) were created for analysis. We counted the number of begging vocalizations and measured the duration, centre frequency and amplitude of begging calls analysed.

3.3.5 Statistical Analysis

3.3.5.1 General statistical methods

To avoid habituation to playback sequences, individual nestlings were only included in one of the two age groups. We included nest identity as a random effect in our statistical analyses to account for shared genetic and environmental backgrounds of nestmates (Hauber and Ramsey 2003; Nelson and Marler 2005) (see below). We had similar numbers of nestlings at 12 days ($n = 10$, from 6 nests) and 16 days ($n = 11$, from 5 nests). We analysed nestlings' response in three different ways: 1) visual displays (video analysis), 2) begging call rate and 3) begging call acoustic structure. Due to technical difficulties, the video analysis of two nestlings (a 12 day and a 16 day) could not be included. All data are reported as means \pm standard error.

3.3.5.2 Visual display

Videotapes were used to score the response of the nestling to each acoustic stimulus, to which they were exposed. The begging display (raised head and open beak) was chosen as a binary response variable (yes vs. no) as it was unambiguous and easily quantified. Using these data, we followed the metric of Hauber et al. (2001), of computing a discrimination score for each stimulus within each individual's response-set. This was done by calculating the number of times nestlings begged for each stimulus class within 4 s of hearing the stimulus, which can then be expressed as a proportion. Two proportions were determined; 1) the 'average score' and 2) the 'specific score'. The average score is the proportion of times that a nestling responds to all of the stimuli heard (e.g. 2 out of 8 = 0.25) and the specific score is the proportion of times that a nestling responds to the stimulus of interest, such as the parental feeding score (e.g. 2 out of 3 = 0.667). The difference between these two scores is calculated to be the 'discrimination score' (e.g. $0.667 - 0.25 = 0.417$). If this score is zero, the nestlings are responding randomly. Negative values indicate that nestlings are avoiding responding, and positive values indicate that nestlings are preferentially responding compared to individually-adjusted random levels of responsiveness to the respective stimulus type.

3.3.5.3 Begging call rate

We modelled the change in calling rate in relation to each playback sequence by using a Generalized Linear Mixed Model with restricted maximum-likelihood estimation (REML) in SPSS 15.0 (Grim 2007). Playback sequence and age of chicks were fixed effects and nest identity was added as a random factor.

3.3.5.4 Begging call structure

As our main aim was to determine how the different stimuli altered the calling structure within each individual, and as we were not concerned with variation among nestlings, we converted the value of each non-begging vocalization into a z-score (Hauber et al. 2007), using all of the measurements taken for each individual nestling. This was done for each of the three response variables for each nestling; amplitude, duration and frequency. To test for effects within each of the sound parameter response variables, three linear mixed models were used for both the begging solicitation call and alarm call playbacks. For each model, the playback stimuli and age were used as fixed effects, and nest number was used as a random effect. This was to ensure that there were not any within nest effect or nestlings that were outliers. Pairwise comparisons (Least Significant Difference) were used to evaluate the significance of group differences for age and playback sequence variables.

3.3.6 Ethical note

Following the playback experiment, all nestlings were returned to the nest and were measured each day until fledgling to ensure no adverse effects from the experiment occurred. All parents resumed feeding nestlings following the experiment and no nestlings experienced undue weight loss in the days following the experiment. No nestlings died during or following the playback due to the experimental procedures. Nest visitation was unlikely to affect predation events, as no nestling mortalities occurred due to natural predation events at nests used for the experiments. Fieldwork

was conducted at Tawharanui Regional Park with permission from the Auckland Regional Council (Permit CHC1004), Department of Conservation (Permit no. AK/15301/RES), and the Massey University Animal Ethics Committee (Permit 05/34)

3.4 RESULTS

3.4.1 Begging Solicitation Calls

3.4.1.1 *Visual display*

The visual displays (gaping) of nestlings were significantly affected by playback stimulus type ($F_{4, 45}=57$, $P < 0.001$), but not by age ($F_{1, 45} = 0.10$, $P = 0.75$) or any interaction of these factors ($F_{4, 45} = 0.043$, $P = 0.99$). Nestlings showed a high degree of discrimination amongst acoustic stimuli, responding almost exclusively to the begging solicitation calls (50 out of 57; discrimination score 0.52 ± 0.04 ; one sample t-test with random expectation of 0, $t_{10} = 16.17$, $P < 0.001$) (Figure 4). Nestlings never responded to the welcome swallow begging solicitation call, the fantail alarm call, or the grey warbler alarm call, which all produced consistently negative discrimination scores (-0.36 ± 0.03 ; $t_{10} = -11.72$, $P < 0.001$). Nestlings occasionally responded to the fantail song (5 out of 34), but still had a trend towards less than random responsiveness (-0.23 ± 0.06 ; $t_{10} = -2.09$, $P = 0.06$).

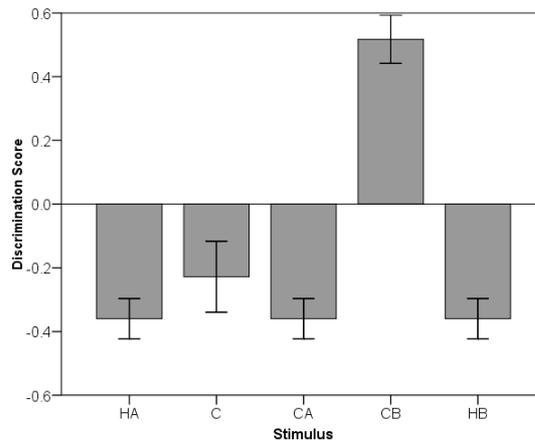


Figure 4: Mean discrimination scores (± 1 standard error) of the begging response for nestlings when presented with each of the five different acoustic stimuli. The five stimuli are fantail alarm call (HA), fantail song (C), grey warbler alarm call (CA), grey warbler begging solicitation call (CB), and the welcome swallow begging solicitation call (HB). Age groups were combined due to no significant difference.

3.4.1.2 Begging Call Rate

There was no significant difference between age groups ($F_{1, 9.1} = 1.965$, $P = 0.194$) or the interaction terms ($F_{2, 45.32} = 1.8$, $P = 0.18$) in begging call rate, although there was a significant difference between playback sequences ($F_{2, 45.324} = 17.61$, $P < 0.001$) (Figure 5a). The random factor of Nest had no effect on the model ($Wald Z = 1.62$, $P = 0.11$). There was a significant difference between the two begging solicitation calls (HB vs. CB; $P < 0.001$) with much fewer calls given in response to the heterospecific control (Mean difference; -3.75 ± 0.65). However, there was no significant difference between the CB and the C (Mean difference; 1 ± 0.65 , $P = 0.133$)

3.4.1.3 Begging Call Structure

The Linear Mixed Models of the begging solicitation calls, indicated that begging call frequency ($F_{1, 22.06} = 0.05$, $P = 0.83$), amplitude ($F_{1, 15.34} = 0.07$, $P = 0.8$) or duration ($F_{1, 18.75} = 2.62$, $P = 0.12$) did not vary with age of chicks (Figure 6). However, the stimuli type was a significant effect for amplitude ($F_{2, 445.87} = 13.05$, $P < 0.001$) and duration ($F_{2, 447.33} = 5.27$, $P = 0.005$), but not the frequency model ($F_{2, 448.47} = 0.81$, $P = 0.45$). The interaction term was not significant for both amplitude ($F_{2, 445.87} = 2.12$, $P = 0.12$) and frequency ($F_{2, 448.47} = 1.45$, $P = 0.24$), but it was significant for duration ($F_{2, 447.33} = 6.19$, $P = 0.002$).

The alteration of begging call structure in response to the begging solicitation call varied among sound parameters (Figure 6). Amplitude increased significantly after hearing a begging solicitation call than a fantail song or welcome swallow begging solicitation call (mean difference \pm standard error of pairwise comparisons: CB vs. C, 0.65 ± 0.15 , $P < 0.001$; CB vs. HB, 1.08 ± 0.34 $P = 0.001$). The duration of begging calls also increased significantly after hearing a begging solicitation call (CB vs. C, 0.3 ± 0.13 , $P = 0.02$; CB vs. HB, 0.7 ± 0.28 $P = 0.01$). There were no significant differences in frequency of begging calls following CB calls and other stimuli (CB vs. C, 0.11 ± 0.23 , $P = 0.65$; CB vs. HB, 0.62 ± 0.51 $P = 0.22$).

3.4.2 Alarm call playbacks

3.4.2.1 Begging Call Rate

There was no significant difference between age groups ($F_{1, 9.18} = 0.3, P = 0.86$), playback sequences ($F_{2, 42.5} = 0.22, P = 0.81$) or the interaction terms ($F_{2, 42.5} = 0.75, P = 0.48$) in begging call rate (Figure 5b). The random factor of Nest had no effect on the model ($Wald Z = 1.48, P = 0.14$).

3.4.2.2 Begging call structure

The Linear Mixed Models of the alarm call playbacks, indicated that begging call frequency ($F_{1, 7.41} = 3.5, P = 0.1$), amplitude ($F_{1, 9.09} = 0.027, P = 0.87$) or duration ($F_{1, 8.41} = 0.16, P = 0.7$) did not vary with age of chicks (Figure 7). However, the stimulus type had a significant effect for all three response variables (frequency; $F_{2, 190.21} = 3.36, P = 0.037$; amplitude, $F_{2, 187.99} = 42.08, P < 0.001$; duration, $F_{2, 190.74} = 3.42, P = 0.035$). The interaction term was not significant for both amplitude ($F_{2, 184.85} = 2.72, P = 0.07$) and frequency ($F_{2, 187.27} = 2.8, P = 0.06$), but it was significant for duration ($F_{2, 185.97} = 8.14, P < 0.001$).

In addition, the way that the begging call structure altered in response to the conspecific alarm call varied among sound parameters (Figure 7). Amplitude was reduced significantly more after hearing a parental alarm call than a fantail alarm call or song (mean difference \pm standard error of pairwise comparisons: CA vs. HA, $-1.29 \pm 0.15, P < 0.001$; CA vs. C, $-0.32 \pm 0.16, P = 0.04$). The duration of begging calls also decreased significantly after hearing a parental alarm call (CA vs. HA, $0.18 \pm 0.09, P = 0.06$; CA

vs. C, $-0.05 \pm 0.1 P = 0.63$). The alteration in frequency was less straightforward, with frequency being lower in CA than both HA and C, with only the difference between CA and C being significant (CA vs. HA, $-0.12 \pm 0.16, P = 0.45$; CA vs. C, $-0.41 \pm 0.16 P = 0.01$).

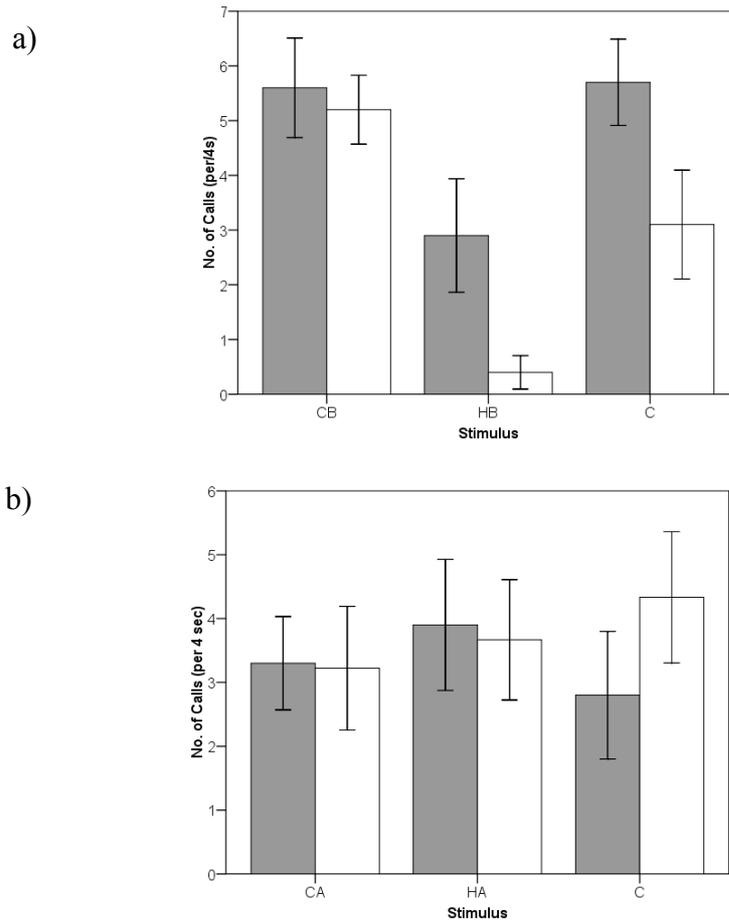


Figure 5: Alterations in calling rate of 12 (■) and 16 (□) days grey warbler nestlings for a) begging solicitation calls and b) alarm calls.

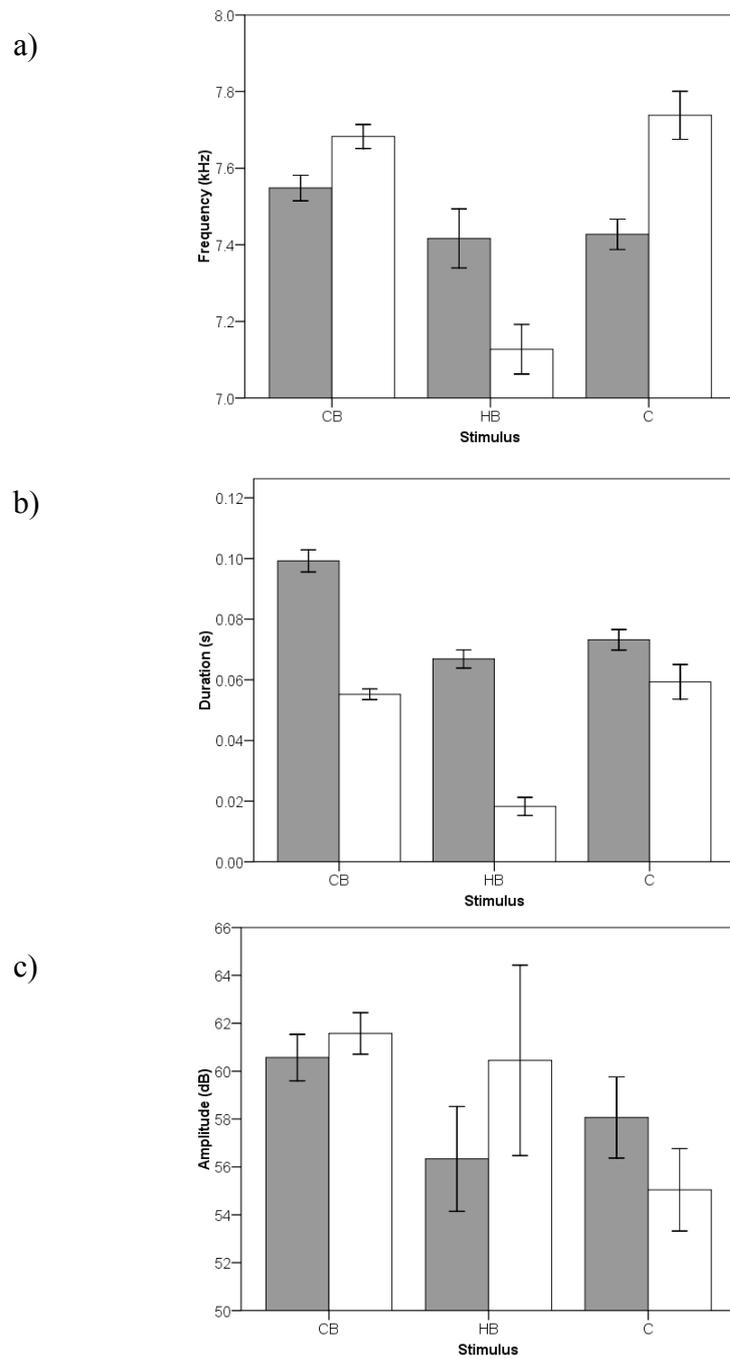


Figure 6: Alterations in the a) frequency, b) duration and c) amplitude of nestling begging calls of 12 (■) and 16 (□) day old grey warbler nestlings in response to the three different begging solicitation calls.

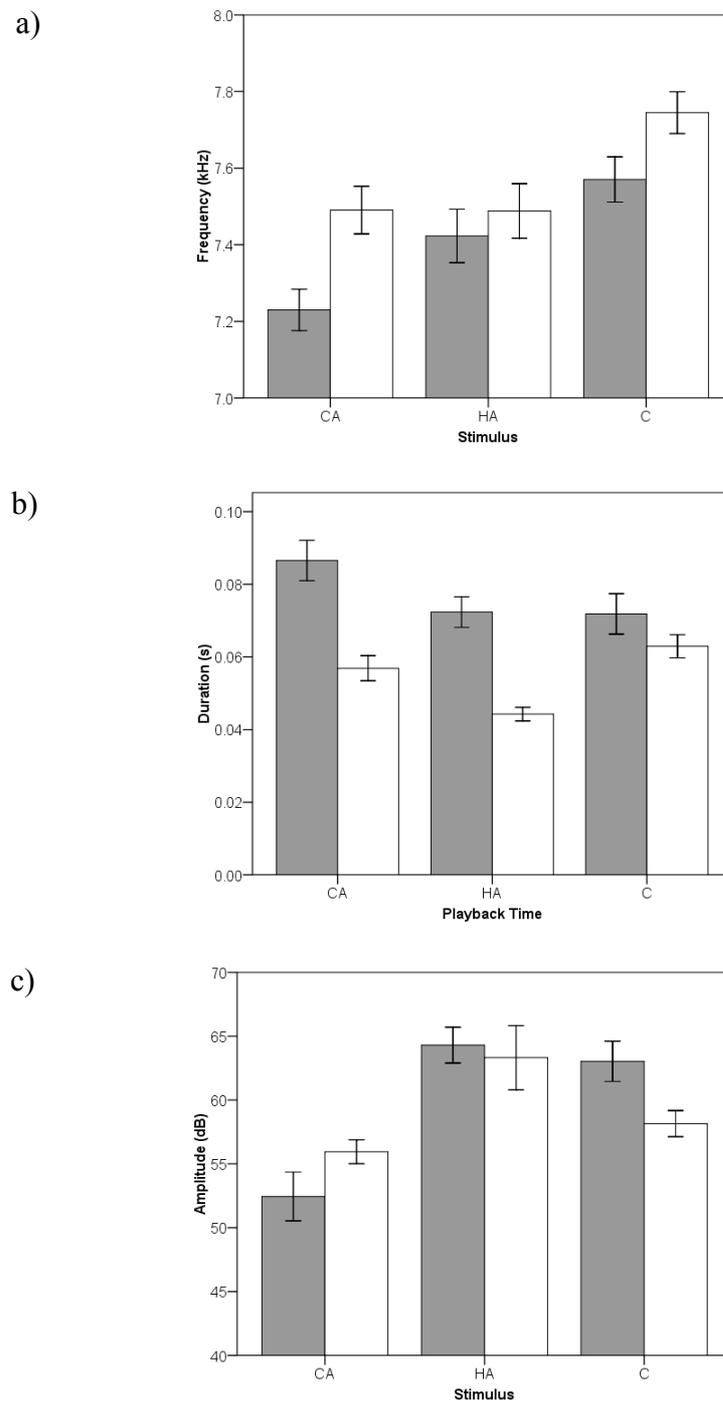


Figure 7: Alterations in the a) frequency, b) duration and c) amplitude of nestling begging calls of 12 (■) and 16 (□) day old grey warbler nestlings in response to the three different alarm stimuli.

3.5 DISCUSSION

The begging behaviours of Grey warbler nestlings conform to several hypothetical scenarios so as to avoid detection by acoustically-oriented predators. This study showed that nestlings preferentially respond to begging solicitation calls over heterospecific begging solicitation calls and control songs, displaying effective species-specific acoustic discrimination. Nestlings also responded appropriately by not increasing their begging call rate to parental alarm calls and also alarm calls of heterospecifics, instead reducing their rate of begging calls. However, chicks did not cease begging altogether following alarm calls. It is acknowledged, however, that the method that we have used may not be entirely adequate, due to nestlings being removed from their nest for experiments, which may not mimic natural situations perfectly.

The sound parameters of begging calls given after parental alarm calls also changed, with a reduction in amplitude. Amplitude was consistently lower for both age groups, following the conspecific alarm call. This is an appropriate response, as one of the best ways to reduce conspicuousness of begging calls is to decrease amplitude (Briskie et al. 1999). The change in frequency of begging calls caused by alarm calls was more variable with age; 12 day old nestlings decreased the call frequency, while 16 day old nestlings did not appear to alter their call frequency. This suggests that this may be due to different selection pressures on the begging call during the nestling and fledgling periods. For example, Magrath et al. (2006) found that nestlings and fledglings behaved differently to specific alarm calls, showing that they only responded to alarm calls that were relevant to their life history stage. Nestlings were unresponsive to aerial

alarm calls, but developed an appropriate response (silence) to aerial alarm calls during the fledgling period, when they are more vulnerable to aerial predators.

Acoustic cues to evoke a begging response from nestlings have been described in many species of birds (Kuhlman 1909; Bengtsson and Ryden 1981; Schuchmann 1983; Khayutin 1985; Clemmons 1995b). Such vocalizations have been shown through playback experiments to act as an antipredator strategy by effectively only “switching on” a begging response in nestlings when parents determine that there are no predators nearby (Clemmons 1995b; Leonard et al. 1997a; Madden et al. 2005a; Magrath et al. 2007). Here we demonstrate that not only do grey warbler nestlings respond strongly to begging solicitation calls, but also that they do not respond to other matched heterospecific acoustic stimuli; thus clearly demonstrating species-specific acoustic discrimination. This makes evolutionary sense in a noisy environment, because a false cue response (Dor et al. 2007), as observed in house sparrows *Passer domesticus*, may be elicited by inappropriate stimuli. Therefore, it appears that grey warblers have a high response threshold, as they only respond to species appropriate stimuli.

Few studies have tested the acoustic discrimination response of nestlings. Magrath *et al.* (2007) found that white-browed scrubwren (*Sericornis frontalis*) nestlings responded appropriately to 5 of the 6 acoustic stimuli used. However, nestlings also showed a begging response to a heterospecific song. Madden *et al.* (2005a) found a similar begging response error in red-winged blackbird *Agelaius phoeniceus* nestlings that responded to eastern phoebe *Sayornis phoebe* begging solicitation calls. The most likely explanation for this, in both cases, is that the inappropriate stimuli that evoked a begging response, shared acoustic features with the begging solicitation call. This

suggests that there is an acoustic similarity threshold that nestlings may use. This was also suggested in our study because some nestlings responded to fantail songs, although at a rate that was still below the random expectation (Figure 4). The ability of nestlings to perceive and discriminate amongst acoustic stimuli can vary with age, as they may be more responsive to particular frequencies, which may also change with age (Khayutin 1985). Parental solicitation stimuli may vary with age, as can the response of nestlings. This may be due to nestlings learning alternative cues with age, such as the sound of parents arriving at the nest, or better responding to parental stimuli (Clemmons 1995b; Clemmons 1995a). It is yet to be determined if this acoustic similarity threshold is present in other species, and if so, what developmental, acoustic, social and ecological factors act to mitigate this threshold.

Nest architecture has been suggested to be an important determinant of the antipredator mechanism used by parents (Madden et al. 2005a). Species that nest on flexible substrates are more likely to possess a switch off mechanism, as nestlings may beg at inappropriate times due to nest movements. Alternatively, species that nest on solid surfaces or cavities are more likely to use a switch on mechanism, as nestlings cannot use vibrational cues to predict parents arriving at the nest. Parents, in some species of birds, are able to use alarm calls to stop nestlings from vocalising (both begging and non-begging calls) in the nest to avoid detection by predators (Platzen and Magrath 2004; Madden et al. 2005a; Platzen and Magrath 2005; Magrath et al. 2007). Madden et al. (2005a) also suggested that it is likely that most species will either possess a “switch on” or a “switch off” mechanism, but rarely both. Magrath et al. (2007) found that white-browed scrubwren use both a “switch on” and “switch off” mechanism. This dual strategy was suggested to be useful as their nests are on or near the ground, where

vibrational cues from parents arriving are limited (Magrath et al. 2007), while alarm calls are also beneficial to silence nestlings when potential predators are nearby (Platzen and Magrath 2004). On average, grey warbler nests are situated at 70% of the trees height, averaging 3.5m above ground (Gill 1982, 1983). Nests are enclosed and typically attached only at the top, though occasionally with lateral attachments (Gill 1983). Therefore, it is likely that nests are prone to frequent vibrations due to wind. When the nest location is combined with the grey warbler's light weight (average 6.44g; (Gill 1982) and ability to hover before entering the nest, begging solicitation calls are probably a more reliable cue than nest or substrate vibrations.

Food availability and differing levels of predation pressure have also been suggested as factors that may mediate nestling begging strategies (Magrath et al. 2007). The grey warbler's response to parental alarm calls differs from other species that have been tested, where nestlings responded to alarm calls by either a reduction in the number of begging calls or by being completely silent (Platzen and Magrath 2004; Madden et al. 2005a, b; Platzen and Magrath 2005; Davies et al. 2006). In the grey warbler, however, it was found that nestlings responded by continuing to call, but with a decreased amplitude and shorter duration of begging calls, both of which are strategies suggested to reduce detection by acoustically oriented predators (Redondo and De Reyna 1988). This modulated response to alarm calls may possibly be due to the grey warbler evolving in an environment that has a lower level of predation than other species that have been tested elsewhere. With a reduced predation pressure, it would make evolutionary sense to still reduce predator detection by altering begging call parameters, while remaining vigilant for the return of parents to the nest to increase the probability of being fed over siblings (Dor et al. 2007). An alternative explanation may be that the

use of alarm calls evolved as an anti-predator response by an ancestral species in a different environment. Indeed, the white-browed scrubwren, which possesses a well developed parental-offspring alarm call system, is in the same family (Acanthizidae) as the grey warbler (Leavesley and Magrath 2005; Magrath et al. 2006).

In conclusion, it appears that the grey warbler has a well developed begging solicitation call, or “switch on” mechanism, and a moderate alarm call response, when compared to other species that use alarm calls to warn nestlings of danger. The reason behind this reduced response to alarm calls is unclear and requires further research. It is possible that it is an intermediate strategy between ceasing begging completely and continuing to beg in preparation for the return of parents to the nest. Future research should also consider what factors lead to the presence of a switch off or switch on strategy, as it has now been found that either strategy or both can be present, as well as potential intermediate strategies.

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4 Egg eviction imposes a recoverable cost of virulence in chicks of the common cuckoo



A young Common Cuckoo chick nestling after hatching (Photo: Miklós Bán)

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Abstract

Chicks of virulent brood parasitic birds eliminate nestmates to avoid costly competition for foster parental care. Yet, efforts to evict nest contents by the blind and naked common cuckoo *Cuculus canorus* hatchling are counterintuitive as both adult parasites and large older cuckoo chicks appear to be better suited to toss the eggs and young of the foster parents. Here we show experimentally that egg tossing imposes a temporary and recoverable growth cost of mass gain in common cuckoo chicks during the nestling period in nests of great reed warbler *Acrocephalus arundinaceus* hosts. In contrast, growth rates of skeletal traits and morphological variables involved in the solicitation of foster parental care were similar between evictor and non-evictor chicks throughout development. We also detected no predation cost of egg tossing behaviour by common cuckoo hatchlings. We argue that the timing of virulence in brood parasites is constrained by two major factors: (1) hosts desert clutches reduced to one (parasite) egg and (2) the cuckoo chick is unable to succeed in competition with older host chicks. Thus, the reversibly costly egg eviction by common cuckoo hatchlings represents an adaptation to counteract the constraints imposed by rejecter host adults and competitive nestmates on the timing and mechanism of parasite virulence.

Keywords: eviction cost, host-parasite coevolution, parental provisioning, rejection strategy, tolerance, virulence

4.1 Introduction

The remarkable ability of the common cuckoo hatchlings *Cuculus canorus* (hereafter: cuckoo) to evict host eggs and nestmates from the nest (Figure 8) has fascinated naturalists since times of Aristotle (Davies, 2000) but was first documented in the scientific literature about 220 years ago (Jenner, 1788). Eviction represents a virulent behavioural strategy by this obligate avian brood parasite to eliminate costly competition with host nestmates (Broom *et al.*, 2008, Kilner *et al.*, 2004). Yet both the mother parasites, that remove one or more host eggs when laying her own egg (Wyllie, 1981), and older cuckoo nestlings that are larger and beg more intensely than host chicks (Davies *et al.*, 1998), appear to be well equipped to eliminate eggs or cohabiting nestmates, respectively. Why does it then fall to the naked and blind cuckoo chick to complete the task of tossing eggs and hatchlings over the rim of the host nest?

Previous work showed that the timing of virulence is prohibitively constrained by hosts, as they frequently desert clutches reduced to one (parasite) egg (Davies & Brooke, 1988, Moskát & Hauber, 2007). Similarly, if cuckoo chicks cohabited with host nestmates, they would face permanently costly competition for foster parental care and suffer from lower growth (Grim *et al.*, 2009, Hauber & Moskát, 2008, Martín-Gálvez *et al.*, 2005) or very high mortality (Grim *et al.*, 2009, Rutila *et al.*, 2002). Therefore, the window of virulence by cuckoo parasites is open only shortly after the hatching. Nevertheless, it is unknown what the relative costs may be of the virulence strategy to evict host eggs and nestmates upon hatching.

In theory, virulence by the cuckoo hatchling may entail several costs for the evictor parasite. For example, egg tossing results in unhatched eggs and live chicks falling to the ground or floating in the water near the nest, thereby potentially attracting more predators. In addition, observations of growth patterns of cuckoo chicks raised by different hosts led to the suggestion that parasites might incur growth costs during eviction behaviour (Kleven *et al.*, 1999) and observations of occasional self-eviction and refusal to beg by some cuckoo chicks likely exhausted after eviction further indicate that this behaviour may really be costly (Molnár, 1944). Although the benefits of eviction are well known in that cuckoo chicks receive parental care without competition (Hauber and Moskát 2008), the relative costs of such behaviour of cuckoo virulence have not previously been investigated.

How the eviction behaviour of brood parasite nestlings evolved is poorly understood. One suggestion postulated by Soler (2001, 2002) is that parasite virulence is determined by the breeding strategy of the host species. Two main breeding strategies have been described for parent birds; 1) clutch size adjustment and 2) brood reduction. Clutch size adjusters allocate food evenly amongst nestlings, so that all members of the clutch fledge. However, in brood reducers, parents lay larger clutches than they are capable of raising, instead reducing the brood at the later stages, by selectively feeding larger nestlings. Soler (2002) suggested that this could act as a mechanism to drive the evolution of eviction behaviour, as brood parasite nestlings in nests of brood reducing species can survive by outcompeting host nestmates. By contrast, cuckoo nestlings in nests of clutch size adjusting will not receive increased parental provisioning with increased begging intensity, and will be less likely to survive to fledge. Therefore, it is likely that the evolution of eviction behaviour was necessary for cuckoos parasitizing

clutch adjusters. To better understand this scenario requires answering the many questions about the potential costs of eviction behaviour that need to be overcome before such a behaviour could evolve, such as reduced growth due to energetic costs or less time begging and increased predation rates.

Here, we tested the idea that eviction behaviour incurs a moderate cost to cuckoo chicks. We removed host eggs when cuckoos hatched in nests of the great reed warbler *Acrocephalus arundinaceus* and measured differences in growth rates between hatchlings that evicted nest contents and those that did not. We propose two hypotheses; 1) the "ghost of past eviction" and 2) "compensatory growth" hypothesis. The "ghost of past eviction" hypothesis predicts poorer growth performance of control, evictor chicks compared to experimental, non-evictor chicks, continuing after the eviction instinct ceases. Alternatively, the "compensatory growth" hypothesis predicts that control chicks, even if experiencing early growth costs of eviction, are able to recover in growth in the latter parts of the nestling period to fledge at similar masses as experimental chicks.



Figure 8: Hatchling common cuckoos in the process of evicting host chicks and eggs [inset] from great reed warbler nests. Photo credit: C. Moskát and M. Honza (inset photo).

4.2 Methods

4.2.1 Field Procedures

We conducted this research in Hungary, about 30–40kms south of Budapest, in the regions of Apaj and Kiskunlacháza (47°09', 19°05'). Great reed warblers are a relatively large and common host of the common cuckoo and breed at these sites in reed *Phragmites australis* beds that grow in 2–4 m wide margins of small channels and experience an unusually high level of parasitism (41–68% nests per year; see Moskát *et al.*, 2008). Field work was conducted from mid-May to mid-July 2008. Host nests were monitored daily during the laying period and again at around the expected hatching dates. Parasitized nests with a single cuckoo egg were randomly assigned at hatching into one of two treatments. In *control* nests, we left the host clutch in the nest and allowed cuckoo nestlings to evict host eggs naturally. In *experimental* nests we removed all host eggs to prevent eviction behaviour.

To analyze differences in the development of cuckoo nestlings, we quantified growth rates using several parameters (mass, tarsus, gape length, gape width). Importantly, these diverse growth parameters cannot be combined into a single measure of growth because they may be subject to life history trade-offs (Saino *et al.*, 1998). For instance, Gil *et al.* (2008) showed that chicks in poorer condition might invest more into structures that serve to increase provisioning, namely gape area. Accordingly, we also calculated gape area because it is one of the factors known to be involved in soliciting sufficient parental resources for the fast growing cuckoo chick (Kilner *et al.*, 1999).

Nestling mass was measured using portable electronic scales (precision: 0.01 g) and morphological measurements were taken using Vernier calipers (precision: 0.05 mm). We measured gape length (GL) from the outside edge of the rictal flange to the tip of the bill and gape width (GW) was the maximum distance between the outer corners of the rictal flange. These two measurements were used to estimate of gape area (GA). We calculated gape area using the formula: $GA = \left(\sqrt{GL^2 - \left(\frac{GW}{2}\right)^2} \right) \times GW$, assuming that the maxilla and mandible of cuckoo nestlings are of equal area and that the shape of each is triangular.

4.2.2 Sample Sizes

Nests were assigned randomly to control (n = 21) and experimental (n = 17) treatments. We confirmed that all host eggs were evicted from control nests. Overall, the dates of measurements taken in two groups were statistically identical: median for control = 13th June (n = 228), experimental = 15th June (n = 149; GLMM controlling for chick identity: $F_{1, 38.1} = 0.44$, $p = 0.51$). We attempted to take measurements every day, but were occasionally unable to do so due to inclement weather; thus, the numbers of measurements per nestling are variable (Suppl. 5). Also, the number of nestlings decreased with age due to predation. However, we also compared predation rates between experimental and control tests to test the prediction that evictor behaviour is costly because it is more conspicuous whereby tossed eggs attract more predators.

4.2.3 Data Analyses

Analyzing growth data presents statistical problems for standard linear model techniques because the sigmoid growth patterns of birds violate the assumption of linearity of effects (Grim 2006a). Therefore, we analyzed the deviations of growth parameters from control cuckoo chicks (i.e., developing under natural conditions), rather than raw growth data. The aim of this approach was to obtain estimates of chick growth performance that would not violate the assumption of linearity of generalized linear mixed models (GLMM). For mass data we fitted logistic growth curves (PROC NLIN in SAS with the Levenberg-Marquardt estimation method; see (Grim, 2006a) to data from control chicks (one random measurement per chick so that there was no pseudoreplication). The resulting logistic growth curve had following parameters: $\text{mass}(t) = 87.66/(1+e^{(-0.35*(t-8.20)})}$ (t = chick age in days). We then calculated differences between observed chick masses and those predicted by this standard growth curve (i.e., residuals). Thus, positive residual values designate better growth performance of an individual chick compared to the average control chick. Data for structural growth were best fitted by second order polynomial regressions in all cases as follows:

$$\text{Tarsus}(t) = 11.61 + 0.82*t - 0.04*t^2$$

$$\text{Gape length}(t) = 10.87 + 0.96*t - 0.03*t^2$$

$$\text{Gape width}(t) = 11.82 + 0.46*t - 0.04*t^2$$

$$\text{Gape area}(t) = 99.42 + 20.80*t - 0.70*t^2$$

The calculated growth parameters, i.e. residuals, were then analyzed using GLMM (PROC MIXED module in SAS; normal error distribution, parameters estimated by

REML, denominator degrees of freedom were calculated using the Kenward–Roger method). We used the variance components covariance structure in all models. Models had nest (cuckoo chick) identity as a random factor, treatment (control vs. experimental) as predictor and chick age as covariate. Age was significant in some periods and so we conservatively controlled for it in all models. However, removal of age did not affect results qualitatively in any model; treatment*age interactions were always non-significant and removed in all cases. All models were checked for the linearity of effects, normality of errors and homogeneity of variances and were found satisfactory (Grafen & Hails, 2002).

Honza et al. (2007) showed that cuckoo chicks in great reed warbler nests start to evict hosts eggs on average 2 days after hatching. Therefore, we began our analyses of the differences between experimental and control nestlings during this initial period. Eviction instinct typically disappears when cuckoo chicks are 5 days old (Davies, 2000, Hauber & Moskát, 2008). Therefore, we conducted tests during the period from 3 to 5 and 6 to 8 days of age. Following these periods, we divided the remainder of the nestling period into 3-day phases subsequent to eviction for the statistical comparisons between treatment groups. We estimated chick fledging age as a mid-point between the last nest check when the chick was in the nest and the first nest check when the nest was empty and there were no signs of predation.

We did not manipulate number of eggs in the nests with control cuckoo chicks. Thus, the number of evicted eggs naturally varied from 2 to 5. We nevertheless tested the correlation between the number of eggs ejected on the growth rates of nestlings within the control group. The same structure of GLMM that tested for the effect of eviction

versus non-eviction on growth was used, but with the number of eggs evicted as the fixed effect, while maintaining nest (cuckoo chick) as a random variable and age as a covariate. We set $\alpha = 0.05$ and report effect sizes for both significant and non-significant comparisons (Nakagawa & Cuthill, 2007).

4.3 Results

Growth parameters of cuckoo hatchlings in the experimental treatment were statistically identical to those of the controls during the period prior to the onset of eviction (experimental/control*100; 92 – 103%) (Table 4, Figure 9). However, during and immediately following the eviction phase (days 3–5 and 6–8), non-evictor cuckoo chicks grew at a faster rate than evictors with respect to mass (110–120%: Table 1 and Fig. 1a). From day 9 until fledging, although the experimental chicks continued to grow faster, the differences between the two treatment groups were smaller and non-significant in all comparisons (Table 4).

As predicted by the compensatory hypothesis, the mass gain of experimental chicks became similar to controls prior to fledging. This result was obtained by comparing the last measured weight of chicks prior to fledging (control: 84.8 ± 1.88 g, experimental: 85.6 ± 2.76 g, $U_{7,7} = 0.13$, $p = 0.90$). Control and experimental chicks were last weighed at similar ages prior to fledging (days 17 – 20; control: 18.0 ± 0.43 vs. experimental: 18.3 ± 0.36 , $U_{7,7} = 0.61$, $p = 0.54$). There was no difference in fledging ages between the two groups (control: 18.11 ± 0.44 days vs. experimental: 19.0 ± 0.48 days, $U_{9,6} = 15.5$, $p = 0.17$).

Although in most comparisons tarsus, gape length, gape width, and gape area were greater for non-evictor than evictor chicks (Figure 9b–e, Table 4), in contrast to mass data, these morphological measurements were highly variable between treatment groups, so that only two of the differences reached statistical significance (Table 4). We did not test differences in parental responses to begging displays of experimental vs. control cuckoo chicks to conclude the biological significance of our morphological comparisons.

The growth rate of mass of cuckoo nestlings differed amongst those that evicted differing number of eggs (Table 5). Our correlational data showed that the mass of nestlings that evicted five eggs was significantly greater than those that only evicted 2, 3, or 4 eggs (2 vs 5, mean difference \pm s.e.: -9.38 ± 4.16 , $df = 13.08$, $p = 0.042$; 3 vs 5, -8.301 ± 2.98 , $df = 17.2$, $p = 0.013$; 4 vs 5, -7.54 ± 2.42 , $df = 14.82$, $p = 0.007$). There was no significant difference amongst nestlings that evicted 2, 3 or 4 eggs (all $p > 0.05$). No other measures of growth correlated amongst control nestlings with the number of eggs evicted (Table 5). The predation rates of experimental versus control groups (3 of 14 nests and 8 of 15 nests, respectively) were also not significantly different (Fisher's exact test, $p = 0.13$).

Table 4: Differences in growth parameters between experimental (chicks raised alone, host eggs removed) and control (host eggs left and evicted) cuckoo chicks in great reed warbler nests. Data from *a priori* defined phases of development were analyzed separately. Growth was estimated as deviations from growth patterns of control chicks randomly sampled in the study population (see Methods). Effect size (mean \pm SE) is the difference between the growth parameter of experimental and control groups (i.e., positive effect = greater growth of experimental chicks). Sample sizes for respective periods are given as number of nests/chicks and measurements and df refers to denominator degrees of freedom from GLMM models controlling for chick identity and age.

Variable	Phase (days)	Effect size	Sample size		F	df	P
			N	n			
<i>Mass</i> (g)	0–2	0.07 \pm 0.37	31	68	0.03	29.5	0.86
	3–5	2.42 \pm 1.04	32	75	5.47	30.2	0.026
	6–8	4.76 \pm 1.99	22	60	5.73	19.9	0.027
	9–11	1.49 \pm 2.40	22	60	0.38	19.4	0.54
	12–14	3.22 \pm 2.95	21	53	1.20	18.7	0.29
	15+	3.04 \pm 2.28	21	52	1.77	17.4	0.20
<i>Tarsus</i> (mm)	0–2	0.16 \pm 0.22	32	46	0.55	19.1	0.47
	3–5	0.41 \pm 0.31	32	64	1.73	25.7	0.20
	6–8	0.55 \pm 0.38	23	55	2.06	19.0	0.17
	9–11	0.13 \pm 0.52	22	57	0.06	19	0.80
	12–14	0.25 \pm 0.37	21	49	0.45	18.1	0.51
	15+	0.19 \pm 0.44	17	50	0.19	13.9	0.67
<i>Gape length</i> (mm)	0–2	–0.58 \pm 0.36	32	47	2.67	25	0.11
	3–5	–0.02 \pm 0.37	32	67	0.00	27.8	0.97
	6–8	0.32 \pm 0.46	23	55	0.49	18.9	0.49
	9–11	0.10 \pm 0.43	22	59	0.05	19.6	0.83
	12–14	0.30 \pm 0.40	21	49	0.56	17.5	0.46
	15+	–0.02 \pm 0.42	17	49	0.00	14	0.97
<i>Gape width</i> (mm)	0–2	–0.03 \pm 0.25	32	46	0.01	22.2	0.92
	3–5	0.19 \pm 0.25	32	67	0.55	26.9	0.47
	6–8	0.75 \pm 0.33	23	55	5.13	19.1	0.035
	9–11	0.32 \pm 0.31	22	59	1.05	20.2	0.32
	12–14	0.46 \pm 0.34	21	50	1.79	17.1	0.20
	15+	0.55 \pm 0.24	17	49	4.98	11.1	0.047
<i>Gape area</i> (mm ²)	0–2	–6.05 \pm 5.26	32	46	1.32	22.8	0.26
	3–5	2.34 \pm 7.03	32	67	0.11	28	0.74
	6–8	14.74 \pm 10.82	23	55	1.86	19	0.19
	9–11	6.28 \pm 10.42	22	59	0.36	19.6	0.55
	12–14	12.65 \pm 12.03	21	49	1.11	17.4	0.31
	15+	10.76 \pm 9.83	17	49	1.20	14.1	0.29

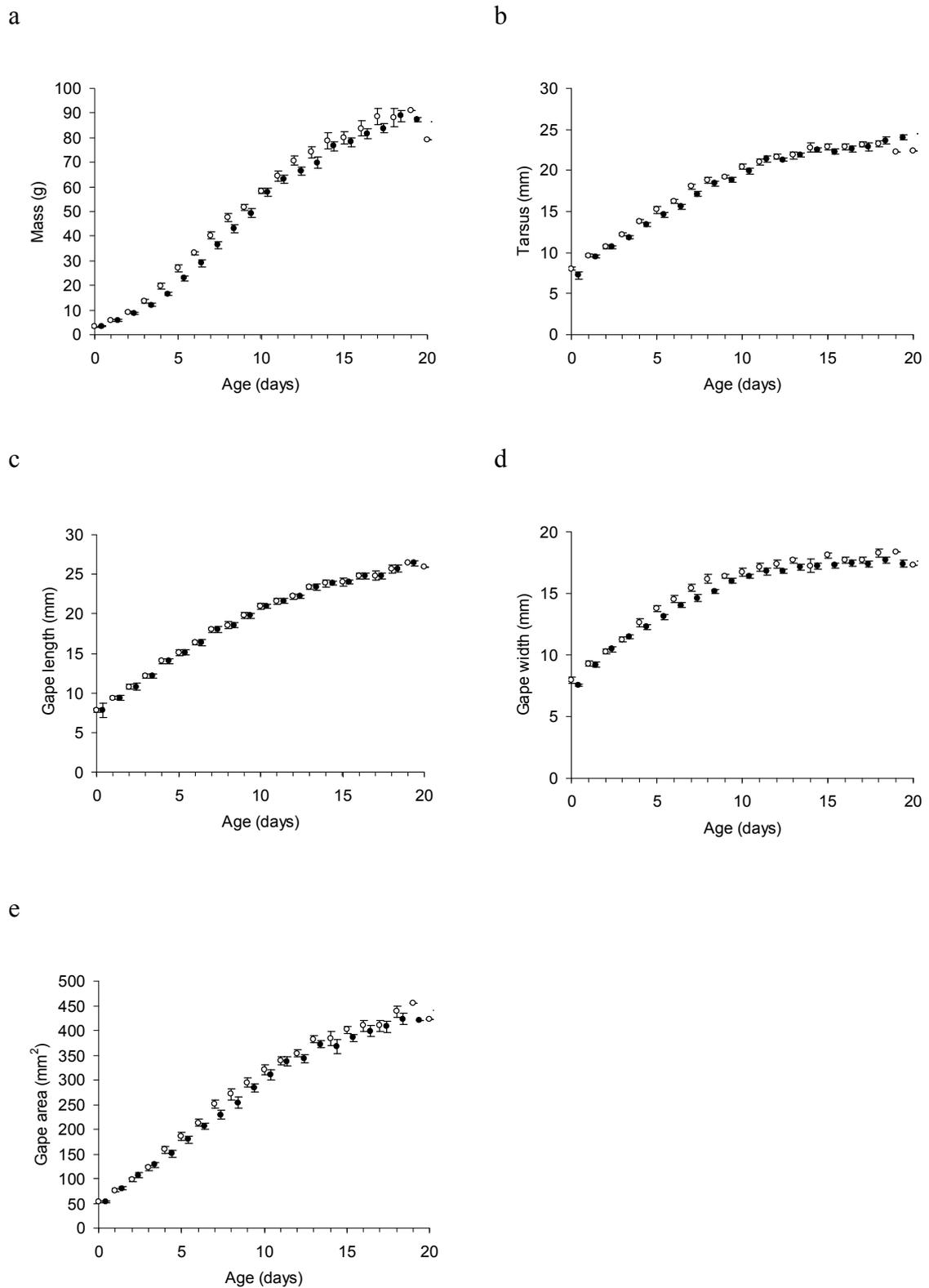


Figure 9: Growth of common cuckoo chicks in great reed warbler nests with host eggs left that had to be evicted by cuckoo chicks (black circles: control/evictor group) or where host eggs were removed (open circles: experimental/non-evictor treatment) for a) mass, b) tarsus, c) gape length, d) gape width, e) gape area. Values are means \pm SE.

Table 5: The effect of the number of eggs evicted by cuckoo nestlings on growth parameters within the control group (nestlings that evicted eggs). Sample sizes for respective periods are given as number of nests/chicks (N) and measurements (n), and df refers to denominator degrees of freedom from the LMM model controlling for chick identity and age.

Variable	Measurements	F	df	P
Mass (g)	206	3.80	15.11	0.03
Tarsus (mm)	173	3.38	9.98	0.06
Gape Width (mm)	180	1.85	12.48	0.19
Gape Length (mm)	180	1.27	15.25	0.32
Bill Area (mm ²)	179	1.23	16.07	0.32

4.4 Discussion

Chicks of the evictor common cuckoo experience a temporary cost of growth due to their virulence to eliminate host progeny in nests of great reed warbler hosts. While we detected no predation cost of egg eviction behaviour by the hatchling parasite, cuckoo nestlings experienced a significant reduction in mass gain during, and immediately following, the eviction period in which they toss host great reed warbler eggs over the rim of the nest. However, the costs of eviction of naturally laid host clutches in great reed warbler nests are compensated during the later stages of the nestling period, leading to no statistically significant differences in nestling fledglings' mass, other growth parameters, or fledging age. It now remains to be determined in future comparative work whether temporary or permanent costs of egg eviction can also be detected in nests of the other host species of cuckoos, varying in body size, nest size and depth relative to parasite hatchling sizes (Kleven et al. 1999).

Our results conform to the compensatory growth hypothesis, as there were no differences between control and experimental nestlings during the late stages of the

nestling period, suggesting that cuckoo chicks are able to increase their rate of mass gain following the eviction period. None of the other morphological variables measured indicated a consistent reduction in growth due to the eviction process. Of particular interest is that bill dimensions were similar between evictor and non-evictor cuckoo chicks. Thus, reduced mass gain was not paralleled by a reduced development rate of the gape area, suggesting that increased allocation may have been channeled towards gape growth relative to mass (Gil *et al.*, 2008), so as to maintain an adequate visual signal of need (Kilner *et al.*, 1999). Compensatory growth (Lepczyk & Karasov, 2000) of cuckoo nestlings regarding mass may be an adaptation that allows parasitic chicks to mitigate the cost of egg eviction. Future research will aim to examine whether there are detectable differences in other sensory modalities of the begging signals between evictor and non-evictor cuckoo nestlings. For instance, it is possible that evictor cuckoo chicks managed to increase their growth rates not by parallel development of gape traits but by faster call rates (Kilner *et al.*, 1999). That foster parents are able to compensate the growth reduction of evictor cuckoo chicks is suggested by our counterintuitive correlation data on cuckoo chick growth. Specifically, we found that cuckoo chicks evicting 5 host eggs grew faster than cuckoo chicks evicting fewer eggs (Table 5). This result is consistent with the pattern of better parental care by foster parents who are also able to lay larger clutches (also see (Avilés *et al.*, 2009, Polačiková *et al.*, in press).

Kilner (2005) applied the use of a cost/benefit model to explain variation in nestling virulence. Under this model, whenever the costs of sharing a nest with nestmates are greater than any potential benefits, such as an increase in the production of begging signals owing to larger number of nestmates (Kilner *et al.*, 2004), then eviction behaviour should evolve. In turn, the costs of virulent eviction behaviours will also alter

the threshold where it becomes beneficial for the parasite chick to be raised alone (Kilner, 2006), resulting in host-parasite systems, where alternative strategies of virulence will be employed, such as increased competitiveness with host nestlings or direct killing of nestmates (Davies, 2000).

Growing up alone, rather than cohabiting with nestmates (Broom *et al.*, 2008, Kilner *et al.*, 2004), is beneficial for cuckoo chicks in terms of higher per capita feed rates, improved growth, survival, and shorter fledging latency (Grim *et al.*, 2009, Hauber & Moskát, 2008, Martín-Gálvez *et al.*, 2005). Nevertheless, experimental evidence has shown that cuckoo chicks lack the ability to outcompete host chicks when sharing a nest. This reduced competitive ability may be an artifact of secondary adaptations of the evictor cuckoo chick to reduce the energetic and predation costs of intensive begging displays in the absence of competitors for parental provisions (Dearborn, 1999, Haskell, 1994, Kilner, 2001). However, our finding that measurable growth costs are detected during and immediately following eviction behaviour by the cuckoo chick should inhibit egg eviction behaviour. Therefore, growing up alone must have had to represent a substantial benefit for the cuckoo chick throughout evolutionary time for egg eviction behaviour to initially appear and be favored by selection (Kilner, 2005).

We suggest that timing of eviction by the naked and blind cuckoo chick can be explained by an ongoing coevolutionary arms race between hosts and parasites (Dawkins & Krebs, 1979), whereby hosts escalate to evolve increasingly specialized responses to reduce the cost of parasite adaptations to circumvent rejection (Langmore *et al.*, 2003). Overall, (1) the potential strategy of the early removal of future competitors at the *egg* stage by female cuckoos leads to unrecoverable costs (e.g.,

desertion of parasitized nests by hosts: Moskát and Hauber 2007), (2) the potential strategy of late removal of competitors at the *chick* stage by the typically older and larger cuckoo chick also leads to unrecoverable costs (e.g., impaired growth, survival and fledging of the parasite chick caused by costly competition with host chicks: Grim et al. 2009, Hauber and Moskát 2008), so that (3) eviction by the blind and naked cuckoo chick remains the only feasible option for the cuckoo to become the sole occupant of the host nest (Jenner 1788). Nevertheless, this cost of early eviction is temporary, recoverable, and compensated for later in the nestling period in broods of great reed warbler hosts (this study). The cost of eviction is also likely to vary with the size of host eggs and nestlings, as well as the nest structure (Grim, 2006b). In turn, the mechanisms of compensatory growth, including possible increases in the cuckoo chicks' signaling of need for parental provisioning following egg tossing, still remain to be elucidated.

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Suppl. 5: Sample sizes for the number of cuckoos at each age class within each experimental group.

Age (days)	Experimental Group		Total
	Experiment	Control	
0	9	10	19
1	15	13	28
2	14	15	29
3	18	14	32
4	13	18	31
5	13	15	28
6	12	13	25
7	13	13	26
8	9	13	22
9	10	12	22
10	12	14	26
11	13	12	25
12	8	14	22
13	10	11	21
14	8	11	19
15	9	9	18
16	8	9	17
17	5	7	12
18	7	4	11
19	1	2	3
20	1	1	2

5 Honest information content of nestling begging calls in the Grey Warbler



Adult Grey Warbler (Photo: Michael Anderson)

This chapter is modified from the manuscript:

Anderson, M.G., Brunton, D. H. and Hauber, M. E. Honest information content of nestling begging calls in the Grey Warbler. (Submitted to *Ethology*)

5.1 Abstract

One critical prediction of communication models regarding parent-offspring conflict is that food solicitation displays of offspring are honest. A common aspect of honesty in begging calls is reliable change with the physiological needs of the dependent young. We experimentally tested whether and how the acoustic structure and begging call rate of individual Grey Warbler (*Gerygone igata*) nestlings change with hunger level and age. We also examined the temporal dynamics of the acoustic structure of begging calls after nestlings heard parental feeding calls. Begging call structure narrowed in frequency range and, surprisingly, decreased in amplitude as hunger levels increased. We also found that begging calls changed with chick age, with frequency increasing and duration decreasing for older chicks. These results indicate that the acoustic properties of nestling Grey Warbler begging calls are complex and may be used to signal several aspects of nestling traits simultaneously, including hunger level and age (or size, a correlate of age). Overall, begging calls of Grey Warbler chicks appear to be honest, implying that parents are likely to benefit from recognizing hunger associated acoustic features of their progeny's calls. Finally, there is an important implication of such signals for the specialist brood parasitic shining cuckoos *Chrysococcyx lucidus* exploiting Grey Warbler parental care, cuckoos would also need to match the dynamics of acoustic features of their host chicks' calls.

Key words: begging call, honesty, parent-offspring conflict, parasite

5.2 Introduction

A critical prediction of communication models regarding parent-offspring conflict is that the solicitation behaviours of offspring are an honest signal (Budden & Wright 2001; Kilner & Johnstone 1997; Royle et al. 2002). Honest signalling implies that there is a reliable relationship between aspects of offspring displays and their real needs (Lotem 1998; Royle et al. 2002; Trivers 1974). For these signals to be evolutionary stable, they must be costly, both for the offspring to produce and for the parents to ignore (Godfray, 1995, Grafen, 1990, Kilner & Johnstone, 1997). Signals can indicate offspring quality (de Ayala et al. 2007; Tanner & Richner 2008) or need (Kilner, 1997, Kilner *et al.*, 1999). Whether offspring signals vary sufficiently for the parents to perceive and what aspects of the signal reflect need or quality have only been examined in a handful of species to date (e.g. Kilner *et al.*, 1999, Leonard & Horn, 2006, Sacchi *et al.*, 2002, Saino *et al.*, 2000).

The begging behaviour of nestling birds has become a model system to test predictions of parent-offspring conflict theory (as reviewed in Kilner & Drummond, 2007), including visual and acoustic aspects of the honest aspects of chicks' displays (e.g. de Ayala *et al.*, 2007, Hauber & Ramsey, 2003). Nestling birds are ideal for testing such hypotheses, as these young are dependent on their parents to provision food, often compete with siblings of varying relatedness (Briskie *et al.*, 1994, Hauber, 2003) and display context-specific behaviours that can be used by parents to determine the need of both the brood and individual nestlings (Dearborn, 1998, Kilner, 1997, Saino *et al.*, 2000).

In contrast to extensive data on the visual (behavioural and colour) displays of begging chicks, the acoustic parameters of begging signals have rarely been examined in the context of honest predictors of offspring need such as hunger or age (Lotem, 1998). Indeed, in enclosed nests such as those of Grey Warblers, the nest interior is a dark environment, which suggests that acoustic signals may be more important than visual signals. Furthermore, begging call mimicry by specialist brood parasites has been observed in this species and its close relatives (Anderson *et al.*, in press, Langmore *et al.*, 2003, McLean & Waas, 1987). Understanding which aspects of the acoustic displays are modulated with varying chick need can provide information about the cost of the signals (Kilner, 2001) and how parents assess this need and respond with appropriate resource allocation (Grodzinski & Lotem, 2007). For example, Leonard and Horn (2001) showed that tree swallow (*Tachycineta bicolor*) nestlings were able to signal both hunger and thermal state by modulating begging call acoustics and delivery rates. Leonard and Horn (2006) later found that this pattern of signalling was consistent throughout the nestling period, although amplitude and frequency range only increased with hunger during the later stages of the nestling period (10 and 15 days). Such studies suggest that particular acoustic components of the begging call can be used to reflect nestling hunger, while others may reveal nestling size, sex, age, health, or other fitness relevant traits (Hauber & Ramsey 2003).

Few studies have integrated the different sensory modalities that form chick begging displays to assess the nature of the information conveyed by each of the signals. Kilner *et al.* (1999) found that parental provisioning rate is determined by visual and acoustic cues, which correlates with nestling age and brood size. These multimodal signals give a rough estimate of the levels of parental provisioning required, which is then adjusted

for offspring short term levels of need indicated by begging vocalisations (Kilner & Davies, 1999, Sacchi *et al.*, 2002, Leonard & Horn, 2001). In turn, brood parasitic chicks which tap into the fine tuned communication system between parents and offspring (i.e. *Cuculus* cuckoos and *Vidua* finches), would need to match the signalling modality and signal strength of the hosts to solicit sufficient parental provisions (Hauber & Kilner, 2007, Kilner *et al.*, 1999, Payne *et al.*, 2000, Schuetz, 2005).

Here we studied the dynamics of the modulation of begging vocalisations of individual chicks of the Grey Warbler *Gerygone igata* to test how begging calls varied with hunger level and age. Grey warblers are also hosts to a begging call mimetic brood parasite, the Shining Cuckoo (*Chrysococcyx lucidus*) (McLean & Waas, 1987), so that begging call dynamics are directly relevant to host-parasite coevolution (Anderson *et al.*, in press). We removed Grey Warbler chicks from their nest during the later stages of the nestling period and tested their response to playbacks of parental feeding calls after 5, 10 and 20 minutes within a sound-isolation chamber. This procedure was carried out with nestlings of two different age groups, 12 and 16 days, to examine if the acoustic parameters that are used to signal need to parents also vary predictably with age in the absence of experimental order effects (Hauber, 2002).

5.3 Methods

5.3.1 Study Site and Species

The Grey Warbler is an endemic New Zealand passerine in the family Acanthizidae (Heather & Robertson, 1997). Grey Warblers build enclosed, pensile nests at heights of

1-10 m, with an average of 3.5 m (Gill 1982). Pairs form prior to the breeding season and are strongly territorial, with some territories being maintained year-round. During the breeding season, pairs usually have two clutches of 3-4 eggs (Gill, 1982). The nestling period is 17-18 days, at which time offspring fledge and remain dependant on parents for a further 28-35 days (Gill, 1982). This research was conducted from August to January during the 2006-2007 and 2007-2008 breeding seasons, at Tawharanui Regional Park (36°22' S, 174°50' N), located 52 km north of Auckland, New Zealand. Nests were located throughout the breeding season by following adult Grey Warblers. Once located, nests were checked daily during the egg laying and hatching periods to be certain of nestling ages. Once females initiated incubation of eggs, nests were enclosed with a large-holed wire mesh for protection from predation. This method has been used in other studies to protect nests from predation (Langmore *et al.*, 2007, Langmore *et al.*, 2003) and in our study this protocol reduced predation rates from 50% to 0%.

5.3.2 Playback experiment

We tested the information content of the begging call structure of individual Grey Warbler nestlings by recording begging calls at differing hunger levels. Nestlings were removed from the nest at 12 or 16 days post hatch and tested in a sound-isolation chamber. Each nestling was fed until satiation, with Wombaroo™ insectivore rearing mix, to standardise hunger levels (Kilner *et al.* 1999; Lichtenstein 2001; Madden *et al.* 2005a; Madden *et al.* 2005b) and then induced to beg after 5, 10 or 20 minutes. Following each begging event, the nestling was removed from the chamber and fed to satiation again before the next trial. The three different food deprivation durations were presented in a random order. This protocol was deemed necessary to avoid the potential

confound of order effects due to the food deprivation period and the time spent within the sound isolation chamber being identical.

Nestlings were stimulated to beg by broadcasting parental feeding calls. Alternative methods of inducing begging were trialled, such as tapping the bill and tapping on the box (Kilner & Davies 1999; Madden et al. 2005a; Madden et al. 2005b), but did not result in a begging response by nestlings. All acoustic stimuli (parental feeding calls) were recorded at the chicks' own nest with a Sennheiser ME 66 microphone onto a HiMD Minidisc as 44.1 kHz, 16 bit .wav files. Recordings from nests were made by attaching the microphone approximately 20-30 cm below the nest, and recording for 90 minutes to obtain parental feeding calls under natural situations. Only nestlings' own parents' feeding calls were used in the playback experiment to avoid pseudoreplication (Kroodsma 1989; Kroodsma et al. 2001) or circumvent parent-offspring recognition errors (Leonard et al. 1997; Medvin et al. 1992). Recordings were subsequently examined in Raven 1.2.1 (Charif *et al.*, 2004) then edited and amplified to achieve standardized call length (4 s) and peak amplitude (20 kU). Parental feeding calls were then played to nestlings with a CD player attached to Sony SRS-A5S portable speakers at standardized amplitude levels, that were comparable to what nestlings would hear at the nest (as measured from nest recordings using the same technique as for the playback experiment, see following paragraph; parental feeding calls, 50-60 dB).

Grey Warbler nestlings have two types of vocalisations; 1) a short call emitted when parents are absent from the nest and 2) a longer call that is given to accompany a raised (begging) posture, with open beak, when parents arrive to feed nestlings (Figure 10). Both vocalisations are high pitched (maximum power at 7.5-9 kHz) and vary with age

(McLean & Waas, 1987). Nestlings start to vocalise at about four days of age (day 0 = hatch day), but it is difficult to elicit a begging response in chicks while out of the nest until 8-10 days (M.G.A., unpub. data). Therefore, we conducted our playback experiments at 12 and 16 days of age. Audio recordings from within the sound isolation chamber were made with a Panasonic RP-VC201 stereo tie-clip microphone (frequency response 100 Hz to 20 kHz), connected to a Sony MZ-NH700 Hi-MD Minidisc. Prior to each trial the amplitude recorded was calibrated by playing a constant tone with an electric metronome (Sabine Metrotune MT9000) at the same distance from the microphone as the nestling, while simultaneously recording the amplitude with a Digitech QM-1589 sound level meter next to the microphone. This measurement was then used to later determine the amplitude of the nestlings' begging calls.

All sound recordings were digitally transferred to Raven 1.2 and spectrograms (Hann window size 5.33 mS, 3 dB bandwidth of 270 Hz, frequency grid DFT size 256 samples and 188 Hz) were generated for analysis. To determine which vocalisations were suitable for analysis, we examined the relationship between time passed after the playback of the parental feeding call was recorded and the structure of nestlings' vocalisations (Figure 11). For all acoustic properties there was a 2 second delay in chicks' response from the time of broadcasting the parental feeding call, followed by an alteration in the acoustic trait after 2 - 8 seconds. Because of this delayed pattern of alteration of vocal displays, the first 5 begging calls after 2 seconds were selected to analyse for changes in begging call traits with hunger levels. For these begging calls, we measured the duration, fundamental frequency, frequency range and peak amplitude. We also measured the begging call rate of these 5 vocalisations (calls/s) following the playback of parental feeding call. We were unable to determine the sex of

the Grey Warbler chicks in this study, which is known to be a predictor of begging displays in some other taxa (Hauber & Ramsey, 2003).

5.3.3 Statistical methods

To avoid pseudoreplication and habituation to playback sequences, nestlings (and nests) were used in only one of the two age groups. This meant that our analyses did not require repeated measures for individuals to be incorporated into the design. The numbers of nestlings differed for the 12 day ($n = 9$, from 5 nests) and 16 day ($n = 4$, from 2 nests) groups.

Within trials, however, we tested for the effect of hunger level on begging call rate by using a repeated measures ANOVA, with age as the between subjects effect and hunger treatment as the repeated measure. All analyses met the tests of sphericity required (Mauchly's Test of Sphericity), so the degrees of freedom were not adjusted.

To examine differences in begging call structure, we used a doubly-repeated measures MANOVA, with age as a between subjects variable and playback and playback-age interaction as within subjects variables. The repeated measure was the playbacks, with four measures of the acoustic properties of the begging calls as response variables: frequency, frequency range, duration and amplitude. The significance of each of these variables was tested with univariate tests for both within and between subjects variables as part of the MANOVA. The degrees of freedom and the significance levels were calculated using the Greenhouse-Geisser epsilon due to violation of sphericity for

several variables. We set $\alpha = 0.05$ and report effect sizes for both significant and non-significant comparisons (Nakagawa & Cuthill, 2007).

5.4 Results

5.4.1 Call rate

The begging call rate of Grey Warbler nestlings did not vary with the hunger treatment (Wilks $\lambda = 0.6$, $F_{2, 10} = 3.33$, $P = 0.78$) and there was no interaction effect between hunger treatment and age (Wilks $\lambda = 0.84$, $F_{2, 10} = 0.95$, $P = 0.42$; Figure 12). The begging call rate varied with age, decreasing from 12 days (mean \pm S.E.: 3.68 ± 0.22 calls / s) to 16 days (2.79 ± 0.32 calls / s; $F_{1, 10} = 6.59$, $P = 0.04$).

5.4.2 Call structure

Begging call structure of Grey Warbler chicks changed significantly with both chick hunger level (Wilks' $\lambda = 0.36$, $F_{8, 51} = 11.3$, $P < 0.001$) and age (Wilks' $\lambda = 0.47$, $F_{4, 55} = 14.56$, $P < 0.001$) and included a significant interaction term (Wilks' $\lambda = 0.41$, $F_{8, 51} = 9.2$, $P < 0.001$).

Grey Warbler nestling calls also varied in amplitude ($F_{1, 82, 58} = 11.01$, $P < 0.001$) and frequency range ($F_{1, 93, 58} = 4.55$, $P = 0.01$) and changed significantly across hunger treatments with frequency range and amplitude decreasing with hunger level (Figure 13). Neither frequency ($F_{1, 48, 58} = 2.74$, $P = 0.09$) nor duration ($F_{1, 77, 58} = 0.88$, $P = 0.41$) varied across the differing hunger levels. Amplitude was the only acoustic variable to

have a significant interaction effect between playback and age ($F_{1.82, 58} = 14.41$, $P < 0.001$). Frequency ($F_{1.48, 58} = 0.35$, $P = 0.64$), frequency range ($F_{1.93, 58} = 2.7$, $P = 0.07$) and duration ($F_{1.77, 58} = 2.19$, $P = 0.12$) all had non-significant interaction terms.

Nestling begging calls significantly increased in frequency ($F_{1, 58} = 35.82$, $P < 0.001$) and decreased in duration ($F_{1, 58} = 32.15$, $P < 0.001$; Figure 13) in older chicks. However, neither frequency range ($F_{1, 58} = 1.88$, $P = 0.18$) or amplitude ($F_{1, 58} = 2.13$, $P = 0.15$) changed with age.

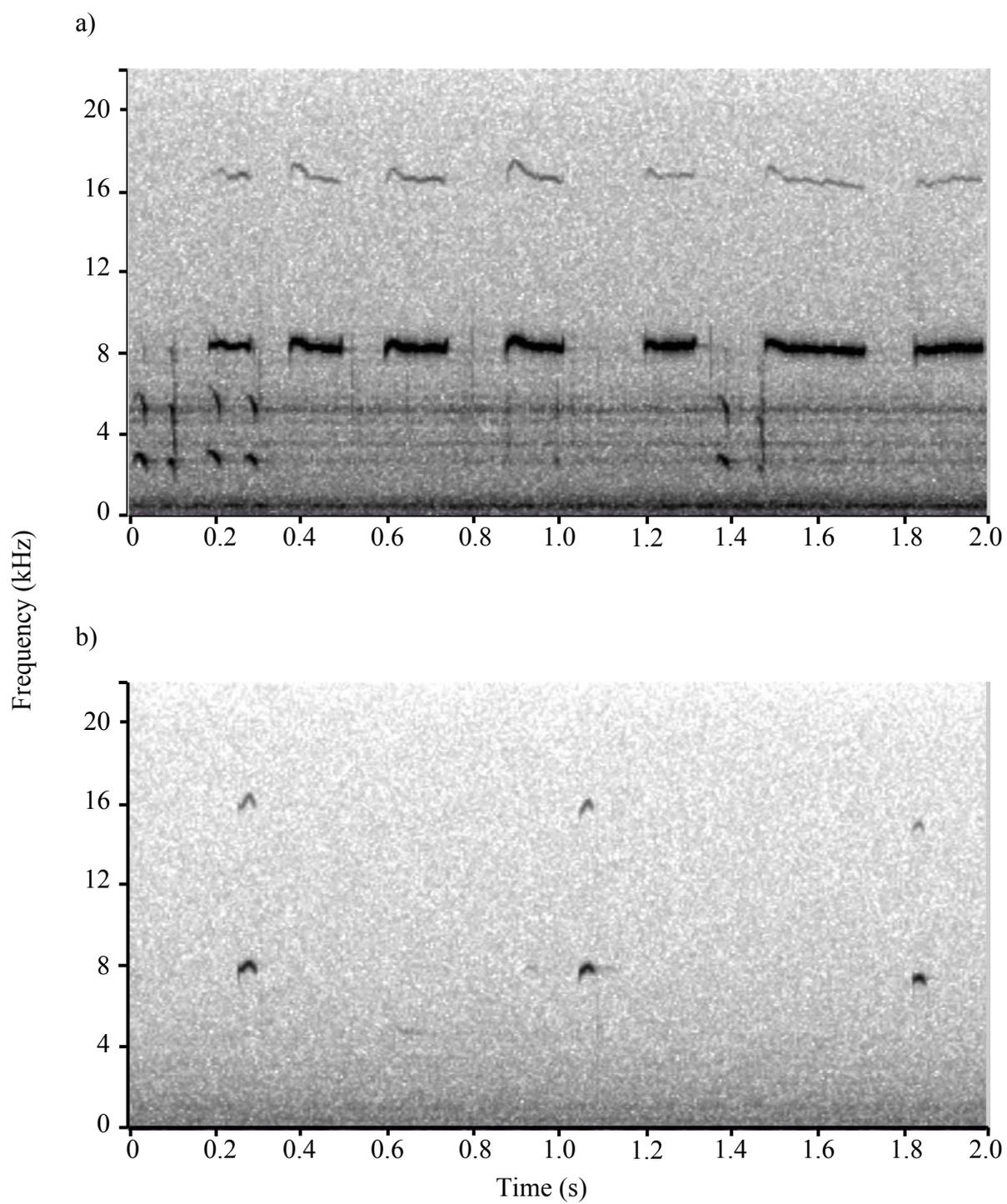


Figure 10: The two typical types of vocalisations given by Grey Warbler nestlings; a) a longer begging call following the parental feeding call and b) the shorter non-begging call.

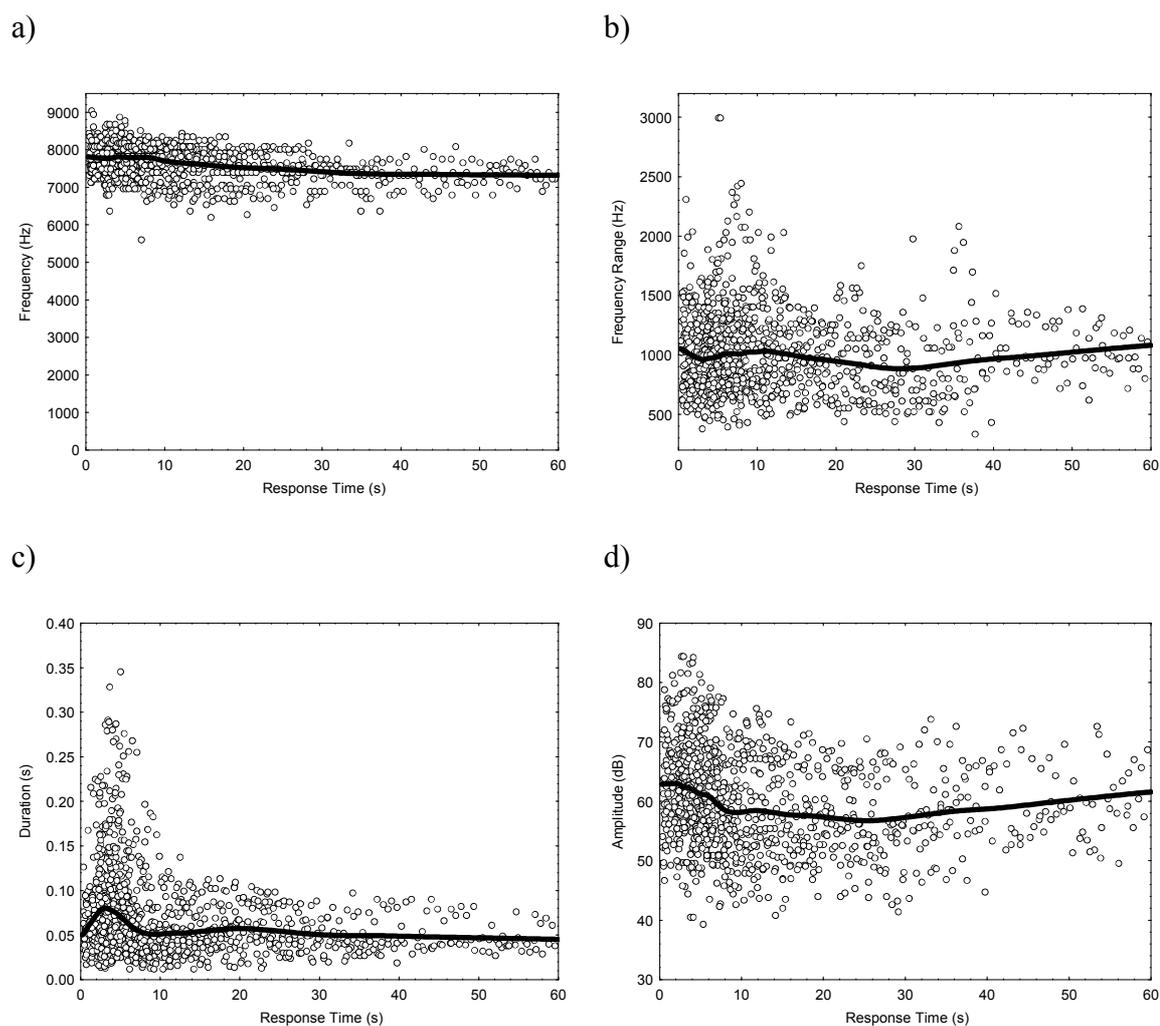


Figure 11: The relationship between the time since nestlings heard their parental feeding call and a) frequency ($r = -0.34$, $p < 0.001$), b) frequency range ($r = -0.06$, $p = 0.06$), c) duration ($r = -0.27$, $p < 0.001$) and d) amplitude ($r = -0.14$, $p < 0.001$) of nestling vocalisations. Lowess smoothing is used to give lines of best fit for all graphs.

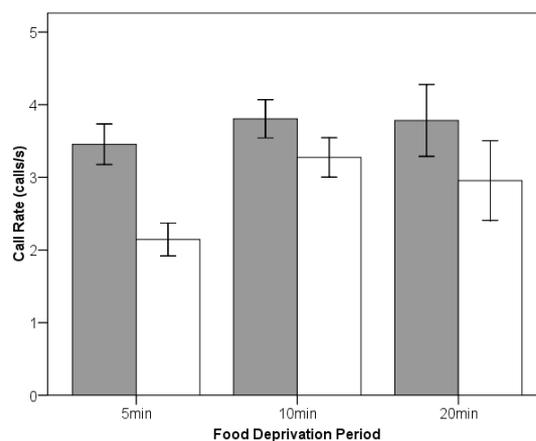


Figure 12: Mean (\pm SE) begging call rate (number of begging calls per second given after parental feeding call) given by Grey Warbler nestlings across three food deprivation periods (i.e. hunger levels) at 12 (■) and 16 (□) days.

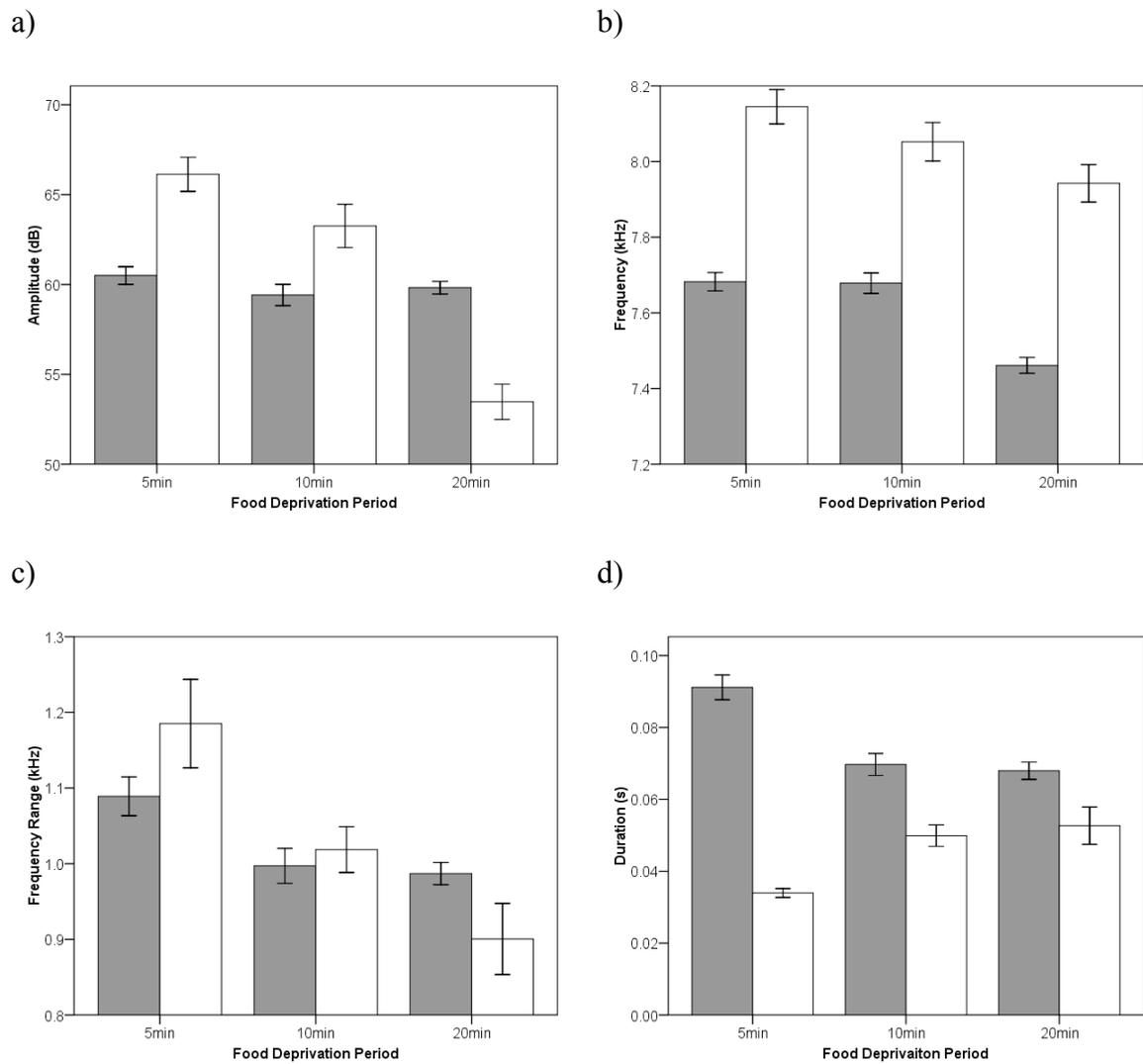


Figure 13: Mean (\pm SE) of (a) amplitude, (b) centre frequency, (c) frequency range, and (d) duration of begging calls for Grey Warbler nestlings across three food deprivation periods (i.e. hunger levels) at 12 (■) and 16 (□) days.

5.5 Discussion

Our main finding was that the begging calls of Grey Warbler nestlings are honest signals of need in that chicks alter specific acoustic properties to reflect proximate hunger levels. In contrast, begging call rate did not change in a pattern that reflected the level of need of nestlings, in contrast to patterns observed in other taxa (Hauber & Ramsey, 2003, Kilner *et al.*, 1999). These results indicate that the acoustic properties of nestling begging calls are complex and may be used to signal multiple aspects of nestling traits simultaneously, including hunger level and age (or size, a correlate of age).

We found that there were distinctive and measurable changes in acoustic structure of begging calls associated with both short term need following food deprivation and nestling age. Begging calls decreased significantly in both frequency range and amplitude, indicating that these acoustic traits can be used by parents to reliably assess nestlings levels of need. Leonard and Horn (2006) found that the begging calls of Tree Swallows (*Tachycineta bicolor*) increased in call rate and duration across all age groups (5, 10 and 15 days), with hunger levels, although amplitude and frequency range only increased for older nestlings (10 and 15 days). This is similar to our findings, suggesting that these particular begging call traits may change more generically across species with chick hunger levels. Comparative studies may reveal the signalling origin and shared perception of such begging call variability amongst species.

Begging calls change with age with both begging call frequency and duration varying significantly between the two age groups. The ontogeny of begging call structure has

been examined in other passerine species (Butchart *et al.*, 2003, Clemmons & Howitz, 1990, Hauber & Ramsey, 2003, Jurisevic, 1999, Leonard & Horn, 2006, Redondo & Exposito, 1990). However, few studies have examined the way in which the acoustic properties of begging calls vary with levels of need across age groups.

Grey Warbler nestlings in this study showed a clear pattern of temporal acoustic structure modulation following the parental feeding call (Figure 11). The most striking changes were in duration and amplitude, with both peaking within eight seconds of a chick responding to parental stimulus. This aspect of parent-chick interactions has rarely been examined, and we predict that the modulation of the acoustic structure of begging calls may reflect the expected duration of parental visits to the nest. In other studies of begging call acoustic parameters there has been a general lack of justification for the selection of the begging call syllables used in the analysis and we suggest that examining temporal variation could be important for future studies.

Our research also found that in general the rate at which begging calls are produced did not alter with nestling hunger levels. Call rate has been used many times as a measure of the nestling honesty or intensity of begging calls, and is almost the standard trait that is measured for begging call studies (e.g. Butchart *et al.*, 2003, Leonard & Horn, 2001, Leonard & Horn, 2006). Given our results, it may be pertinent for future studies of chick signalling to examine additional characteristics of the begging call, such as the acoustic parameters even when call rate is constant. It is possible that the number of different signal modalities (e.g. begging call rate, begging call structure and begging call posture) that are used to signal offspring need is related to other factors that are known to affect signalling intensity. Signals of need are known to vary in intensity

with such factors as sibling relatedness (Boncoraglio *et al.*, 2008a, Boncoraglio & Saino, 2008, Briskie *et al.*, 1994) and provisioning ability of parents (i.e. resource availability) (Royle *et al.*, 2002). Therefore, as signalling becomes more intense, it is possible that more modalities are required to signal need and outcompete siblings.

Other factors may affect the number of signalling modalities used by nestlings to convey hunger levels due to cost involved in signalling need. Such costs may be metabolic, or through nestlings mortality, caused by either predation or brood parasitism. Predation is known to be a selection factor for offspring signals (Briskie *et al.*, 1999, Dearborn, 1999, Haskell, 1994, Leech & Leonard, 1997), which may lead to silent signals (i.e. begging posture, gape colour) offering an adaptive advantage over conspicuous signals (i.e. begging calls). If this is occurring, the selection for less conspicuous signalling modalities is likely to also be mediated by predation pressure and nest architecture. Brood parasitism may be also alter the begging call of nestlings due to evolutionary history with begging call-mimetic brood parasites, such as the specialist Shining Cuckoo of the Grey Warbler in New Zealand (McLean & Waas, 1987). Begging call mimetic brood parasites may also contributed to the modulation of need-dependent signalling in the host species (Boncoraglio *et al.*, 2008b). Accordingly, it remains to be determined which aspects of host begging displays that are required to be displayed by the foreign parasite to avoid rejection and to solicit sufficient provisioning (Langmore *et al.* 2008).

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6 Counterintuitive patterns of breeding phenology variation with latitude in the Grey Warbler (*Gerygone igata*) and implications for its brood parasite, the Shining Cuckoo (*Chrysococcyx lucidus*).



A Grey Warbler nest (Photo: Michael Anderson)

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Counterintuitive patterns of breeding phenology variation with latitude in the Grey Warbler (*Gerygone igata*) and implications for its brood parasite, the Shining Cuckoo (*Chrysococcyx lucidus*).

6.1 Abstract

The Grey Warbler has one of the most widespread distributions of any endemic passerine species within New Zealand, making it a suitable candidate for investigating theoretical predictions and empirical correlates of latitude on breeding phenology along the length of the archipelago. We examined differences in the timing of breeding, including dates of egg laying, clutch completion, and incubation and nestling periods between two sites: Kowhai Bush, Kaikoura, South Island, and Tawharanui Regional Park, northern North Island. These two sites are currently the only locations where the breeding biology of the Grey Warbler has been intensively studied. Theory predicts that the breeding biology of birds should change with increasing latitude; clutch size should increase, the number of broods should decrease and the breeding season should shorten. Nest record data suggested that the nationwide average was 3.5 eggs per clutch. However, as predicted, modal clutch size was larger (4 eggs) at Kaikoura's higher latitude and smaller (3 eggs) at Tawharanui. However, in contrast to patterns from the Northern hemisphere, the onset of breeding occurred later and finished earlier at Tawharanui, which suggests that only one brood can be completed at lower latitudes, as opposed to two in Kaikoura. Latitudinal differences in the breeding biology of the Grey Warbler will also have critical implications for its specialist migratory brood parasite, the Shining Cuckoo. Changes in the timing of breeding affects the availability of nests at different locations, whereas increases in nestling body size and brood size with latitude means that hosts may be more suitable further south.

6.2 Introduction

The evolution of avian life-history traits with geography has been the focus of both empirical and theoretical research (Jetz *et al.*, 2008b, Martin, 2004, McNamara *et al.*, 2008). Specifically, why do avian life-history traits, such as clutch size, number of clutches and timing of breeding, vary amongst and within species (Lack, 1947, Moreau, 1944, Skutch, 1949). One of the key factors that affects these traits is latitude. Latitude is linked to changes in many reproductive parameters, and can be invoked as either a proximate or ultimate explanation. The large number of studies conducted on the effect of latitude has helped to establish general patterns of variation in many breeding biology traits (see

Table 6 for summary), including clutch size (Evans *et al.*, 2005, Dunn *et al.*, 2000), timing of breeding (Schoech & Hahn, 2008, Lambrechts *et al.*, 1996), number of broods and duration of breeding (Boehning-Gaese *et al.*, 2000).

Avian clutch size is known to vary considerably within species. An increase in clutch size with increasing latitude is well known and has been documented in many species since the pioneering work of Moreau (1944) and Lack (1947). Since then, numerous studies have investigated breeding variation with latitude, showing that both avian life history and in particular clutch size are influenced by intrinsic (e.g. phylogeny) and extrinsic factors (i.e. ecological) (Böhning-Gaese *et al.*, 2000, Hauber, 2003, Jetz *et al.*, 2008a, Travers *et al.*, 2006).

The pattern of increasing clutch size with increasing latitude is closely linked with the number of broods an individual has per season (Böhning-Gaese *et al.*, 2000). This is

primarily due to the effects of seasonality, which dictates the length of time that is suitable to breed, combined with the predation pressure experienced by a species (Martin *et al.*, 2000, McNamara *et al.*, 2008, Skutch, 1949). The longer the season, the greater the possibility of having more clutches, which increases the chances of reproductive success by lowering the risk that predation or brood parasitism will cause a reproductive failure for that season (Hauber, 2003). In contrast, species breeding near the poles experience high seasonality and thus a shorter window of opportunity for breeding (Evans *et al.*, 2005). A general pattern of breeding behaviour emerges from these patterns, with single large clutches near the poles and tropical species that have multiple smaller clutches and breed almost year round. These factors also mean that the onset of breeding occurs later in the season, as the duration of the breeding period is reduced. Therefore, at higher latitudes, we predict that species have fewer, but larger clutches and start breeding later in the season than more temperate species (Farnsworth & Simons, 2001, Böhning-Gaese *et al.*, 2000).

Interspecific brood parasitism is another factor that may cause a change in the clutch size of species that act as hosts (Hauber, 2003, Lyon, 1998, Rothstein, 1990). Life-history theory predicts that clutch size should be adjusted according to the risk of failure of each breeding attempt. As risk increases, through either predation or brood parasitism, the investment within each clutch should decrease. This has been shown for cowbird hosts (Hauber, 2003), where those hosts that have been in contact with cowbirds for longer periods of time have reduced their clutch size, thus reducing the cost of parasitism to host parents. Therefore, brood parasitism can act as another extrinsic factor that can shift the optimal clutch size for a species.

Latitude is also known to affect body size across and within species, which has implications for breeding traits such as relative egg size and the relative amount of resources required to raise offspring for altricial species (Murphy, 1978). This relationship between body size and latitude is known as Bergmann's rule (Bergmann, 1847), which in its original form states that when other factors are constant, the smaller species in a genus will occur in a warmer climate, due to the relationship between heat loss and surface area (cited in (James, 1970). This rule applies for both increasing latitude and cooler habitats associated with an increase in altitude (Blackburn *et al.*, 1999). This was originally proposed as a comparative pattern, which has general support, but has also been found to apply with intraspecific studies (James, 1970, Monahan, 2008). This is known as the neo-Bergmannian rule or James's rule (*sensu* (Blackburn *et al.*, 1999)) (Gaston *et al.*, 2008). This rule has been found to hold true for over 72% of birds, with sedentary birds being more likely to follow the pattern than migratory species (Meiri & Dayan, 2003).

Finally, the onset of breeding in birds is known to be affected by many factors. Resource availability can be used as a cue to trigger the onset of reproduction, as there should be sufficient resources available to raise offspring (Noordwijk *et al.*, 1995). Environmental cues are frequently used by animals to predict the appropriate time for reproduction to occur. This has been demonstrated in several species, where the onset of breeding has advanced as temperatures have increased due to climate change (Crick *et al.*, 1997, Dunn & Winkler, 1999). Food supply is also critical for reproduction, as resource availability is known to mediate the onset of breeding (Schoech & Hahn, 2008, Thomas *et al.*, 2001).

Here we examine the intraspecific variation in breeding phenology with latitude in a New Zealand passerine, the Grey Warbler (*Gerygone igata*). The Grey Warbler is the most widely distributed New Zealand endemic terrestrial species, found throughout the country (Robertson *et al.*, 2007). Despite this widespread distribution, little is known about variation in morphological and breeding biology traits of Grey Warblers across their range. As yet, to the best of our knowledge, there have been no studies of latitudinal variation of breeding biology traits in any New Zealand passerines, even though the New Zealand archipelago covers over 1400 kilometres in the North – South axis. Here, we use several studies of the Grey Warbler to compare key features of their life-history to examine differences that occur with latitude, and where possible, examine temporal changes in breeding patterns in the nearly three decades between studies at Kaikoura. We predict that an increase in latitude should be associated with 1) an increase in clutch size, 2) an increase in body size of adults and nestlings (Bergmann’s rule), and 3) later onset of breeding and fewer clutches. Also, we compared the variation in parasitism rates amongst studies to examine the relationship between brood parasitism and the breeding characteristics of its host.

Table 6: A summary of the factors that are known to affect various breeding parameters for birds and the change caused by each effect.

Factor	Breeding Parameter	Effect
Predation	Clutch size (<i>Skutch’s Hypothesis</i>)	Decreased clutch size with increased levels of predation
Latitude	Clutch size (<i>Ashmole’s Hypothesis</i>)	Increase in clutch size with latitude
	Number of broods	Decrease in the number of broods with latitude
	Timing of breeding	Shorter breeding season and breeding will start later
Brood parasitism	Clutch size	Decreased clutch size
	Number of broods	Increased number of broods
Resource availability	Timing of breeding	Increased resource availability can initiate earlier breeding

6.3 Methods

6.3.1 Historical nesting records

Data on Grey Warbler breeding was collected by volunteers for the Ornithological Society of New Zealand (OSNZ) on nest cards from 1934-1998. There were 90 nesting records available, which were used to analyse the breeding parameters of the Grey Warbler. Only those records where the final clutch size was determined by multiple visits to the nest to ensure that egg laying had finished were included in the clutch size analysis. Timing of breeding was determined by using the same criteria as in the other studies (see following section).

6.3.2 Study Sites and Species

The Grey Warbler is an endemic New Zealand bird species (family Acanthizidae: (Heather & Robertson, 1997). Grey Warblers build enclosed, pensile nests at heights of 1-10 m, with an average of 3.5 m (Gill, 1982a). Pairs are formed prior to the breeding season and are highly territorial, with some territories being maintained year-round. The nestling period is 17-18 days, at which time offspring fledge and remain dependant on parents for a further 28-35 days (Gill, 1982a).

Information about breeding biology of the Grey Warbler was compiled from four sources; two detailed studies of breeding biology, a more general study and nest record data. The two detailed breeding biology studies were conducted at Tawharanui Regional Park (36°22' S, 174°50' E), located 52 km north of Auckland in the North

Island and Kowhai Bush, near Kaikoura (42°22'S, 173°35' E) in the South Island of New Zealand. The research conducted at Tawharanui Regional Park was done in the Southern Hemisphere summers between August and January during the three breeding seasons between 2005 and 2008.

The breeding biology data from Kaikoura comes from two separate studies. The first was conducted between 1976 and 1979 on the breeding biology of the Grey Warbler and the Shining Cuckoo (*Chrysococcyx lucidus*) at this site (Herein referred to as Kaikoura Study 1; Gill, 1980b, Gill, 1982b, Gill, 1982a, Gill, 1983a). More recent data from Kaikoura were collected from a general study of songbird breeding. These data were opportunistically collected from a general survey of passerine breeding biology (Barnett & Briskie, 2007, Briskie, 2003, Briskie, 2007, Massaro *et al.*, 2008) during the breeding seasons between 2001 and 2007 (Herein referred to as Kaikoura Study 2). We compared breeding biology traits between the two locations and between the two time periods from the studies conducted at Kaikoura.

We examined several life-history traits of the Grey Warbler, particularly those that are known to vary with latitude; 1) clutch size, 2) timing of breeding, 3) adult body mass and 4) nestling growth patterns. Nests were located throughout the breeding season and monitored to determine the timing of key events, such as egg laying. Only those records where clutch size could be confirmed through multiple visits to the nest to confirm that the laying period had been completed were included. Both predation and brood parasitism of eggs can reduce clutch size during the breeding season. To control for this only nests where the final clutch size was confirmed were included. The criteria that was used for this, was that the clutch size needed to remain constant at the end of the

laying interval for more than the inter-laying interval (i.e. more than 2 days). Nests that experienced egg loss during this period were excluded from the analysis, as the final clutch size could not be confirmed.

The brood parasitism rates by the Shining Cuckoo on the Grey Warbler were also compared amongst the studies. Grey Warblers often start breeding before the arrival of the migratory Shining Cuckoo into New Zealand from its non-breeding grounds. To account for this, we used the same protocol as Gill (1983b), by only including hosts nests that had clutches initiated by mid-October or later, when Shining Cuckoos began laying eggs. Nests were considered unparasitized if it was either observed during the laying and first half of incubation without parasitism being noted, or if it held either four eggs or nestlings close to the date of hatching.

To quantify the timing of breeding, the laying date of each egg was determined, which were then grouped into weekly intervals. This was calculated using either multiple nest visits during the laying period or by determining key events, such as hatching date or fledging date then using average incubation (20 days) and nestling period (17 days) values (Gill, 1982a) to determine laying date. The clutch size was also incorporated into this method, as Grey Warblers lay eggs every second day (Gill, 1982a) (i.e. clutch size of 3 requires a laying period of 5 days).

We also compared the adult mass of birds that were captured using mistnets at each site, but only included those caught between May and July to control for potential annual fluctuation in mass that is known to occur in other New Zealand passerines (Low, 2006). Nestling mass was measured daily to determine growth rates. Nestlings

were weighed using pesola scales (± 0.5 g) at Kaikoura and with electronic scales (± 0.01 g) at Tawharanui. Tarsus length was also measured using callipers (± 0.05 mm) at both sites.

6.4 Data Analysis

We used the OSNZ data to test the effect of laying date on clutch size and latitude on clutch size using non-parametric techniques. Clutch sizes were compared between the three more detailed data sets; Kaikoura study 1, Kaikoura study 2 and Tawharanui as the assumption of homogeneity of variance between groups was not met.

Nestling growth patterns were fitted by using Curve Expert[®] (version 1.37) for data collected in Kaikoura study 1 and Tawharanui. The nestling growth patterns of Grey Warbler mass were best fitted by logistic models (Kaikoura study 1: $R^2 = 0.97$, Tawharanui: $R^2 = 0.96$; equations 1 and 2), whereas tarsus growth was best fitted by a third degree polynomial fit (Kaikoura study 1: $R^2 = 0.97$, Tawharanui: $R^2 = 0.92$; equations 3 and 4) where t is time (days) since hatching (day 0):

$$1) \text{ Kaikoura: } mass(t) = \frac{7.16}{1 + 5.16e^{(-0.38t)}}$$

$$2) \text{ Tawharanui: } mass(t) = \frac{6.7}{1 + 4.95e^{(-0.39t)}}$$

$$3) \text{ Kaikoura: } tarsus(t) = 5.99 + 1.36t + 0.03t^2 - 0.003t^3$$

$$4) \text{ Tawharanui: } tarsus(t) = 6.77 + 0.55t + 0.1t^2 - 0.005t^3$$

Growth patterns of mass and tarsus length were analysed using an Analysis of Covariance (ANCOVA) with site as an independent variable and age as a covariate. To remove problems of pseudoreplication for nestling growth patterns that occurs with

repeatedly measuring the same nestling, a single weight and tarsus measurement was taken at a random age from each nestling (Grim *et al.*, 2009). Analyses were carried using SPSS v.15.0, and were tested for normality and homogeneity of variance, and non-parametric tests were carried out where appropriate. All other tests used are stated and effect sizes are reported where necessary (Nakagawa & Cuthill, 2007).

6.5 Results

6.5.1 Clutch Size

Clutch size varied significantly between the three data sets (Kruskal-Wallis: $\chi^2=83.335$, d.f. = 2, $p < 0.001$). Clutch size was considerably smaller at Tawharanui ($n = 57$, mean \pm standard error: 2.94 ± 0.05 eggs) (Figure 14) than in either of the studies at Kaikoura. Interestingly, the average clutch size has decreased within the Kaikoura site between study 1 ($n = 59$, 3.93 ± 0.04 eggs) and study 2 ($n = 38$, 3.58 ± 0.1 eggs) data sets (Mann-Whitney test: $U = 784$, $p = 0.001$). The OSNZ data were not included in this analysis, as they were collected from multiple locations from throughout New Zealand. However, the average clutch size from these data were intermediate to our two study sites ($n = 66$, 3.52 ± 0.07). The effect of latitude on clutch size was also tested more directly with the OSNZ data and we found a significantly positive relationship between latitude and clutch size (Spearman's rank correlation: $n = 66$, $R = 0.25$, $p = 0.04$; Figure 15).

We examined the effect of the timing of breeding on clutch size. Data on the laying dates from Kaikoura study 1 were not available, so we examined the more recent study from this site and the data from Tawharanui. There was no relationship between laying date and clutch size for Kaikoura (Study 2 only: $n = 32$, linear regression: $R^2 = 0.10$, P

= 0.07; see Figure 16), Tawharanui ($n = 57$, $R^2 = 0.02$, $P = 0.28$), OSNZ nest records ($n = 59$, $R^2 = 0.04$, $P = 0.12$) and all studies combined ($n = 147$, $R^2 = 0.02$, $P = 0.1$).



Figure 14: Average Grey Warbler clutch sizes (eggs) from the two sites in New Zealand, Tawharanui and Kaikoura. Kaikoura is shown as two separate columns for the two studies conducted at the same site. Bars are means \pm standard error.

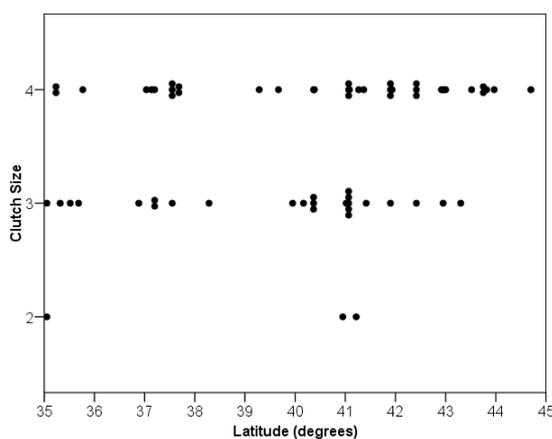


Figure 15: The effect of latitude on clutch size for Grey Warblers throughout the range of New Zealand. Data is from OSNZ nest records.

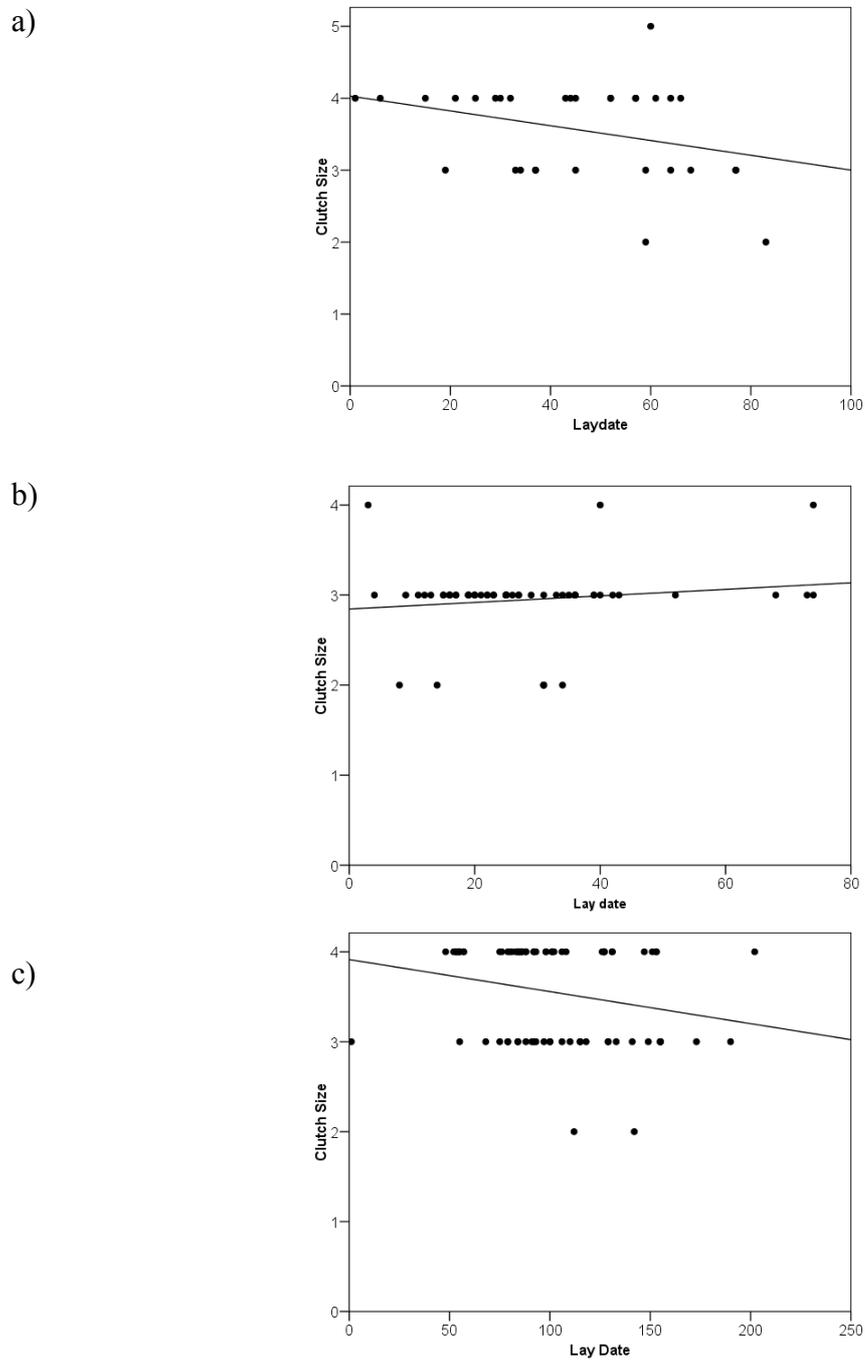


Figure 16: The relationship between lay date (5th of September = Day 1) and clutch size for a) Kaikoura study 2, b) Tawharanui, and c) OSNZ nest record data (25th of June = Day 1).

6.5.2 Frequency of broods and timing of breeding

Grey Warblers at from the Kaikoura study 1 typically laid two clutches, with the first eggs laid in the last week of August and the last being laid in mid-December (Figure 17b). The first clutches were laid between late August and late September, with a second wave of clutches from the last week of October and the first week of December. This pattern was not observed for Kaikoura study 2 (Figure 17c), but this is likely to be due to the much smaller sample size and the less intense searching for Grey Warbler nests earlier in the season, rather than a change in the timing of breeding. By contrast, in Tawharanui Grey Warblers only laid a single wave of clutches starting in the second week of September and lasting until the second week of October (Figure 17a). Both at Kaikoura study 1 and Tawharanui, each clutch laying period for a single set of clutches of the population was typically a 6 week period. When we compared the number of eggs laid during the 6 week period of the first clutch at the two sites, we found no difference (mean \pm s.e.; Kaikoura study 1: 24.7 ± 4.6 , Tawharanui: 21.7 ± 6 ; paired t -test: $t_{10} = 0.397$, $p = 0.7$). Tawharanui birds did lay some eggs after the second week of October, but these were only replacement clutches for first clutches lost to predation. We then compared the sites during the latter six weeks of the nesting period (assuming a three week period between clutches, due to egg laying patterns observed in Figure 17b) and found that there were significantly more eggs laid during this time period at Kaikoura (mean \pm s.e.; Kaikoura study 1: 14.3 ± 1.41 ; Tawharanui: 2.17 ± 1.51 $t_{10} = -5.89$, $p < 0.001$). No observations occurred of banded Grey Warblers successfully fledging a brood and then subsequently laying a second clutch at Tawharanui, further supporting the conclusion that Tawharanui birds only lay a single, early clutch. Despite the OSNZ dataset being less rigorous in its collection methods, these records still

showed an early peak in laying date, primarily during September, with a second peak during late October to late November (Figure 17d).

6.5.3 Brood parasitism rates

The parasitism rates for Kaikoura study 1, has previously been published elsewhere (Gill, 1983b). During this study, annual brood parasitism rates varied from 50% to 63% for clutches laid after mid-October, giving an average parasitism rate of 55% (22 of 40 nests). The Kaikoura study 2 found similar rates of parasitism, with an overall parasitism rate of 30% (18 of 60 nests) for clutches initiated during the same time period. In contrast, the Tawharanui study had a parasitism rate of 0% (0 of 13 nests). However, as the birds at Tawharanui finished breeding earlier, this may not be a fair comparison. The overall brood parasitism rate for all host nests was still 0% (0 of 63 nests where non-parasitism could be confirmed). The OSNZ nest records indicated that only 8.3% of nests (3 of 36 nests) were parasitized. However, it is possible that this lower rate is due to less careful checking of nest contents to ensure that nests were not parasitized with a cuckoo egg.

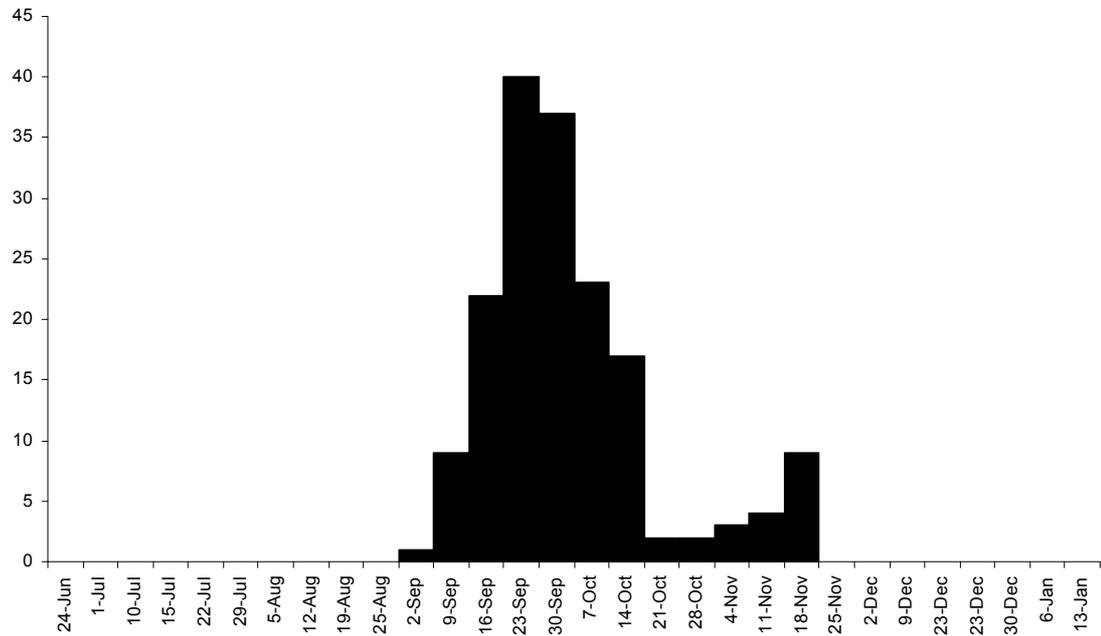
6.5.4 Adult Mass

Adult mass was significantly different between the two study sites (*t*-test, $t_{111} = 8.096$, $p < 0.001$), with the birds from Kaikoura study 1 ($n = 59$, 6.3 ± 0.6 g) significantly larger than those from Tawharanui ($n = 63$, 5.61 ± 0.41 ; see Figure 18).

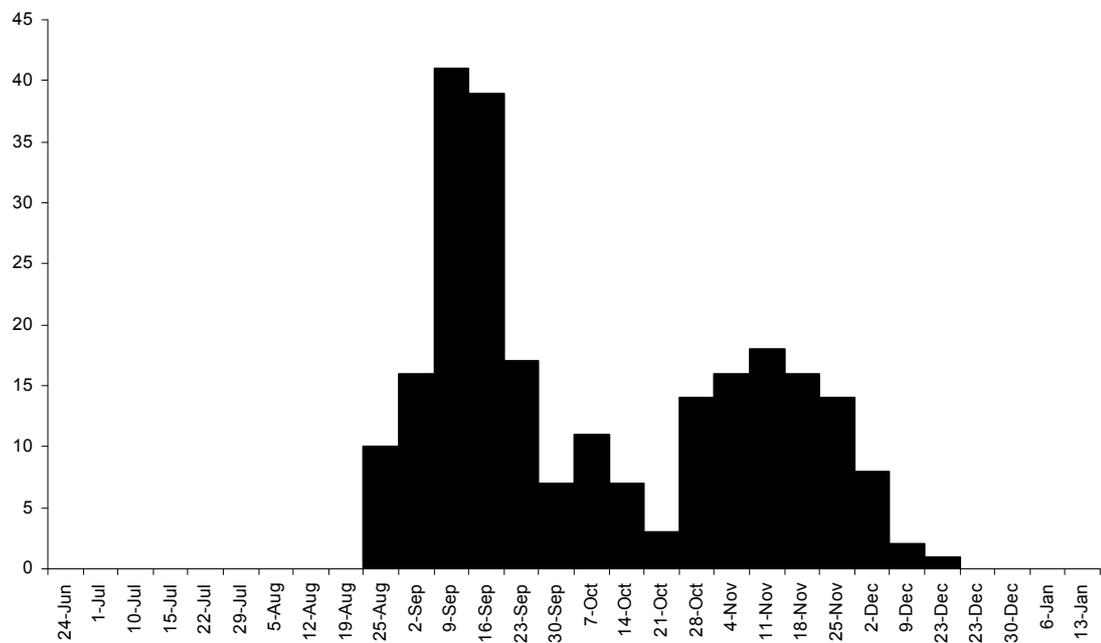
6.5.5 Nestling Growth

Grey Warbler nestlings from Kaikoura study 1 generally grew heavier and larger than those from Tawharanui (Figure 19). There was no statistical difference between sites in growth dynamics of nestling mass ($F_{1, 234} = 2.654, P = 0.11$). As expected, age was a significant covariate of nestling mass ($F_{1, 234} = 1412.3, P < 0.001$). In contrast, growth of nestling tarsus length was significantly different between sites ($F_{1, 167} = 26.3, P < 0.001$) with age as a significant covariate ($F_{1, 167} = 1626.7, P < 0.001$) in the model.

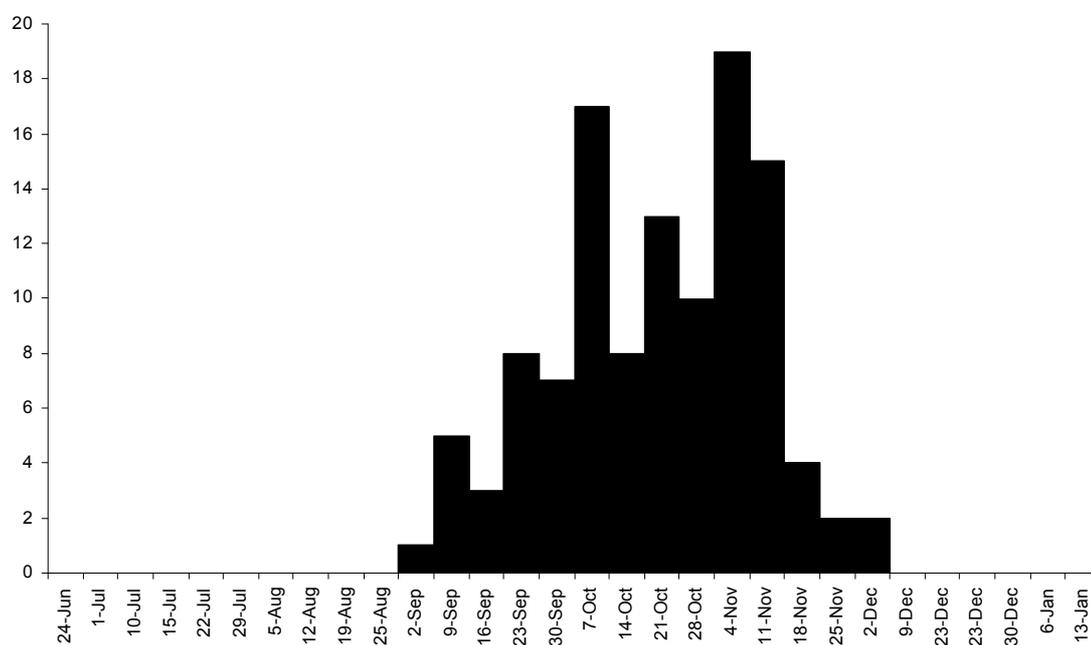
a)



b)



c)



d)

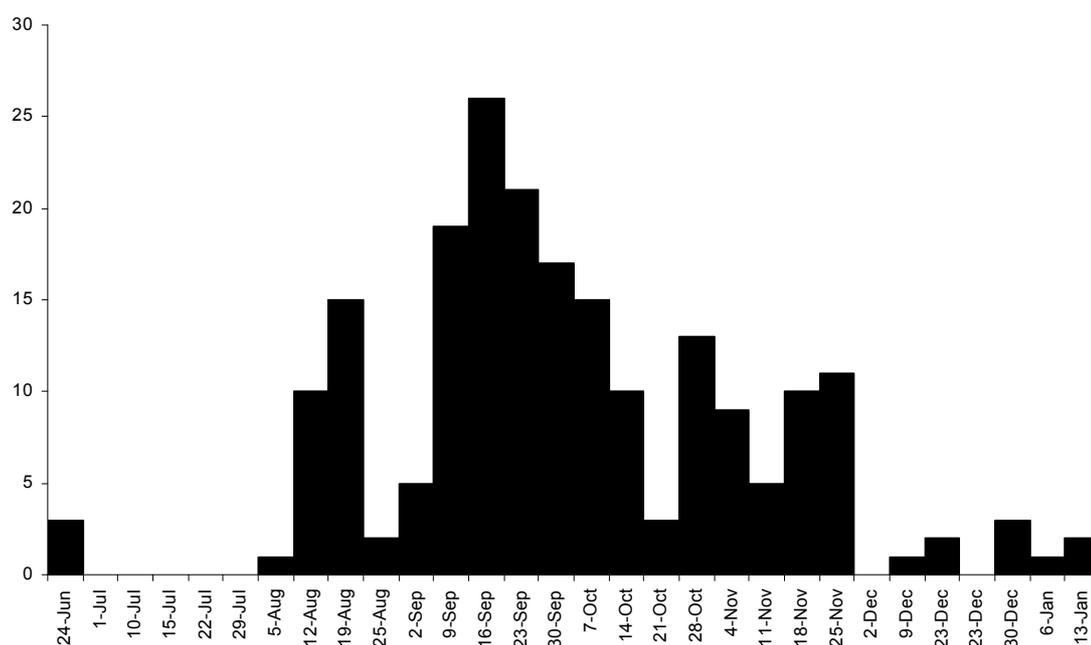


Figure 17: Seasonal patterns of egg laying in the Grey Warbler in a) Tawharanui and b) Kaikoura study 1(1976-1979), c) Kaikoura study 2 (2001-2007), d) OSNZ records. The number of eggs laid are grouped into weekly intervals.

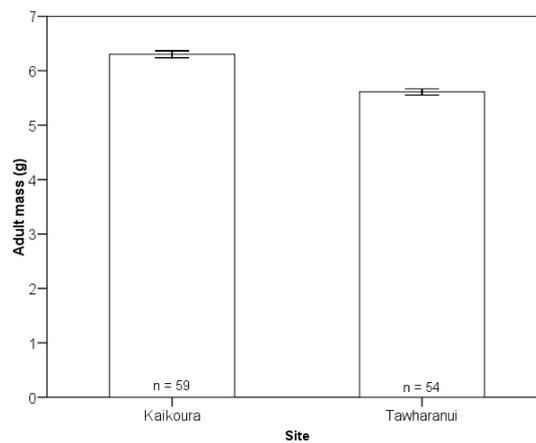
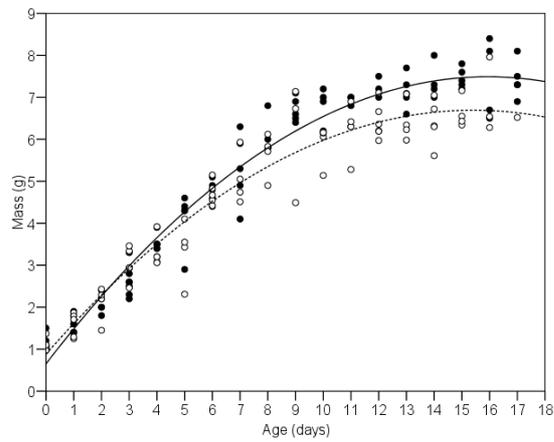


Figure 18: Differences in adult Grey Warbler mass between Kaikoura and Tawharanui. Adults were caught by mist netting birds from May to July at each site. Bars are means \pm standard error.

a)



b)

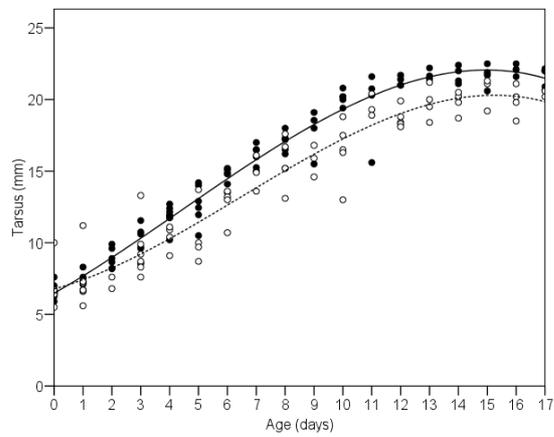


Figure 19: Growth rates of a) mass and b) tarsus of nestlings at Tawharanui (○) and Kaikoura (●). Lines of best fit are logistic curves for mass and a third degree polynomial fit for tarsus (see Methods for equations). Lines of best fit are denoted as solid lines for Kaikoura and dashed lines for Tawharanui data

6.6 Discussion

Our research shows that the Grey Warbler conforms to some of the well established latitudinal rules, but not others. The patterns of body size, for both adults and nestlings, as well as clutch size follow Bergmann's rule and Ashmole's hypothesis, respectively, in that body size and clutch size increases with latitude. In contrast, we found that both the timing of breeding and the number of clutches per season showed the opposite patterns of what was expected, with birds at higher latitudes breeding earlier, breeding longer and producing more clutches. This effectively means that birds at higher latitudes typically have two clutches of four eggs, whereas those at lower latitudes have a single clutch of three eggs.

Differences in clutch size were found at the main study sites regarding both the different decades of study (Kaikoura study 1 versus study 2) and the covariant of latitude (Kaikoura 1 versus Tawharanui). First, there are several explanations that have been put forward to explain variation in clutch size across latitudes; 1) a reproduction versus survival trade off (Lack, 1947, Moreau, 1944), 2) food availability (Lack, 1947), 3) thermal constraints (Cooper *et al.*, 2005), 4) predation (Martin *et al.*, 2000, Skutch, 1949) and 5) brood parasitism (Hauber, 2003). Of these, the reproductive versus survival trade-off could only apply if Grey Warblers at higher latitude had a substantially shorter lifespan, which is unlikely, as adult Grey Warblers at Kaikoura have a high annual survival rate (82%; (Gill, 1982a).

The food availability hypothesis is a more likely explanation, as Grey Warblers are insectivores (Gill, 1980a). Lower availability of resources can be manifested in the

breeding biology of insectivores through shorter breeding seasons, reduced egg and nestling mass (Zanette, 2000), or by reducing the number of clutches laid in a season (Nagy & Holmes, 2005). However, even though two of the main correlates of food availability (e.g. day length and seasonality) may explain the observed results for clutch size, they do not explain the differences in total reproductive output per season between sites. The only possibility is that there is an increase in both food resources and the duration that it is available, at higher latitudes in New Zealand. New Zealand lowlands are moderated by the nearby sea, climatically equable, lacking in marked seasonality and with vegetation that grows continuously or for protracted periods (e.g. Hurnard, 1978, Wardle, 1978). Intensive entomological trapping studies in the Orongorongo Valley (41°21'S, c. 140 m asl), near Wellington, found that although fewest invertebrates were caught in winter, many were active throughout the year (Moed & Meads, 1985). The pooled abundance of all invertebrates in forest litter samples was virtually uniform in all seasons (Brockie, 1992: p129). Flies emerged throughout the year from litter and dead wood, and some species of caterpillars were found in every month (Brockie, 1992: p141).

Gill (1982a) hypothesised a paradoxical food shortage to explain the slow breeding of grey warblers at Kaikoura, with their long breeding season and small clutches compared to songbirds of Northern Hemisphere temperate regions (see (Woinarski, 1985) for similar arguments for small Australian insectivores). He suggested that food is always available at Kaikoura, but that grey warbler populations are set close to the even year-round limit set by food, and extra food for breeding is hard to obtain. Perhaps this is not a general characteristic throughout New Zealand forests, and that at Tawaharanui peculiarities of the site or habitat produced a more seasonal spring flush of invertebrates

which dictated in the grey warblers a shorter breeding season than at Kaikoura. More work is needed on the seasonal availability of food for insectivorous birds in New Zealand forests.

Differing predation pressures between latitudes (Skutch's hypothesis) also does not explain the observed patterns, as an increase in predation pressure would predict an increase in the number of broods and an associated decrease in clutch size (Martin *et al.*, 2000). The third and more recent hypothesis of thermal constraints is also a possible explanation for the counterintuitive patterns of clutch size and number of broods, as it predicts that clutch size should increase with latitude, either due to the clutch cooling hypothesis (Reid *et al.*, 2000) or the egg viability hypothesis (Stoleson & Beissinger, 1999); for review see (Cooper *et al.*, 2005). Unfortunately, none of these explanations are completely suitable to explain the patterns of life history traits observed in the Grey Warbler.

There are very few other studies that have observed similar patterns of life-history traits across latitudes to those that we found in the Grey Warbler. König and Gwinner (1995) investigated the patterns in the timing and frequency of breeding in African and European stonechats (*Saxicola torquata*), a species that shows similar breeding patterns to the Grey Warbler in terms of how the number of clutches and clutch size vary with latitude. European stonechats can have two or three broods per season, with an average clutch size of five, meaning they may raise 15 young per year. In contrast, the East African subspecies of stonechats only raise one brood with a clutch size of three. Through captive experiments with the two subspecies, König and Gwinner (1995) were able to determine that these breeding patterns were not genetically determined. Instead,

it was more likely that wild African Stonechats experience poorer nutrition during the feeding season that inhibits a second clutch. Food availability during the breeding season may therefore be one of the better explanations for the observed patterns of life-history traits found in the Grey Warbler. Especially as birds at higher latitude not only can raise eight young in a season (as opposed to three), but their nestlings are also larger meaning that they require more food to raise them to fledging.

We also observed a decrease in clutch size within the Kaikoura site in the ~30 years between the two studies. This may potentially be associated with climate change that has occurred within New Zealand (Plummer *et al.*, 1999), as this phenomenon has been reported elsewhere for birds (e.g. (Sanz, 2003). Climate change may directly affect clutch size, or indirectly due to laying date becoming earlier, resulting in an increase in average clutch size, as earlier clutches have been shown to be larger in some species (Crick *et al.*, 1997, Dunn & Winkler, 1999, Winkler *et al.*, 2002).

These overall patterns of life-history traits also have implications for the Shining Cuckoo (*Chrysococcyx lucidus*), which is a migratory brood parasite, and uses the Grey Warbler as it's sole host species in New Zealand (Gill, 1982a, Gill, 1983b). The arrival patterns of the Shining Cuckoo has not been studied in depth, although Cunningham (1953, , 1955) collected records on the dates that they were first heard after arrival. The dates that Shining Cuckoos were first heard varied from late July to early December, but the majority of records peaked from mid-September to mid-October, indicating that this was the main arrival period. Gill (1982c) found that shining cuckoos laid eggs from mid-October to early January, and only the Grey Warbler's second clutch was parasitized at Kaikoura. At Tawharanui, none of the nests found during the three year

study were parasitized by Shining Cuckoos. Our findings that Grey Warblers in the North of New Zealand only have a single clutch suggest that many Shining Cuckoos may not arrive in time to parasitize this host's nests. Alternatively, Shining Cuckoos may only arrive in time to act as a nest predator during the later stages of breeding (Briskie, 2007). This lower rate of brood parasitism in the North of New Zealand may be one explanation for why northern birds have only a single clutch. Brood parasitism has been shown to affect both clutch size and the number of broods, with hosts in more heavily parasitized locations investing less in each brood by reducing clutch size (Hauber, 2003, Soler *et al.*, 2001). These lower parasitism rates in the Northern regions indicate there is less selective pressure to decrease clutch size due to loss from brood parasitism. As the opposite of this pattern occurs, it is likely that Grey Warbler clutch size is under stronger selection pressure from the latitudinal factors, but rather, it is the number of clutches that have been modified to mitigate the reproductive failure that occurs from higher rates of brood parasitism. Further research is required to disentangle any possible effects of parasitism rate on clutch size and the timing of breeding in Grey Warblers in New Zealand.

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7 Conclusions and future directions



7.1 Brood parasitism research

The idea of one species using another to raise their offspring, through brood parasitism, has fascinated naturalists since Aristotle (384-322 BC) (Davies, 2000). The phenomena has raised many questions and has been the subject of research since Jenner (1788) first described aspects of the breeding biology of the Common Cuckoo (*Cuculus canorus*), and later fascinated Charles Darwin in chapter 8 of *The Origin of Species* (Darwin, 1859). Since then there has been a large increase in the number of studies conducted on brood parasites, and it has become a model system for testing ideas such as coevolution (Hauber *et al.*, 2004, Langmore *et al.*, 2003), particularly the concept of an evolutionary arms race (Dawkins & Krebs, 1979), cognition (Moskát & Hauber, 2007) and communication (Hauber & Ramsey, 2003, Kilner *et al.*, 1999). Within this thesis, I have tested some of these ideas, which has as a consequence raised many other questions that can be used as future directions for research.

The idea of brood parasite hosts possessing the ability to discriminate amongst their own and foreign eggs has been well established in the literature (Lawes & Kirkman, 1996, Lyon, 2003, Davies *et al.*, 1996). Up until recently, it had been suggested that discrimination of nestlings was not possible (Lotem, 1993). It has since been shown, through either begging calls (Langmore *et al.*, 2003) or duration of care required (Anderson & Hauber, 2007, Grim, 2007), that the ability to discriminate foreign nestlings is feasible. Many questions about this system still remain: 1) what are the physiological mechanisms (i.e. hormonal changes) behind rejection of nestlings based on duration of care?; 2) is the rejection abilities of hosts under genetic control? If so, this would make these traits heritable and therefore, evolvable: a pivotal assumption of

coevolutionary theory. These findings also suggest that the rules of nestling discrimination are varied and quite different from those of egg discrimination (Lotem, 1993), thus inviting more research into the genetic, developmental, physiological and perceptual bases of host–parasite chick discrimination.

Discrimination based on degree of begging call similarity between hosts and parasites is another parasite nestling rejection mechanism that has been demonstrated (Langmore *et al.*, 2003). Despite this finding, few brood parasite studies, either at the egg and nestling stage, have examined the degree of similarity of the parasite to the host in relation to other available non-hosts. In chapter two (Anderson *et al.*, in press), the similarity in the begging call between a brood parasite and its host was tested in a system that had previously been suggested to be mimetic (McLean & Waas, 1987). We found that not only were the parasite and host more similar than expected by chance, but also, through the use of bioinformatic techniques, that it is possible to detect the process of coevolution that is occurring in this system. This is a new technique for brood parasite systems, and has the potential to be used elsewhere to test such ideas as the similarity threshold that is required before rejection occurs (Hauber *et al.*, 2006).

There is the potential for future studies to further investigate the begging call system of Grey Warblers and Shining Cuckoos in New Zealand. Cross-fostering experiments may elucidate the acceptance threshold of foreign nestlings by Grey Warblers based on begging call similarity. Also, it is still unknown to what degree Shining Cuckoo nestlings have a genetic component to their begging calls that has adapted through time, or if the begging call similarity is based more on learning within the nest environment, as has been demonstrated with the Horsfields bronze-cuckoo (*Chalcites basalis*) in

Australia (Langmore *et al.*, 2008). This study system offers the potential to test many more ideas about brood parasite coevolution and mimicry.

In chapter four, the idea that egg-eviction behaviour, used by many cuckoo species, could have a cost on nestling growth was tested. It was found that there was indeed a growth cost that was imposed on the nestling by such behaviour, although it was temporary and recoverable. The growth cost experienced by the nestling was primarily restricted to during and just after the eviction phase, suggesting that nestlings are able to compensate for this lost growth potential. It still remains to be tested how nestlings are able to perform this compensation. Comparing the begging call signals of evictor and experimentally induced non-evictor nestlings, may show if begging call signals are modified during this period to solicit increased provisioning by host parents. Previous research on nestling eviction behaviour, has generally considered such behaviour to be beneficial, as it is known that Common Cuckoos are poor competitors within the nest environment (Hauber & Moskát, 2008), unlike Brown-headed Cowbirds, that can benefit from sharing the nest with host offspring (Kilner *et al.*, 2004). By using a costs and benefits model within brood parasitic systems (Kilner, 2005), and in particular with such behaviours as eviction behaviour by brood parasitic nestlings, it is possible to understand the evolutionary hurdles that must be overcome before these behaviours can become adaptive.

7.2 Parent-offspring communication

Intrafamilial interactions within the nest environment have been used extensively to test several intraspecific communication ideas; 1) parent-offspring communication (Kilner

et al., 1999, Kedar *et al.*, 2000), 2) parent-offspring conflict (Kilner, 1999, Mathevon & Charrier, 2004), 3) sibling competition (Leonard *et al.*, 2000, Fujioka, 1985), 4) sexual conflict (Kilner, 1999), and 5) alarm signalling (Platzen & Magrath, 2004, Madden *et al.*, 2005a). These ideas have particular importance within the nest environment when brood parasite nestlings are in the nest, as they are unrelated to parents, and need to be able to cue into communication systems to respond appropriately to parental cues (Hauber, 2003, Madden & Davies, 2006, Madden *et al.*, 2005b).

In chapter three, I investigated the parent-offspring communication systems in Grey Warblers that are used by parents to influence nestling begging behaviour, ensuring that chicks beg at the right time. Previous studies have found that nestlings of some species only respond to either a parental feeding call or an alarm call, depending on the nest architecture (Madden *et al.*, 2005a, Madden *et al.*, 2005b). Few other species have been found to use both signals (Platzen & Magrath, 2004) and rarely has it been tested whether these cues are species-specific (Madden *et al.*, 2005a). These results are interesting, as they suggest that other species may use such parent-offspring communication signals, and there is potential for the assessment of such signals in multiple species, allowing for comparative studies to test why, when and what type of factors result in the evolution of such calls.

The honesty of begging call signals is an idea that is widely thought to be true, but requires testing before many assumptions about parent-offspring communication can be considered valid. In chapter five, I test the honesty of begging call signals in Grey Warbler nestlings. It was found that the begging call signal was complex, and instead of modulating begging call rate as has been found in many other species, it is the acoustic

structure that is altered to signal both age and hunger level of the nestling to parents. This observed temporal and condition-dependent modulation of the begging call structure is something that has rarely been described before (Leonard & Horn, 2006). As more similar studies are conducted, it may be possible to test what factors may lead to the evolution of different types and numbers of signalling modalities within the nest environment.

7.3 Conservation

“...a monstrous outrage perpetrated on maternal affection” – Gilbert White

The above quote by Gilbert White was used when describing the brood parasitic behaviour of cuckoos, and is so apt that Davies (2000) used it to title the first chapter of his frequently referenced book. This perspective is often heard when discussing brood parasitism amongst scientists, conservationists and the general public. Such anthropomorphism is concerning, as it may lead to the conservation of brood parasites being neglected. Some brood parasites are well known to have increased in range and population size through human induced habitat modification, such as the Brown-headed Cowbird (*Molothrus ater*), which has resulted in the brood parasite becoming the conservation threat to other species (Rothstein & Robinson, 1994). However, the population status of many cuckoo species and their hosts, are less well understood (Payne, 2005). In general, cuckoos are not considered threatened (Collar *et al.*, 1994), but the added problem of conserving both the brood parasite and its host adds an additional level of complexity.

The cuckoo species most at risk are those that inhabit forest habitat, particularly tropical forests, that are being cleared (Payne, 2005). Both of New Zealand's cuckoos are long distance migrants that inhabit tropical forests during their non-breeding season (Heather & Robertson, 2005). Both species are also host specialists, with the Shining Cuckoo only parasitizing the Grey Warbler, and the Long-tailed Cuckoo (*Urodynamis taitensis*) only parasitising the three Mohua species, the Yellowhead (*Mohua ochrocephala*), the Whitehead (*Mohua albicilla*) and the Brown Creeper (*Mohua novaeseelandiae*). Additionally, of the hosts of the Long-tailed Cuckoo, the Yellowhead populations (O'Donnell, 1996) are particularly under threat from introduced mammalian predators.

Future conservation research should consider the conservation status of both hosts and brood parasites in order to maintain a functioning evolutionary relationship between the two species. Previously established conservation techniques should be employed and modified for the conservation of brood parasites. One example of a well established technique that could be utilised is translocations (Wolf *et al.*, 1998, Armstrong & Craig, 1995, Armstrong & McLean, 1995). This could allow the creation of new cuckoo populations. As New Zealand cuckoos are migratory (Gill, 1983, Payne, 2005) and potentially philopatric (Gill, 1980), the best approach would be to harvest eggs or nestlings from parasitized nests and move them to the destination site prior to fledging, so they can be placed into a suitable host nest. Locating and monitoring of host nests, at both the source and release sites, would be critical in order to allow the translocation of cuckoos during the incubation or nestling period.

Chapter six highlighted the decline in brood parasitism through time at one site, and differences in brood parasitism rates in two disparate sites within the country.

Monitoring of brood parasitism rates through time has been conducted in other species to ensure population stability (Lindholm, 1999). Using this technique, combined with regular censuses (Robertson *et al.*, 2007), may help to monitor the population status of New Zealand cuckoos. These techniques could be applied to other brood parasite species that are thought to be at threat.

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8 Appendices

8.1 Chapter 1: Published Version

Update

TRENDS in Ecology and Evolution Vol.22 No.8

283

Species Act, the Arctic Wildlife Refuge and federally owned lands in North America with widespread corruption but a range of success stories in the Old-World tropics (e.g. four new national parks have been gazetted in Tanzania alone within the past four years)?

Conclusion

Clearly, there is much to discuss. The re-wilding concept invites conservation practitioners to revisit the ecological and evolutionary targets that they want to shoot at; it calls paleontologists to work with conservationists in understanding stasis and change in Pleistocene ecosystems; it challenges captive-breeding institutions to rethink the conventional wisdom of keeping exotic species in the confinement of standard zoos, now under renewed scrutiny [13]; and it asks conservation biologists to reopen debate on the nature of the historical, geographical, genetic and ecological differences between past (re)introductions of California condors *Gymnogyps californianus* to Big Sur, wolves *Canis lupus* to Yellowstone, peregrine falcons *Falco peregrinus* from many continents to North America, south American cougars *Puma concolor* to the Everglades, wild turkeys *Meleagris gallopavo* to California; Arabian oryx *Oryx leucoryx* to Arizona; and African cheetahs to Texas.

On the other side of the coin, uncertainty about so many Pleistocene re-wilding issues; the understandable difficulties that its proponents have in facing these criticisms head-on using data; and conventional conservation dogma, backed up by pest biology, that novel introductions are hazardous for both ecological communities and agribusiness all argue against Pleistocene re-wilding. There is an air of desperation in the Pleistocene re-wilding idea to which we are all sympathetic. Conservation biology has developed into a science of documenting population

declines, species losses and habitat destruction in excruciating detail but sadly doing little about it. Pleistocene re-wilding is a proactive idea that could galvanize the conservation community out of its helplessness and, for that alone, deserves merit.

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A recognition-free mechanism for reliable rejection of brood parasites

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Hosts often discard eggs of avian brood parasites, whereas parasitic chicks are typically accepted. This can be explained theoretically by fitness losses associated with adults learning to recognize parasitic young and mistakenly rejecting their own young. A new experimental study confirms that rejection of parasitic chicks, without relying on memory to discriminate between foreign and own young, is a feasible and potentially cost-free mechanism used by reed warblers to reject

common cuckoo chicks. By abandoning broods that are in the nest longer than is typical for their own young, parents can reliably reject parasite nestlings and reduce fitness losses owing to having to care for demanding parasitic young. Discrimination without recognition has important implications for the realized trajectories of host-parasite coevolutionary arms races.

Introduction

Social parasites exploit the foraging and breeding efforts of their hosts. Obligate brood parasitic birds, for instance, lay

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their eggs in the nests of other species and reduce the reproductive output of hosts that care for unrelated young. Despite fitness losses, hosts of some brood parasites, including *Molothrus* cowbirds, accept distinctive foreign eggs and chicks in their nest. By contrast, victims of *Clamator* and *Cuculus* cuckoos often reject parasitic eggs, despite the typically close visual match between foreign and host eggs [1]. The mimicry of host chick phenotypes is rare among the different avian brood parasite lineages [2], yet discrimination of parasite and host chicks by foster parents is even more infrequent [3,4]. How can foster parents in the few species where hosts do reject parasitic young, discriminate between their own and foreign chicks? In a recent experimental study, Grim [5] demonstrates that rejection of common cuckoo *Cuculus canorus* chicks by host reed warbler *Acrocephalus scirpaceus* parents is based on intrinsic differences in the duration of parental care required by broods of host versus parasite young.

Darwinian algorithms to reject parasites

The diversity of strategies by which avian brood parasites overcome host defences has offered one of the best opportunities for studying coevolution through observation and experimentation [1]. The cognitive processes used by hosts to defend against mimetic parasite eggs involve recognition through the assessment of the match between a learned template of own eggs and the phenotype of the potential parasite egg [6]. By contrast, theoretical models demonstrate that, even in the absence of costly neural structures associated with memory formation and storage, chick discrimination through learning might be maladaptive. This is because the cost of discrimination errors would be too high for both evicting and non-evicting cuckoo [7] and cowbird [8] chicks. Specifically, misimprinting on a parasitic young during the first nesting attempt by a host would lead to mistaken rejection of its own chicks in all subsequent broods.

In line with this theory, there are few reported examples of brood parasite discrimination at the nestling stage, although this might instead reflect less research effort in this area [9]. However, the experience of the hosts with raising young and, thus, learning about offspring, might not be required to identify parasites [4]. For example, just as memory might not be required to locate and benefit from caching seeds [10], the rejection of brood parasites might not require the recognition of foreign nestlings [3].

Nestling discrimination without recognition

Grim [5] illustrates how a custom-designed cross-fostering experiment can test between different proximate cues that are used by host parents. Initial observations revealed [3] that some common cuckoo chicks were abandoned during the advanced stages of the nestling period by reed warbler hosts. The recognition of nestlings based on phenotype alone (e.g. appearance or vocalizations) was unlikely as other experimental work already showed that reed warblers readily accept and feed heterospecific nestlings [11]. Three possible explanations for nestling rejection remained feasible: (i) the parental-fatigue hypothesis; (ii) the time-limit hypothesis; and (iii) the single-chick hypothesis (Box 1).

Box 1. Mechanisms of nestling rejection

For host parents to be able to reject brood parasite nestlings, some form of proximate cue is required to discriminate foreign chicks from their own nestlings. These can take the form of recognition-based (1) or recognition-free (2–4) mechanisms of discrimination.

1. Begging-call mimicry

Nestlings give begging calls when being fed by parents. These calls can vary between species and offer a cue that host parents can use to discriminate brood parasite nestlings. Brood parasites are able to counteradapt by mimicking the begging calls of their host [4]. Nestlings that do not show an acceptable level of vocal mimicry should be rejected near the age at which host chicks typically start to vocalize.

2. Parental-fatigue hypothesis

Parents might desert nestlings that require too much care to avoid excessive loss of future reproductive potential. This can occur if parasite nestlings require more food than does a brood of host nestlings. Parents might be physiologically unable to provide for the larger parasite nestling and so might either abandon when their exhaustion levels are too high or use the total amount of care required by young to discriminate between their own and foreign chicks. The desertion of parasite nestlings should occur once food provisioning levels are greater than the normal range observed for parents at unparasitized nest.

3. Time-limit hypothesis

Parasite nestlings fledge after a considerably longer period of time than do the offspring of their hosts, owing to the larger size of the parasites and the physiological constraints placed on their growth. Host parents can use this duration cue as a method to discriminate brood parasites from their own young [5]. Nestling rejection should therefore occur once the duration of parental care exceeds that required for host nestlings.

4. Single-chick hypothesis

Many brood parasite nestlings evict their nest mates, leaving a sole parasite chick for foster parents to feed. Brood loss could be used as a cue by parents to assess the risk for (partial) predation or to identify the nestling that they are feeding as a parasite. According to this scenario, broods with single nestlings should be disproportionately rejected. Nestling desertion should occur within the first few days of hatching, once a nestling is found to be alone in the nest after accounting for natural levels of hatching asynchrony.

Through a series of experiments, Grim and helpers created 'shortened' nests in which younger broods were swapped with older broods and 'prolonged' nests in which older broods were replaced with younger broods. Switching warbler chicks of different ages generated broods that received significantly extended or shortened parental care periods compared to what is typical for non-parasitized reed warbler broods (Figure 1). In addition, broods of four versus single warbler chicks were also generated, thereby creating variation in the overall amounts of care required for each brood within both shortened and prolonged treatments. Two types of nest served as controls: handling-only and cross-fostering of same age broods. The variations in the duration and the amount of parental care received then enabled the author to disentangle the three possible recognition-free mechanisms (Table 1).

The results on nest desertion rates were clear cut with regards to crucial predictions of the alternatives (Table 1). In support of the time-limit hypothesis, nest desertion only occurred in prolonged nests. A finding of similar rejection rates of single and four-chick broods was contrary to both



Figure 1. A typical brood of reed warbler chicks (depicted) demands much parental care. Broods of one or four reed warblers or a single common cuckoo chick that remain in the nest beyond the typical nestling period of the host, face abandonment by parents [3,5]. Reproduced with permission from T. Grim.

the parental fatigue hypothesis and the single-chick hypothesis. Furthermore, the single-chick hypothesis was also rejected because no desertions occurred in single-versus four-chick nests within either the shortened or the control treatments.

Desertions occurred in prolonged nests at a rate of 22% which closely reflected the observed desertion rate (15.8%) of nests naturally parasitized by cuckoos at the same study area [3]. This implies that similar proximate mechanisms for nest desertion might be utilized by natural and experimental foster parents. However, the average nestling age at which chicks died was lower for experimental broods with warbler chicks [5] than for sympatric, natural broods with cuckoo chicks [3].

Implications for host–parasite coevolutionary processes

Previous models of parasite rejection mechanisms led researchers to conclude that it would be maladaptive to learn to recognize nestlings for cuckoo hosts because of costly errors of accepting parasitic young and rejecting own young [7]. However, under this novel mechanism of discrimination without recognition, rejection errors are not made because nest abandonment occurs solely after the typical length of the host nestling period. In support of such a cost-free mechanism, Grim found no evidence at this research site for rejection errors where broods of reed warbler young were abandoned by parents [3,5]. Nonetheless, discrimination without recognition is not a strictly

cost-free rejection mechanism. This is because, in 78% of the cases, parents did fledge chicks from prolonged nests, thereby accepting the cost of longer parental care provided for experimentally ‘parasitized’ nests. Second, parents might not always reliably abandon parasitized broods in host species whose typical nestling period overlaps in duration with that of the nestling periods of the parasitic species [12].

Theoretical scenarios of coevolutionary arms races have also typically evoked escalating cycles between antiparasite defences by hosts and counteradaptations by parasites [1,4]. When foreign eggs are rejected because they look different, egg mimicry evolves [1]. In turn, when nestlings are rejected because their begging displays look or sound different, mimicry of begging behaviors evolve [4]. However, it appears that there is little defence against having a nestling period that is too long compared to that of the reed warbler, as common cuckoo chicks tend to have similar nestling periods regardless of host species size [13]. The absence of additional reduction in the duration of parasite nestling periods might represent the endpoint for any future coevolutionary process within this particular host–parasite system.

Alternatively, brood abandonment by reed warblers might represent a trait that evolved independently of cuckoo parasitism as a life-history tradeoff between current and future parental investment. If longer nestling periods are predictive of lower success of the current brood, owing to disease or weather-related slowing of growth, then parents might abandon current broods and attempt to breed later. Determining whether the abandonment by reed warblers of prolonged broods is a specific anti-parasite response will require conducting Grim’s experiments in genetically isolated populations of reed warblers that have never been exposed to brood parasitism, or in a series of a sister taxa of host and non-host species.

Recognition-free discrimination of brood parasites raises additional research questions and possibilities in coevolution and cognition. This mechanism not only shows that nestling discrimination is possible for evicting parasites raised alone, but also confirms that discrimination might not require prior learning or parental experience by hosts [4]. What then are the phenotypic and cognitive tricks used by single cuckoo chicks that cause naturally parasitized nests to be abandoned after a longer period of care than what is seen for experimentally prolonged broods of warbler chicks? And why did chicks in the shortened treatment consistently remain in the nest longer to receive more parental care than did control and prolonged host broods?

Table 1. Suggested mechanisms of brood abandonment in evicting brood parasites

Hypothesis	Age at abandonment*	Parasite mimicry expected	Reason for abandonment at given brood age
Recognition-based mechanism			
1. Begging call mimicry	4–5 days	Yes	Age when chicks begin to vocalize
Recognition-free mechanisms			
2. Parental fatigue	8 days	No	Age when the cumulative amount of provisioning by parent exceeds that required by brood of host
3. Time limit	12 days	No	Nestling period exceeds that of healthy host chicks
4. Single chick	1–3 days	No	Extent of maximum hatching asynchrony in host broods

*A hypothetical host with a nestling period of 11 days.

Differences in the duration of parental care across treatments might be due to differences in the proximate, solicitation stimuli given by nestlings. The endogenous cues used by host parents to determine the appropriate duration of nestling care are also unknown. If the duration of parental care is under hormonal control [14] in reed warblers, it might be pertinent to test for hormonal titer differences between chick rejecters and acceptors. Most importantly, the causes of sensory and endocrine differences when responding to prolonged parental care would also need to be explored because, to date, we lack direct evidence about the genetic control of parasite-rejection mechanisms in any avian hosts [15], even though heritability and, thus, evolvability, of rejection decisions are pivotal assumptions of coevolutionary theory.

Conclusion

Our knowledge of the evolutionary diversity and frequency of nestling discrimination abilities by host parents has increased considerably over recent years. New findings add to this knowledge and offer several additional lines of research into the cognitive and physiological basis of recognition systems. They also suggest that the rules of nestling discrimination are varied and quite different from those of egg discrimination [7], inviting more research into the genetic, developmental, physiological and perceptual bases of host-parasite chick discrimination. These results will, in turn, be incorporated into evolutionary models of host-parasite systems and shape our understanding of the complexity of the arising coevolutionary processes.

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Letters

Maximizing the efficiency of conservation

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We welcome Naidoo *et al.*'s recent review in TREE [1] highlighting the importance of measuring the costs of conservation directly, instead of relying on proxies, such as the area conserved. However, we are surprised that they advocate using biological proxies (e.g. the number of species conserved) to estimate the benefits of conservation, when calculating cost effectiveness. Similar to costs, the benefits of conservation, which include existence values, can be hard to measure, and we recognize that, by not directly considering benefits in the planning process, Naidoo *et al.* [1] reflect the prevailing tendency in conser-

vation [2]. Nevertheless, this approach concerns us for two reasons. First, we believe that measuring the benefits of conservation is no more difficult than collecting data on biological proxies, which could involve mapping the distributions of all species [3]. Second, irresolvable disagreement exists over the choice of which biological variables to maximize [3–5] and we are concerned that, in using these purely biological measures of conservation effectiveness, important value judgements are concealed.

Given that value is created by the interaction of humans with the environment, the benefits of conservation (similar to its costs) are anthropocentric. Although studies demonstrating the general importance of wild nature to humans abound [6], those examining the relationship between

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8.2 Chapter 2: Published Version

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Begging call matching between a specialist brood parasite and its host: a comparative approach to detect coevolution

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Studies of avian brood parasite systems have typically investigated the mimicry of host eggs by specialist parasites. Yet, several examples of similarity between host and parasite chick appearance or begging calls suggest that the escalation of host–parasite arms races may also lead to visual or vocal mimicry at the nestling stage. Despite this, there have been no large-scale comparative studies of begging calls to test whether the similarity of host and parasite is greater than predicted by chance or phylogenetic distance within a geographically distinct species assemblage. Using a survey of the begging calls of all native forest passerines in New Zealand, we show that the begging call of the host-specialist shining cuckoo (*Chrysococcyx lucidus*) is most similar to that of its grey warbler (*Gerygone igata*) host compared to any of the other species, and that this is unlikely to have occurred by chance. Randomization tests revealed that the incorporation of the shining cuckoo's begging calls into our species-set consistently reduced the phylogenetic signal within cluster trees based on begging call similarity. By contrast, the removal of the grey warbler calls did not reduce the phylogenetic signal in the begging call similarity trees. These two results support a scenario in which coevolution of begging calls has not taken place: the begging call of the host retains its phylogenetic signal, whereas that of the parasite has changed to match that of its host. © 2009 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2009, **, ***–**.

ADDITIONAL KEYWORDS: nestling rejection – recognition systems.

INTRODUCTION

Coevolution is a reciprocal process whereby an alteration in a trait of one species causes a change in a second species, leading to a further response in the first species (Janzen, 1980; Futuyma, 1998). In a linear form of coevolution, two species reciprocally evolve in response to each other in what has frequently been termed an evolutionary arms race (Dawkins & Krebs, 1979; Futuyma, 1998). The

relationship between avian hosts and their brood parasites offers some of the best examples of this type of coevolution (Rothstein & Robinson, 1998). A potentially useful way of detecting the coevolution is to apply a comparative method to detect deviation from the phylogenetic position of both host and parasite taxa with respect to their specific trait-sets. In the present study, we applied randomization tests to a comparative dataset for this aim.

Previous phylogenetic methods to explicitly test for host–parasite coevolution (Johnson, Drown & Clayton, 2001; Banks, Palma & Paterson, 2006) showed that speciation events of the parasite reflect

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bij_1256

2 M. G. ANDERSON *ET AL.*

those of the host, resulting in parallel phylogenies of host and parasite taxa (Paterson & Banks, 2001). However, these methods have typically tested host-parasite systems with only pairs of species of hosts and their respective species-specific parasites. We adapted this approach specifically to avian brood parasites where the parasite has multiple hosts available but only exploits one host species (Payne, 2005a). If traits of brood parasites are coevolving with traits in their host (Davies & Brooke, 1989; Davies, 2000; Langmore, Hunt & Kilner, 2003), then trait similarity trees of taxa that include actual and potential hosts, as well as their parasites, would indicate how similar parasites actually are to hosts. Grim (2005) suggested numerous alternative explanations to trait similarity that are not the result of coevolved mimicry (e.g. random matching, crypsis in the shared environment). Several of these can be tested by the use of phylogenetic methods, including: (1) phylogenetic constraints (i.e. being closely related); (2) random matching (i.e. similarity as a result of chance, not coevolution); and (3) nonrandom matching (i.e. as a result of similar selection pressures on both host and parasite).

In the present study, we tested for coevolution of begging call signals between a specialist native brood parasite, the shining cuckoo (*Chrysococcyx lucidus*) and its host the grey warbler (*Gerygone igata*) (Gill, 1983, 1998). Previous work suggests begging call mimicry in this system based on the pairwise acoustic similarity of host and parasite nestlings' (McLean & Waas, 1987). We specifically evaluated whether this is a result of a coevolutionary process; with begging call mimicry evolving in the parasite and begging call discrimination evolving in the host. In this scenario, the parasite would evolve a similar begging call to the host as a result of host rejection of vocally dissimilar nestlings (Langmore *et al.*, 2003; Grim, 2006). In response, the host would be expected to alter its begging call, increasing its ability to discriminate parasites. This process would repeat as a coevolutionary arms race, leading to the loss of any phylogenetic signal (i.e. tendency for closely-related species to resemble each other) in the begging calls of both host and parasite.

To test this coevolutionary scenario, we first generated a similarity tree of begging calls using cluster analysis methods with native passerines in New Zealand to quantify the acoustic distance between host and parasite. We then used this tree to evaluate the chance that these species would be the most closely-matching taxa based on randomization procedures. Second, we applied phylogenetic tree comparison techniques to evaluate the extent of the phylogenetic signal in the interspecific acoustic similarity patterns. Finally, we examined the effects that

the inclusion or exclusion of either the parasite or its host had on the phylogenetic signal in the acoustic similarity tree to evaluate whether coevolution occurred.

We predicted one of three outcomes: that the host and parasite similarity would (1) not be greater than predicted by chance, (2) have matching traits, but the host trait was not altered in response, and (3) have matching traits, which were both altered from their original evolutionary position through an arms race. In the first and second cases, no coevolution occurred, whereas the third scenario would suggest that coevolution occurred in the form of chase-away selection (Hauber & Kilner, 2007), where the trait deviated from what would be expected from phylogenetic history (Fisher, 1930; Gavrillets & Hastings, 1998; Servadio & Lande, 2003). This strategy would benefit the host because altering the structure of nestling begging call would potentially improve discrimination. Alternatively, under the second scenario, host parents respond by increasing their threshold of discrimination for begging calls, progressively selecting for similar sounding parasite nestlings. However, cases (2) and (3) are also consistent with the scenario that either host and parasite traits evolved in parallel owing to a shared ecological variable, such as mortality caused by acoustically oriented predators, during ontogeny (i.e. host and parasite chicks both grow up in host nests) (Grim, 2005), whereas case (2) is also consistent with the possibility that the evolutionary response of parasites involves learning to match host begging calls (Madden & Davies, 2006; Langmore *et al.*, 2008).

MATERIAL AND METHODS

BEGGING CALL RECORDINGS

Begging calls were recorded from nestlings of native New Zealand passerines, including all forest species that are found on the North and South Islands. In total, there are 20 such extant species in New Zealand, of which two were not sampled because they are only located on the Chatham Islands (black robin, *Petroica traverse*; Chatham Island warbler, *Gerygone albofrontata*) and we were not permitted to gain access to nestlings. We were also unable to record the remaining native New Zealand passerine (Fernbird, *Bowdleria punctata*) as a result of difficulty in locating nests. The other 17 species were recorded from locations throughout the country (see Supporting information, Table S1). The begging calls of three nonpasserine species were also used in the analysis: (1) the shining cuckoo, (2) orange-fronted parakeet (*Cyanoramphus malherbi*), and (3) the New Zealand kingfisher (*Halcyon sancta*). The shining cuckoo was

added to test the similarity of its begging call to its host, the grey warbler. It is widespread in New Zealand, and all the species recorded have the potential for sympatry (Robertson *et al.*, 2007), with the exception of the alpine rock wren. The two other species were used as opportunistic outgroups for the analysis.

Begging calls were recorded from broods under natural situations during parental feeding visits by setting up a microphone as close as possible to the nest without causing disturbance (usually 20–30 cm). The nest was subsequently observed from a distance (typically 10–15 m) to ensure that normal parental behaviours resumed. We controlled for nestling development by attempting to record nestlings on the day that primary feathers emerged from the sheaths (Briskie, Martin & Martin, 1999), as determined by either direct inspection or the age of nestlings. However, some instances required nestlings to be recorded opportunistically. If age could not be determined, nestlings from the mid to late stages of development that were responding vocally to parental nest visitations were recorded. Calls were then recorded for up to 90 min to ensure that several feeding bouts occurred. Nestling begging calls were recorded with a Sennheiser ME 66 microphone or a Panasonic RP-VC201 stereo tie-clip microphone, depending on nest accessibility, onto a Sony MZ-NH700 Hi-MD Minidisc, with a sampling rate of 44.1 kHz. Recordings were subsequently examined in RAVEN, version 1.3 (Charif, Clark & Fristrup, 2007). Sound recordings were digitized and visualized as spectrograms (Hann, window size 5.33 mS, 3-dB bandwidth of 270 Hz, frequency grid DFT size 256 samples and 188 Hz) for analysis.

For each species, attempts were made to record at least three nests, although this was not always possible (for sample sizes, see Supporting information, Table S1). Only one shining cuckoo nestling was recorded during the nestling stage, and so the begging calls of two fledglings were used. To ensure that the fledgling begging calls did not alter the results, cluster analysis was conducted separately for both nestling and fledgling stages. The overall tree topology was identical for both analyses, and this topology did not change when the two age groups were combined. Only begging calls given by nestlings when parents were at the nest were used, thus avoiding parent-absent vocalizations (Šicha, Procházka & Honza, 2007). From each nest, ten individual begging calls were used that did not overlap with begging calls of siblings.

Begging calls were analysed using Sound Analysis Pro (Tchernichovski *et al.*, 2000) and relevant sound parameters were measured for each begging call. These measures were: (1) mean frequency modula-

tion, (2) mean amplitude modulation, (3) mean entropy, (4) mean frequency, and (5) call duration (for explanations of parameters, see Supporting information, Table S2' and, for further definitions of measurements, see Tchernichovski *et al.*, 2000,).

PHYLOGENY OF NEW ZEALAND PASSERINES

An unweighted phylogeny of New Zealand passerines was compiled from the available molecular phylogenetic relationships (Keast, 1977; Sibley & Ahlquist, 1987; Barker *et al.*, 2004; Miller & Lambert, 2006; Driskell *et al.*, 2007). Where analyses of the species in question were unavailable, their position could generally be resolved by the position of higher taxonomic levels. The only unresolved group was for the family Pachycephalidae (genus *Mohoua*). The three endemic species of this genus, are considered to be closely related (Keast, 1977; Sibley & Ahlquist, 1987) and were thus put as a polytomy.

STATISTICAL ANALYSIS

Generation of phylogenetic species sets and begging call similarity trees

Phylogenetic trees of three sets of taxa were used in the analysis: (1) all 17 recorded New Zealand passerines, the shining cuckoo, and two nonpasserines as outgroups (20 species); (2) all recorded New Zealand passerines and the shining cuckoo (18 species); and (3) all recorded New Zealand oscines and the shining cuckoo (16 species). The final tree was added to reflect the possibility that the begging calls of New Zealand wrens (Acanthisittidae) may be anomalous amongst New Zealand's passerines because wrens are an ancient precocene passerine lineage (Barker, 2004).

Hierarchical cluster analyses were employed to reveal the structure of begging calls amongst New Zealand passerines using the five sound variables that were extracted from the begging calls. Cluster analyses at the species level were conducted in STATISTICA, version 6.0 (Statsoft, 2001) for the three sets of species (as above) using average linkage (unweighted pair-group average) as the fusion strategy and Euclidean distances as the distance metric (McGarigal, Cushman & Stafford, 2000). The dendrograms produced were used as the trees for randomization analyses of tree topology and phylogenetic signal.

Probability of parasite and host being sister taxa

The results of the begging call cluster analyses consistently found that the shining cuckoo and the grey warbler were a sister pair (see Results). To test the statistical probability of this occurring by chance, we conducted two randomization procedures using PAUP,

bij_1256

4 M. G. ANDERSON *ET AL.*

version 4 (Swofford, 2002). First, we estimated the probability of two designated taxa forming a sister pair on a randomized tree by creating trees of random topology, with a constant number of species, and calculating how frequently the species pair clustered together. We repeated the randomization procedure using 10 000 iterations because increasing the number of iterations by a factor of 10 had little effect on the results.

Second, we estimated the probability that the two designated taxa occur as a species pair on the observed topology by chance. This procedure used the existing tree created from the cluster analysis and randomization of the position of the species on the tree (10 000 iterations). Both of these randomization procedures were conducted on the nestling begging call tree for each of the three taxonomic groups.

Similarity between begging call and phylogenetic trees

To test the effect of phylogeny on the structure of begging calls of New Zealand passerines, the topologies of the phylogenetic trees were compared with the begging call trees using two tree-comparison metrics: (1) the symmetric difference or 'partition' metric and (2) agreement subtree metrics (largest common pruned trees) (Penny & Hendy, 1985; Goddard *et al.*, 1994) using PAUP, version 4 (Swofford, 2002). Both metrics have a value of zero when the topologies under comparison are identical.

For each metric, its sampling distribution under the null hypothesis that begging call similarity was random with respect to phylogeny was determined empirically. First, the topology of the acoustic similarity cluster diagram was randomized. Next, its similarity to the topology of the phylogeny was estimated using the two metrics. This procedure was repeated one million times to produce a frequency distribution of the topology comparison metric under the random hypothesis. Then, the observed similarity cluster diagram was compared with the phylogeny by computing the metric. The empirical probability of the observed value of the metric was estimated as the percentile of the corresponding value in the frequency distribution. If there is close agreement in the topologies of the two trees, the observed metric will fall at a low percentile of the null distribution. However, if the two trees have effectively random topologies with respect to one another, the observed metric will be expected to occur at a higher percentile.

These tree comparison metrics were calculated for the three different sets of trees. For each of the three species sets, the analysis was performed three times: (1) with the shining cuckoo present, (2) with the shining cuckoo absent, and (3) with both the shining cuckoo and grey warbler absent. Therefore, nine tree

comparison metrics were calculated. By comparing begging call similarity and phylogenetic trees without the shining cuckoo, we tested whether begging call similarity is the result of a shared evolutionary history or relatedness. This first test of a phylogenetic signal is useful because it was then used to test what effect the addition/removal of (1) the parasite (second analysis) and (2) the parasite and its host (third analysis) has on the phylogenetic signal. Any effect on the phylogenetic signal might be an indication of the evolutionary and/or coevolutionary processes that have occurred between parasite and host.

RESULTS

HOST-PARASITE BEGGING CALL SIMILARITY

The begging call of the shining cuckoo and the grey warbler consistently grouped together as sister taxa in the cluster analyses, in all three taxonomic data sets (Fig. 1). Both of the randomization tests indicated that the probability of this occurring by chance was in the range 2–5% (Table 1).

SIMILARITY BETWEEN BEGGING CALL AND PHYLOGENETIC TREES

The cluster analysis dendrograms of begging call similarity were compared with the phylogeny of the corresponding species to test whether begging call similarity results from evolutionary proximity or relatedness. We tested this by quantifying the similarity between trees when the shining cuckoo was included or excluded from the species set. We predicted that the presence of the shining cuckoo would reduce the phylogenetic signal of begging calls. The observed value of the symmetric difference metric fell between the 16th and 18th percentile of the distribution of this metric on randomized cluster diagrams (Table 2). There was little change in the signal by varying the number of taxa included in the phylogeny.

By contrast, when the agreement subtree metric was used (Table 2), the percentile at which the metric fell decreased as we increased the number of species

Table 1. Empirical probability that two designated taxa form a species pair on a tree of random topology, or when the leaves are randomized on the observed topology of begging call similarity

	Trees randomized	Species randomized
16 species	0.036	0.049
18 species	0.031	0.036
20 species	0.027	0.033

In each case, 10⁴ randomizations were performed.

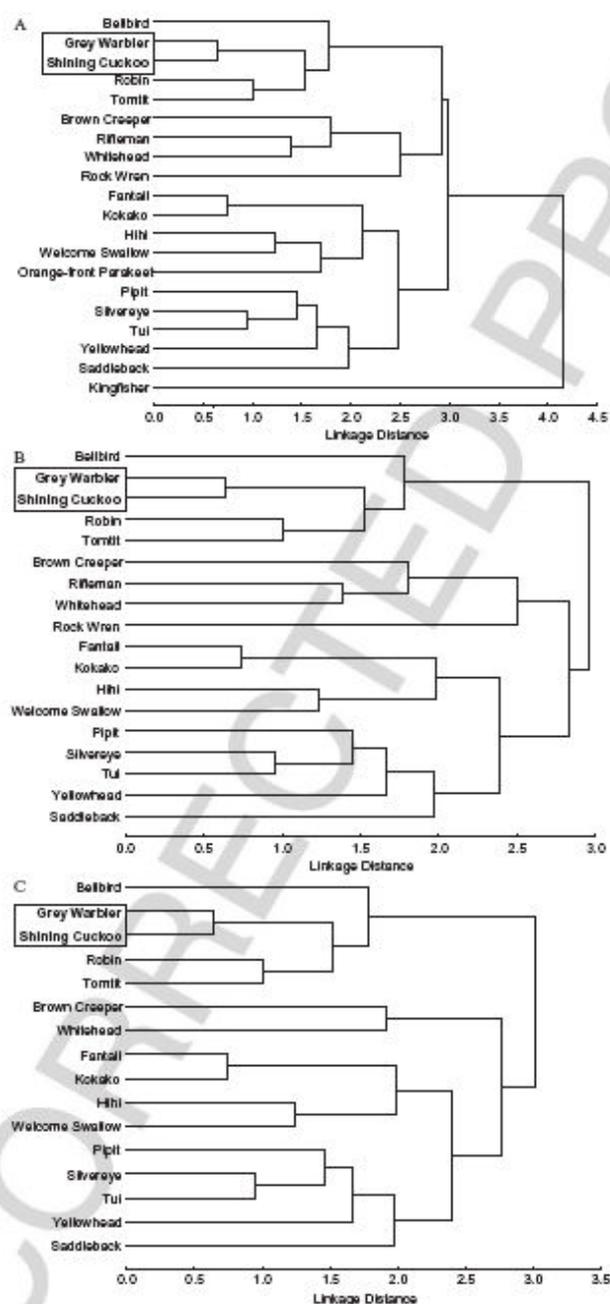


Figure 1. Dendrograms of begging call similarities created by cluster analysis based on acoustic features. Three species sets were used: all passerines and out groups (A), passerines (B), and oscines (C). The host and brood parasite species are shown in bold.

bij_1256

6 M. G. ANDERSON *ET AL.*

Table 2. The congruence of the topology of the call similarity cluster diagram with respect to phylogeny

Taxonomic group	Symmetric difference metric			Subtree agreement metric		
	With parasite	Without parasite	Without parasite or host	With parasite	Without parasite	Without parasite or host
New Zealand oscines	15.2%	16.4%	1.8%	78.7%	13.1%	7.5%
New Zealand passerines	16.1%	17.0%	18.1%	7.0%	4.1%	7.9%
New Zealand passerines and outgroups	16.7%	17.6%	18.5%	16.1%	1.1%	6.9%

The underlying null distribution of each metric was obtained by randomizing the topology of the cluster diagram and then comparing it with the known phylogeny. The 'randomness' of the observed cluster diagram is indicated by the percentile at which it fell on the null distribution. Low percentiles are indicative of nonrandomness. In each case, 10^6 randomizations were performed.

in the analysis (16 species, 13.1%; 18 species, 4.1%; 20 species 1.1%). This suggests that the agreement subtree metric was more sensitive to changes in tree topology and that the phylogenetic signal in begging call similarity was present; a feature that was enhanced with increased taxon sampling.

THE EFFECT OF PARASITE AND HOST ON THE PHYLOGENETIC SIGNAL OF THE BEGGING CALL SIMILARITY TREE

We tested how the strength of the phylogenetic signal in the begging call dendrogram was affected by both the host and the parasite by assessing the effect of their addition and removal from the tree comparisons. First, we asked whether the addition of the shining cuckoo makes the begging call similarity diagram more random-like by virtue of its placement. We detected no change in the percentiles at which the symmetric difference metric fell when we added the shining cuckoo (Table 2).

By contrast, for each case involving the agreement subtree metric, the presence of the shining cuckoo increased the percentiles at which the observed diagram fell sharply, indicating a more random cluster diagram topology and, thus, a less phylogenetic signal. Accordingly, the placement of the shining cuckoo was consistently different to that expected given its phylogenetic position (Fig. 1, Table 2).

Conversely, the presence/absence of the grey warbler, but not the shining cuckoo, had a minimal effect on the symmetric difference metric, but a more marked effect on the subtree agreement metric (Fig. 1, Table 2). Specifically, for the latter metric, in two of the three data sets, the inclusion of the grey warbler increased the phylogenetic signal in the begging call cluster diagram (Fig. 1, Table 2).

DISCUSSION

Several studies have invoked mimicry as the evolutionary explanation of the similarity between the begging call of nestling brood parasites and their hosts (Davies, Kilner & Noble, 1998; Langmore *et al.*, 2003; Langmore *et al.*, 2008). However, in studies of focal host-parasite taxa, it can remain unclear how similar the taxon-specific begging calls are with respect to a diverse suite of available or potential hosts. In the present study, we have shown that the begging calls of a specialist avian brood parasite and its host are more similar to each other compared to all other available hosts and that this level of similarity was unlikely to have occurred by chance.

Several previous studies demonstrated that avian acoustic signals, both songs and flight calls, can have phylogenetic signals (McCracken & Sheldon, 1997; Päckert *et al.*, 2003). Our tree comparison methods also showed that the acoustic structure of the begging calls of New Zealand forest birds retained a considerable phylogenetic signal. It is known that the frequencies of bird songs are influenced by habitat (Slabbekoorn & Smith, 2002; Seddon, 2005) and may change through time due to cultural evolution (Jenkins, 1978; MacDougall-Shackleton & MacDougall-Shackleton, 2001). The retention of a phylogenetic signal requires that the ecological conditions that are necessary for the behaviour to occur remain constant through phylogenetic history (Paterson, Wallis & Gray, 1995). Begging calls may be a useful trait in this respect because they are less influenced by sexual selection or cultural evolution compared to adult vocalizations. Nevertheless, begging calls are also extensively shaped by ecological factors, including predation (Haskell, 1994; Briskie *et al.*, 1999), relatedness (Briskie, Naugler & Leech, 1994; Boncoraglio

& Saino, 2008), and learning by nestlings (Madden & Davies, 2006; Langmore *et al.*, 2008).

The use of comparative methods in the study of avian host–parasite coevolution has been limited. For example, most studies of egg mimicry have typically compared parasite egg appearance directly with host egg appearance in a species-pair design (Davies & Brooke, 1989; Soler, Aviles, Soler *et al.*, 2003; Langmore *et al.*, 2005; Starling *et al.*, 2006; Cherry, Bennett & Moskat, 2007). In addition, Soler & Moller (1996) and Hauber (2003) used comparative analyses on the egg appearances and clutch sizes, respectively, of potential or actual hosts to test for the effects of evolutionary history with an egg-mimic cuckoo, *Cuculus canorus* and the generalist brown-headed cowbird, *Molothrus ater*. Payne (2005b) used a comparative framework to test the possibility of coevolution between *Vidua* parasites and their hosts by looking at nestling mouth markings and coloration compared with that in the old world finches (Krüger & Davies, 2002; Mermoz & Ornelas, 2004; Hauber & Kilner, 2007) used comparative methods to detect interspecific brood parasitism, specific life history, and morphological adaptations within parasite lineages of cuckoos and cowbirds. However, none of these prior analyses used quantitative comparative methods to evaluate the phylogenetic signals of host traits with respect to the evolutionary history of parasitism. Our comparative approach shows how similar host traits actually are to parasites, which is important for invoking mimicry as an explanation for similarity (Grim, 2005).

An ideal context to use this technique in future studies would be one where the brood parasite is known to be mimetic, in the trait that is being tested, of several host species. One example is egg mimicry in the European cuckoo or the pallid cuckoo, where distinct gentes are known (Davies, 2000; Gibbs *et al.*, 2000; Starling *et al.*, 2006). Each gens should match its own host in the mimetic trait more closely than the match by other gentes, or any of the other available hosts (Langmore *et al.*, 2005). Alternatively, the coevolving trait in the host may not be the begging call itself but the ability to recognize and discriminate between their own and foreign begging calls (Hauber & Sherman, 2001). Finally, the shining cuckoo uses other host species in Australia (Payne, 2005a), and may have evolved strategies to evade the host defences of Australian species, whereas the grey warbler may lack such host defences. Further comparative research into the begging call of the shining cuckoo in both Australia and New Zealand should help to elucidate the degree of similarity and explanations for the presence or absence of coevolution with different host species.

The present study has shown that an avian brood parasite is more similar to its host species than any of the other available hosts. Using a comparative method combined with randomization techniques, we have shown that coevolution with respect to reciprocal changes in the begging call is not present within this brood parasite system. Instead, the parasite has closely matched the begging call of its host, but the host has not altered its begging call in response, a pattern suggesting a process of sequential evolution. It also remains possible that coevolution has occurred in the host perceptual system of call recognition rather than in the host begging call. However, it remains unclear whether the matching of host calls by the parasite is an evolved inflexible display or if it is the cuckoo's ability that has evolved to learn and match the most effective begging signal to solicit parental care from foster parents (i.e. by matching host begging calls; Langmore *et al.*, 2008). Future studies of mimicry should consider how closely matched avian brood parasites actually are to their hosts, by comparing brood parasites with more species than just the host and another nonhost. This may contribute to our knowledge of the threshold that is required for parasite rejection to occur in the host (Reeve, 1989) and the perceptual mechanisms used for host selection by the parasite (Cherry, Bennett & Moskat, 2007).

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bij_1256

8 M. G. ANDERSON ET AL.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1. Phylogeny of the 20 New Zealand species used in comparative analysis of begging calls.

Figure S2. Example spectrograms of the begging calls of (A) shining cuckoo and three New Zealand passerine species: grey warbler (B), bellbird (C), and whitehead (D).

Table S1. Locations and samples sizes for the begging call recordings made for each species.

Table S2. Example spectrograms of the begging calls of (A) shining cuckoo and three New Zealand passerine species: grey warbler (B), bellbird (C), and whitehead (D).

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