An Investigation on the Ecological Significance of the Terrestrial Context in Predator-Prey Interactions between Echolocating Bats and the Australian Field Cricket (*Teleogryllus* spp.)

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Abstract
The Australian field cricket has been a model system for addressing the behavioural and acoustic interaction between echolocating bats and their insect prey. This understanding is based largely on inferences from aerial encounters. However, there is much evidence for terrestrial associations, wherein models of interaction between predator and prey do not apply. Moreover, the ecological significance of the ground environment likely plays an important extrinsic role in shaping the animals' behaviours, especially for the prey's (unknown) response. In Australia, *Teleogryllus* crickets occur widely and in sympathy with a number of bats well-suited for terrestrial foraging. This dissertation aimed to investigate the interactions between Australian bats and crickets, with an emphasis on elucidating how the terrestrial setting has shaped their association.

I describe one example of setting in the field where interactions between a range of bats and crickets (*Teleogryllus commodus*) may be occurring in close proximity and over successive years. From the perspectives of crickets on the ground, I aimed to evaluate what the acoustic environment might be like for these individuals as echolocating bats forage overhead. Extrapolations on the estimated audibility of echolocation calls from two bats (*Scotorepens greyii* and *Nyctophilus gouldi*) that were detected directly above, indicates they are probably inaudible to the grounded males at this site. The estimated distance at which sounds might be heard suggests potentially greater distances for detection of *S. greyii*, but the gleaner *N. gouldi* is probably inaudible unless very close.

Investigations in the laboratory targeted confirmation or otherwise that bat-avoidance behaviour (negative phonotaxis) in *T. commodus* is context-dependent, and whether this is the case in both sexes. Freely-moving male and female crickets were exposed to echolocation calls from bats representing a range of possible risks, and signals design to simulate proximity of a bat. To address the relevance of the terrestrial setting in this paradigm, I then examined how shelter use is affected by bat cues. Walking crickets do not demonstrate any avoidance behaviour in response to bat echolocation, irrespective of the species or call repetition rate presented. This was consistent between the sexes, and agrees with past conclusions that ultrasound sensitivity is context-dependent (behaviourally) in *Teleogryllus* crickets. Only female crickets show recognition of and preference for sheltered (versus open) space, but their movement to shelter indicates it may represent a passive source of defence. However, these females delay moving to shelter when this preferred environment is compromised by the simulated presence of a
bat. This change in behaviour indicates crickets are recognising a threat and are staying away.

Finally, I bring together predator and prey under controlled conditions to examine their interactions within a terrestrial context. Using wild caught, naïve *Nyctophilus* bats, I aimed to characterise their behaviour and (to some extent) acoustic repertoire during foraging for grounded female *T. commodus*. In turn, these live interactions also aimed to further characterise the prey’s response in the presence of the real, dynamic predator.

These experiments established that *N. gouldi* and *N. bifax* are very capable, agile and precise in preying on these large, hard-bodied insects, readily using surface capture techniques (gleaning/perch hunting). Their foraging was independent of prey type (moths and crickets), suggesting this hunting strategy is utilised to exploit available food in a context- rather than prey-dependent manner. Passive localisation was consistently evidenced, based on measurements of last detected emission prior to contact with attacked insects. However, the duration of this silent period was highly variable so their acoustic repertoire may be quite dynamic. The inactivity of *T. commodus* during live interactions with bats potentially reflects generalised avoidance strategy; remaining immobile to minimise detection. Active responses were however, elicited upon direct attack from a bat; crickets consistently performed a rapid, powerful startle response. This escape behaviour therefore constitutes the late-stage, emergency response to bat predation, and one that would be sufficient and highly effective for evasion of bat attacks in the cluttered setting of the terrestrial environment.

These findings support that context is an important factor for influencing the terrestrial interactions between *T. commodus* and echolocating bats. The environment poses limitations for both animals in their capacity to detect and respond to one another. Whilst bats may be well-adapted for such encounters, in close engagements the terrestrial setting may play to the benefit of the prey.
Declaration by author

This thesis is composed of my original work, and contains no material previously published or written by another person except where due reference has been made in the text. I have clearly stated the contribution by others to jointly-authored works that I have included in my thesis.

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**Publications during candidature**

Conference Abstracts:

2012

Oral Presentation (3 Minute Thesis – People’s Choice Winner)
The School of Biomedical Sciences International Postgraduate Symposium
Three Evils of Meeting a Bat on the Ground: See No, Hear No, Do...?

Poster Presentation
The 15th Australasian Bat Society Symposium
Encounters of the terrestrial kind: Long range detection of aerial hawks by ground dwelling field crickets (*Teleogryllus commodus*) is possible, but requires close proximity to a gleaning predator.

Poster Presentation
The 15th Australasian Bat Society Symposium
Bat evasion by the field cricket *Teleogryllus commodus*, is context and environment dependent: cover elicits passive avoidance behaviour in walking crickets.

2008

Oral Presentation
The Royal Zoological Society of NSW and Australasian Bat Society Symposium on the Biology and Conservation of Australasian Bats
The predator-prey relationship between field crickets (*Teleogryllus* spp.) and echolocating bats in Australia

2006

Oral Presentation
Australian and New Zealand Entomological Societies Conference
The sensory ecology of predator-prey interactions: echolocating bats versus field crickets

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Moggill Creek Catchment Group Brisbane, Spring 2009
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Contributions by others to the thesis

Invaluable expertise was provided by some people, which contributes significantly to this dissertation.

Many acoustic aspects of experimental design, testing, analysis and interpretation would not have been possible without the assistance and expert advice of Dr Roger Coles. In particular, Dr Coles contributed significantly in the recording of echolocating bats in the field, and subsequent identification by acoustic analysis (Chapter 2), and in set-up and calibration of acoustic equipment for laboratory investigations on crickets (Chapter 4).

Critical statistical contribution came from Dr Simon Blomberg for the analysis and interpretation of cricket behaviour in Chapter 4 (Open Space Experiments). The description of these statistics in the Methods and Results sections were originally written by Dr Blomberg (but subsequently modified to suit this dissertation), in preparation for submission of the Chapter as a paper to Behavioral Ecology (rejected and currently under revision).

A final review and corrections were carried out through the proofreading services of Carl J Smith (Just Proofreading).

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Statement of parts of the thesis submitted to qualify for the award of another degree

None
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*Teleogryllus commodus*, *Nyctophilus*, echolocation, behavioural, passive listening, passive localisation, avoidance, escape, shelter, cover, ground, terrestrial context

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ANZSRC code: 060801, Animal Behaviour, 25%
ANZSRC code: 060304, Ethology and Sociobiology, 15%

Fields of Research (FoR) Classification

FoR code: 0602, Ecology, 80%
FoR code: 0608, Zoology, 20%
# Table of Contents

Title Page .............................. ii  
Abstract .......................................................... ii  
Declaration by Author ........................................ iv  
Publications During Candidature ................................. v  
Publications included in this thesis ............................. vi  
Contributions by Others ....................................... vi  
Acknowledgements ............................................. vii  
Keywords ....................................................... ix  
ANZSRC and FoR Classifications ............................... ix  
Table of Contents ............................................. x  
List of Figures and Tables ..................................... xiv  
List of Abbreviations .......................................... xvi

## Chapter 1:
Acoustic and Behavioural Correlates of Terrestrial Interactions between Echolocating Bats and Field Crickets

1.1 Introduction ................................................. 2  
1.2 The Terrestrial Predator....................................... 2  
1.2.1 Direct Evidence for Cricket Predation ............... 2  
1.2.2 Behavioural Adaptations ................................ 7  
1.2.3 Acoustic Adaptations .................................... 9  
1.2.4 Opportunities with Aerial Hawkers Near the Ground 11  
1.2.5 Candidate Bat Species for Study ..................... 12  
1.3 Implications of Context for Prey Defence ............... 12  
1.3.1 Auditory Processing of Ultrasound .................. 13  
1.3.2 Limitations to Detection and Avoidance Behaviour 16  
1.3.3 The Environment as Passive Defence .............. 18  
1.4 Research Aims and Key Considerations .................. 19  
1.5 References .................................................. 20

## Chapter 2:
General Methodologies and the Context of Association

2.1 Introduction ................................................ 28  
2.2 Field Work Methodologies ................................ 29  
2.2.1 The Field Study Site .................................... 29  
2.2.2 Assessing Distribution and Diversity of Prey and Predator 31  

Crickets ..................................................... 31  
Bats ......................................................... 34  
2.3 Resident Taxa and their Overlap .......................... 37  
2.3.1 Overview of Field Seasons ............................. 37  
2.3.2 Summary of *Teleogryllus* Population at Enoggera State Reserve 39  
2.3.3 Summary of Bat Population at Enoggera State Reserve 43  
2.4 Focal Species and their Context of Association ......... 51  
2.5 References .................................................. 55
Chapter 3:
Estimation of the Audibility of Echolocation Calls for *Teleogryllus commodus* on the Ground

3.1 Introduction ........................................................................................................ 59
3.2 Methods ................................................................................................................ 62
  3.2.1 Field Recordings of Bat Echolocation Foraging Sequences .......................... 62
  3.2.2 Calibrations to Determine Relative Peak Equivalent Intensity of
       Echolocation Calls .................................................................................................. 63
  3.2.3 Extrapolation of Threshold Sound Pressure Levels for Field
       Crickets .................................................................................................................. 64
  3.2.4 Data Transformation to Account for Sound Attenuation ............................. 65
  3.2.5 Data Analysis .................................................................................................. 67
3.3 Results .................................................................................................................... 69
  3.3.1 Within-Species Differences Across Call Phase ............................................. 70
  3.3.2 Between-Species Differences Across Call Phase ......................................... 70
  3.3.3 Audibility of Bat Emissions – Call Phase and Signal Intensity at
       the Ground .............................................................................................................. 74
  3.3.4 Audibility of Bat Emissions – Distances Required for Detection ............... 77
3.4 Discussion ............................................................................................................. 80
  3.4.1 Implications of Estimated Audibility on Cricket Detection Ranges .......... 80
3.5 References ............................................................................................................ 85

Chapter 4:
Responses of Walking *Teleogryllus commodus* to Bat Echolocation:
Differences Between the Sexes and the Relevance of Shelter

4.1 Introduction .......................................................................................................... 90
4.2 Methods ................................................................................................................ 94
  4.2.1 Animals ......................................................................................................... 94
  4.2.2 Experimental Set up .................................................................................... 94
  4.2.3 Acoustic Stimuli ........................................................................................... 95
  4.2.4 Open Space Experiments: Effect of Call Design between
       Sexes ..................................................................................................................... 98
  4.2.5 Cover Experiments: Significance of Shelter in Response to
       Echolocation ......................................................................................................... 99
  4.2.6 Data Analysis ................................................................................................. 100
4.3 Results ................................................................................................................... 102
  4.3.1 Open Space Experiments ............................................................................. 102
  4.3.2 Cover Experiments ....................................................................................... 104
    *Male and Female Shelter Seeking Behaviour* .................................................. 104
4.4 Discussion ............................................................................................................. 107
  4.4.1 Absence of Cricket Response to Echolocation in Open
       Terrestrial Settings ............................................................................................... 107
  4.4.2 Shelter Elicits Changes in Behaviour in the Presence of
       Ultrasound ........................................................................................................... 109
Chapter 5: Live Interactions Between Naïve Nyctophilus Bats and Teleogryllus commodus

5.1 Introduction .................................................................................................................. 120
5.2 Methods ........................................................................................................................ 123
  5.2.1 Study Site ................................................................................................................. 123
  5.2.2 Animals .................................................................................................................... 123
  5.2.3 Experimental Setup ............................................................................................... 125
  5.2.4 Interactions Between Bats and Insects ................................................................. 126
  5.2.5 Data Analysis ......................................................................................................... 126
5.3 Results ............................................................................................................................. 129
  5.3.1 General Acoustic and Behavioural Activity across Prey Conditions .................. 129
  5.3.2 Echolocation Patterns During Prey Capture ......................................................... 131
  5.3.3 Behavioural Patterns During Prey Capture ......................................................... 136
    Capture Success ............................................................................................................. 137
    Capture Precision ........................................................................................................ 138
    Restriction, Manipulation and Consumption of Captured Insect Prey ..................... 139
    Incidental Behaviours Exhibited by Nyctophilus ......................................................... 140
  5.3.3 Observations on the Responses of Insect Prey ..................................................... 140
5.4 Discussion ....................................................................................................................... 142
  5.4.1 Acoustic Strategies of Terrestrial Predation by Nyctophilus ................................. 142
  5.4.2 Foraging Behaviour during Terrestrial Predation by Nyctophilus ....................... 145
  5.4.3 Significance of Cricket Emergency Response to Bat Attacks ............................. 148
5.5 References ....................................................................................................................... 152

Chapter 6: General Discussion

6.1 Background and Study Findings ................................................................................. 159
6.2 Implications, Limitations and Future Directions ....................................................... 160
6.3. References .................................................................................................................... 166

Appendices:

Appendix 1 Bat species diversity at Enoggera State Reserve, as determined through echolocation call profiles (where available) and trapping 171

Appendix 2 Calibration response plot of mean sound pressure level (dB SPL re20μPa) measured for a 40 kHz reference signal recorded over distance (1 – 20 m). 178

Appendix 3 Descriptive statistics of call parameters recorded from little broad-nosed bats, S. greyii, in April 2007. 179
| Appendix 4 | Descriptive statistics of call parameters recorded from Gould’s long-eared bat, *N. gouldi*, in April 2007. | 180 |
| Appendix 5 | Example observation record from focal sampling used in Chapter 5 for characterisation of behaviours (type and frequency) exhibited by wild caught *Nyctophilus* bats during interactions with field crickets, in an arena. | 181 |
| Appendix 6 | Descriptive statistics of scored behaviours exhibited by *Nyctophilus bifax* (n = 2) and *Nyctophilus gouldi* (n = 3) during live interaction trials with live and intact crickets, deaf crickets, dead crickets and moths. | 185 |
| Appendix 7 | Extracts from a video sequence illustrating typical attack and capture by *Nyctophilus* bats of *Teleogryllus commodus*. | 186 |
| Appendix 8 | Extracts from a video sequence illustrating typical attack and capture by *Nyctophilus* bats of moths (perched on arena wall in this example). | 189 |
## List of Figures

### Chapter 1.

| Figure 1.1 | Neural processing of auditory information in the cricket (Gryllidae). | 14 |
| Figure 1.2 | Neural audiogram of peak hearing sensitivity in crickets. | 15 |

### Chapter 2.

| Figure 2.1 | Location of South D’aguilar National Park and field study site. | 30 |
| Figure 2.2 | Overview of the south-east wall of Gold Creek Reservoir, site of resident *Teleogryllus* cricket colony. | 32 |
| Figure 2.3 | Sites of acoustic and harp trap surveys across Enoggera State Reserve. | 34 |
| Figure 2.4 | Monthly climactic data during active field work months. | 38 |
| Figure 2.5 | Population structure of field cricket colony. | 40 |
| Figure 2.6 | Comparative cricket specimen for species identification. | 41 |
| Figure 2.7 | Comparison of song structure from male *Teleogryllus* crickets. | 42 |
| Figure 2.8 | Bat species diversity at Enoggera State Reserve including characteristic call profiles for taxa acoustically detected. | 45 |

### Chapter 3.

| Figure 3.1 | Audiogram of the Australian field cricket (*Teleogryllus oceanicus*). | 64 |
| Figure 3.2 | Example echolocation call pattern recorded from *Scotorepens greyii*. | 67 |
| Figure 3.3 | Echolocation call parameter analysis in Cool Edit Pro | 68 |
| Figure 3.4 | Representative search phase pulse patterns and frequency spectra from *Scotorepens greyii* and *Nyctophilus gouldi*. | 93 |
| Figure 3.5 | Comparison of echolocation call parameters between *Scotorepens greyii* and *Nyctophilus gouldi* in search, approach and terminal buzz phase emissions. | 72 |
| Figure 3.6 | Estimated sound intensity (dB peSPL) at the ground for calls from the little broad-nosed bat (*S. greyii*) during foraging compared to minimum hearing threshold in *T. oceanicus*. | 75 |
| Figure 3.7 | Estimated sound intensity (dB peSPL) at the ground for calls from the Gould’s long-eared bat (*S. greyii*) during foraging | 76 |
compared to minimum hearing threshold in *T. oceanicus*.

**Figure 3.8** Proximity (distance closer to bat, m) required for estimated call amplitude from an echolocating bat to activate AN2 in *T. oceanicus* crickets (*d₀*), at different auditory sensitivity thresholds.

**Chapter 4.**

**Figure 4.1** Pulse patterns and frequency spectra of echolocation calls presented during playback trials to grounded, freely moving male and female *Telegryllus commodus*.

**Figure 4.2** Mean ± SEM time taken by female (*n* = 10) and male (*n* = 8) crickets to move to cover following two experiences in the testing arena with cover.

**Figure 4.3** Mean ± SEM time taken by female crickets to move to cover in silence (-Bat Call, *n* = 10) and in the presence of echolocation calls (+Bat Call, *n* = 7), following two experiences in the testing arena with cover.

**Chapter 5.**

**Figure 5.1** Exemplary frequency of echolocation behaviour recorded from *Nyctophilus* bats during interactions with insect prey.

**Figure 5.2** Proportional frequency of behaviours exhibited by naïve, wild *Nyctophilus* bats (*n* = 5) during interactions with crickets (live, deafened and dead *T. commodus*) and wild caught moths.

**Figure 5.3** Mean ± SEM duration (sec) of flight bouts exhibited by naïve, wild *Nyctophilus* bats (*n* = 5) during interactions in an arena with insect prey.

**Figure 5.4** Example echolocation repertoire during one capture sequence from naïve *Nyctophilus* bats (*N. gouldi* in this case) during interactions with insect prey.

**Figure 5.5** Spectrogram of echolocation behavioural sequence depicted in Figure 5.4, for the period just prior to attack up to capture and take-off flight to wall. Time between last detected emission and capture in this example was 3 seconds.

**Figure 5.6** Spectrogram of *Nyctophilus* echolocation behaviour during captures of *Telegryllus commodus* crickets, depicting examples of short duration of time for last detected emission prior to contact, for *N. gouldi* and *N. bifax*.

**Figure 5.7** Capture Success Rate for naïve, wild *Nyctophilus* bats offered live crickets, deaf crickets and moths, as a product of first time attacks and subsequent attacks following missed attempts.
List of Tables

Chapter 1.
Table 1.1 Composition of orthopteran insect prey in the diets of echolocating insectivorous bats from Australia. 4
Table 1.2 Bat assemblage at Enoggera State Reserve. 7

Chapter 2.
Table 2.1 Bat fauna composition at Enoggera State Reserve determined from acoustic surveys and harp trap catches. 44

Chapter 4.
Table 4.1 Spectral and temporal characteristics of stimuli broadcast to male and female T. commodus in open field experiments. 97
Table 4.2 Mean response probabilities of field crickets (T. commodus) compared for stimulus type (controls and bat species). 102
Table 4.3 Mean response probabilities of field crickets (T. commodus) compared for echolocation pulse repetition rate (in pulses per second). 102

Chapter 5.
Table 5.1 Median and range (minimum and maximum) time (seconds) between last detected echolocation emission and point of first contact with prey by naïve Nyctophilus bats during their live interactions. 132
Table 5.2 Total capture events from the number of prey available to Nyctophilus bats across all prey condition trials, and the position of captured insects at time of Attack and Capture. 137

List of Abbreviations

AN1 Auditory Interneuron 1
AN2 Auditory Interneuron 2
ON1 Omega Interneuron 1
spp. species (plural)
Chapter 1

Acoustic and Behavioural Correlates of Terrestrial Interactions between Echolocating Bats and Field Crickets.
1.1. Introduction

Adaptation of the sense of hearing is key for survival in terms of predator-prey interactions between echolocating bats and insects. For bats, spatial orientation, prey detection and localisation are achieved by auditory processing of the echoes returning from their ultrasound emissions (Schnitzler et al., 2003). Many of their prey, nocturnal insects, are highly specialised to detect and encode these cues, enabling them to avoid capture (Neuweiler 1983; Ratcliffe et al., 2005). The past 50 years of research provides an extensive characterisation of the sensori-motor responses of insects to the dynamic acoustic properties of bat emissions (for reviews, see Neuweiler 1990; Hoy 1992; Michelsen 1998; Miller and Surlykke 2001; Stumpner and von Helversen 2001; Hennig et al., 2004; Mason and Faure 2004) and the evolutionary implications of these interactions on the prey (Fenton and Fullard 1979; Fullard 1984; Belwood and Morris 1987; Ratcliffe et al., 2005; ter Hofstede and Fullard 2008; ter Hofstede et al., 2009). This large body of work has focused predominantly on aerial encounters; yet, there is significant evidence of context-dependent associations between bats and insects (Miller and Surlykke 2001; Schnitzler et al., 2003). The relevance of the terrestrial setting shaping the acoustic and behavioural responses of predator and prey is however, an under-developed area of the research field. In Australia, the extent of research effort is particularly lacking. This country offers a valuable opportunity for such investigations, given the presence of one of the key insect models (Teleogryllus crickets) and a diversity of bat species suited for foraging in terrestrial settings that are widely distributed in sympatry with these insects. For the purposes of this dissertation, the terrestrial setting incorporates cases where insect prey are walking, grounded, or substrate bound.

1.2 The Terrestrial Predator

1.2.1 Direct Evidence for Cricket Predation

There is a relatively large body of research on the diet and foraging behaviour of Australian bat species (Vestjens and Hall 1977; Fenton 1982; Tidemann et al., 1985; O'Neill and Taylor 1986; Jones and Rayner 1991; Churchill 1994; Pavey and Burwell 2004; Churchill 2008). However, investigations of the interactions between bats and
insects are quite limited, and especially so in the terrestrial context (Woodside and Long 1984; Grant 1991; Cronin and Sanderson 1994; Hosken et al., 1994; Bailey and Haythornthwaite 1998). Globally, there is an established body of research substantiating and describing the correlates of terrestrial encounters between bats and crickets (Bogdanowicz et al., 1999; Miller and Surlykke 2001; Schnitzler et al., 2003; Surlykke and Kalko 2008; ter Hofstede et al., 2009; Whitaker and Karatas 2009; Holderied et al., 2011; Jones 2013). Therefore, this work uses knowledge from other continents as a base for extending understanding of Australian bat and cricket species.

In Table 1.1 dietary evidence from Australian bats is collated, illustrating some evidence for predation on crickets and similar Orthoptera by a range of endemic species. Many of these insects are anatomically similarity, being relatively hard-bodied, and in some cases, large sized (Otte and Alexander 1983). This imposes morphological constraints to which bats can feed on crickets, including factors like body size (for handling and over-powering prey), jaw mechanics and gape size (Freeman 1981; Norberg and Rayner 1987; Freeman 1992; Ober and Hayes 2008), but does not exclude them from feeding on other (e.g. small, soft-bodied) prey. It is not surprising therefore, that predation on crickets (and Orthoptera) is not extensively evidenced in Table 1.1, if other insects are also available and in greater abundance (Müller et al., 2012). Where relatively large values are cited (e.g. % volume of Orthoptera for *N. geoffroyi* and *T. kapalgensis*), some preferential feeding on crickets may be indicative but is limited to just a few animals sampled (see sample sizes in Table 1.1).

Field work for this dissertation was carried out at one site in South East Queensland. The bats that may be relevant in the terrestrial lives of field crickets here are therefore dictated by sympatric species at this location. There are evidently 20 species of bats local to the study site (Hall 2013), and these are identified in Table 1.2. Of these, dietary evidence in Table 1.1 supports predation on crickets and cricket-like prey in eight species. Only some however, will be directly relevant for terrestrial encounters since the cluttered space here would require particular specialisations in the bats’ foraging repertoire (Denzinger and Schnitzler 2013).
Table 1.1. Composition of orthopteran insect prey in the diets of echolocating insectivorous bats from Australia. Depending on the literature source, prey identification is provided at the family level (Gryllidae (crickets), Acrididae (locusts and grasshoppers) and Tettigoniidae (bush crickets)) or collectively for the order Orthoptera. Nomenclature of bat species is written as cited in the original reference source with current taxonomic synonyms provided beneath tables for those bats species that have undergone re-classification, based on Churchill (2008). Key to abbreviations:

Methods

Source of sample – **fa**, faecal analysis; **pr**, prey remains collected from feeding perch or roost site; **sc**, stomach contents.
Quantitative analysis – #, absolute incidence; %f, percentage frequency; %o, percentage occurrence; %v, percentage volume.
Sample sizes

n = number of pellets (for **fa**); number of pieces of prey (for **pr**); or, number of animals (for **sc**).

n, n indicates samples taken over multiple seasons; n/n indicates sample sizes corresponding to two different methods carried out by Milne (2006) and quantified as the overall mean %v from the two sampling procedures.

✓ = source cites presence of prey items or direct observation of feeding activity, but no data given.

Where evidence is unquantified, data are not provided.

<table>
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<td>Family, Species</td>
<td>Methods</td>
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<td>Source</td>
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<tr>
<td>Emballonuridae</td>
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<td>10</td>
<td>✓</td>
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<td>8</td>
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<td>sc, %v</td>
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<td>11.9</td>
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<td></td>
<td></td>
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<td>Pavey et al., 2004</td>
</tr>
</tbody>
</table>

Current nomenclature of indicated species:
* Rhinolophus robertsi ** Rhinonicteris aurantia; †Scotorepens balstoni; ††Austronomous australis
Table 1.2. Bat assemblage at the field study site, Enoggera State Reserve, South East Queensland, Australia, as evident from published records (Hall 2013). Nomenclature based on Churchill (2008).

<table>
<thead>
<tr>
<th>Genus, Species</th>
<th>Common Name</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Rhinolophidae</strong></td>
<td></td>
</tr>
<tr>
<td><em>Rhinolophus megaphyllus</em></td>
<td>Eastern horseshoe bat</td>
</tr>
<tr>
<td><strong>Vespertilionidae</strong></td>
<td></td>
</tr>
<tr>
<td><em>Chalinolobus gouldii</em></td>
<td>Gould's wattled bat</td>
</tr>
<tr>
<td><em>Chalinolobus morio</em></td>
<td>Chocolate wattled bat</td>
</tr>
<tr>
<td><em>Chalinolobus nigrogriseus</em></td>
<td>Hoary wattled bat</td>
</tr>
<tr>
<td><em>Nyctophilus bifax</em></td>
<td>Eastern long-eared bat</td>
</tr>
<tr>
<td><em>Nyctophilus geoffroyi</em></td>
<td>Lesser long-eared bat</td>
</tr>
<tr>
<td><em>Nyctophilus gouldi</em></td>
<td>Gould's long-eared bat</td>
</tr>
<tr>
<td><em>Phoniscus papuensis</em></td>
<td>Golden-tipped bat</td>
</tr>
<tr>
<td><em>Scotanax rueppellii</em></td>
<td>Greater broad-nosed bat</td>
</tr>
<tr>
<td><em>Scotorepens greyii</em></td>
<td>Little broad-nosed bat</td>
</tr>
<tr>
<td><em>Scotorepens orion</em></td>
<td>Eastern broad-nosed bat</td>
</tr>
<tr>
<td><em>Vespadelus pumilis</em></td>
<td>Eastern forest bat</td>
</tr>
<tr>
<td><em>Vespadelusroughtoni</em></td>
<td>Eastern cave bat</td>
</tr>
<tr>
<td><em>Myotis macropus</em></td>
<td>Large-footed myotis</td>
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<td><strong>Miniopteridae</strong></td>
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<tr>
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<td>Little bentwing bat</td>
</tr>
<tr>
<td><em>Miniopterus orianae oceanensis</em></td>
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<td><strong>Mollosidae</strong></td>
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<td><em>Mormopterus beccarri</em></td>
<td>Beccarri's freetail bat</td>
</tr>
<tr>
<td><em>Mormopterus ridei</em></td>
<td>Eastern freetail bat</td>
</tr>
<tr>
<td><em>Austronomus australis</em></td>
<td>White-striped freetail bat</td>
</tr>
<tr>
<td><strong>Emballonuridae</strong></td>
<td></td>
</tr>
<tr>
<td><em>Saccolaimus flaviventris</em></td>
<td>Yellow-bellied sheathtail bat</td>
</tr>
</tbody>
</table>

### 1.2.2 Behavioural Adaptations

The foraging guild that bats are associated with (e.g. aerial hawking or gleaning) are derived from: (1) wing morphological indices (aspect ratio, loading, span and tip shape); (2) flight performance in terms of manoeuvrability (angle of turn) and agility (rate of turn); and, (3) the vegetation strata within which particular behaviours are
possible (for reviews, see Norberg and Rayner 1987; Arita and Fenton 1997). Classification of foraging guilds is variable throughout the literature. For the purposes of this dissertation, the description of foraging guilds drawn from the substantial research conducted by Bullen and McKenzie (2001, 2004) is most appropriate because they describe Australian species, and take into account an extensive range of factors to characterise variable foraging strategies and niches. For example, this system recognises that preferential hunting in open space does not necessarily reflect incapacity to glean. The criteria of Bullen and McKenzie (2001, 2004) are also consistent with the most recent revision of the system by Denzinger and Schnitzler (2013). Given this dissertation is an Australian study this classification system thus has the closest relevance to the focal bat species.

The foraging classification described by Bullen and McKenzie (2001, 2004) recognises five groups: Interceptor (I), Air-superiority (A), Ambusher-surface (P), 3D-surface (3D-S), and Horizontal-surface (H). Bats within these groups also exhibit diverse foraging capacity across multiple niches. These are defined by the relative amount of open space and vegetation: open space that is unobstructed in all directions (OC); above canopy that is unobstructed above and beside (AC); edge or contour tracking with partial clutter below and on at least one side (BS/O); flying through gaps within canopy clutter (BS/A); and dense vegetation with clutter all around (IS). The terrestrial context of predation on crickets will likely include ground cover within forest (BS/A and IS) or open grassland (AC or BS/O); or crickets taken from substrate (IS) or whilst approaching the ground (BS/O or BS/A). Irrespective of whether crickets are attacked on surfaces or as females approach the terrestrial environment (Otte and Alexander 1983), the common limitation to capture in terrestrial or near-terrestrial contexts is the level of strata and how clutter obstructs bat flight and acoustics (Denzinger and Schnitzler 2013).

The three surface guilds of bats ascribed by Bullen and McKenzie (Ambusher, 3D and Horizontal; 2001, 2004) describe species that forage by taking prey from substrates (ground and vegetation). Firstly, because there is typically dense vegetation (clutter) below the canopy level or on the ground, bat flight is typically slow and fluttery with high manoeuvrability (Fenton 1982; Taylor et al., 1987; Fullard et al., 1991; Jones and Rayner 1991; Cronin and Sanderson 1994; Brigham et al., 1997; Churchill 2008).
Secondly, capture of substrate-bound prey by a bat requires the ability to land on the ground, then lift off from a horizontal surface (Bullen and McKenzie 2001). Lastly, if the bats remain in the air for final, precise localisation of the prey prior to a directed attack, they will need to be highly manoeuvrable and potentially with the capacity to hover (Faure and Barclay 1994; Churchill 2008; Geipel et al., 2013). All of the surface guild species in Table 1.2 that have been shown to feed on crickets and Orthoptera (*R. megaphyllus, H. diadema, N. geoffroyi*) have these attributes (Pavey and Burwell 2004; Churchill 2008). For some others (*N. bifax* and *N. gouldi*) dietary evidence for predation on crickets is entirely absent, but these species are described to glean and forage within cluttered environments (Fenton 1982; Lumsden and Bennett 2005). If ground foraging is a well-established strategy in these bats, such techniques should be readily displayed during controlled trials (Grant 1991; Cronin and Sanderson 1994).

All of these bats are also capable of aerial feeding across a matrix of habitats, reflecting a group of predators with high foraging plasticity (Lee et al., 2012).

**1.2.3 Acoustic Adaptations**

The acoustic repertoire of echolocation emissions across bat species are shaped by the habitats within which they hunt (Neuweiler 1983; Schnitzler and Kalko 2001; Schnitzler et al., 2003; Boonman and Schnitzler 2005). For bats exploiting prey within terrestrial settings, echoic information is greatly impacted upon by the physical obstructions within this context (clutter). The emissions of clutter zone specialists are typically characterised by short-duration, low-intensity, broad-band signals (Fullard et al., 1991; Denzinger and Schnitzler 2013). Such calls improve the ability to distinguish and locate target prey at close-range, and against the background clutter of dense vegetation to some extent (Ostwald et al., 1988; Moss and Zagaeski 1994; Moss and Schnitzler 1995; Schnitzler and Kalko 2001; Moss and Sinha 2003). Hipposiderid and rhinolophid bats exhibit an extension of this generalised acoustic classification for clutter, using constant frequency emissions to differentiate between flutter echoes arising from insect wing beats and the constant background vegetation structure (Schnitzler et al., 2003). Australian long-eared bats (see local species in Table 1.2) are described to be especially ‘soft’ callers (Pennay et al., 2004; Kutt et al., 2008) although characterisation of the intensity of source emissions for this genus is absent throughout literature. In other comparable bat species, source emissions range between 80 – 110 dB Sound Pressure Level (SPL) during gleaning (Miller and Treat
In addition to acoustic diversification, many terrestrial specialists exhibit the capacity to passively listen for prey-generated sounds (Fiedler 1979; Tidemann et al., 1985; Guppy and Coles 1988; Fuzessery et al., 1993; Fuzessery 1997; Bailey and Haythornthwaite 1998; Schmidt et al., 2000; Swift and Racey 2002). In addition to the use of soft calls, these strategies ultimately circumvent the capacity for many of their insect prey, to acoustically detect the bats (Miller and Surlykke 2001). Most notable are the European Plecotus auritus (Coles et al., 1989; Obrist et al., 1993), the North American Antrozous pallidus (Bell 1982; Fuzessery et al., 1993), Paleotropical Megadermatids Megaderma lyra and Cardioderma cor (Fiedler 1979; Obrist et al., 1993; Hubner and Wiegrebe 2003), and in Australia, some Nyctophillus species and Macroderma gigas (Tidemann et al., 1985; Grant 1991; Cronin and Sanderson 1994; Hosken et al., 1994; Bailey and Haythornthwaite 1998). Not surprisingly, hearing sensitivity is very well developed in these bats including high to extreme thresholds in the Australian N. gouldi (Guppy and Coles 1988), which is ideal for the detection of an insect moving on a substrate, at least under laboratory conditions (Grant 1991; Goerlitz et al., 2008).

Substantial work on A. pallidus demonstrates that concurrent processing of both echoic and prey-generated cues are possible (Razak and Fuzessery 2002; Razak et al., 2007) through auditory neural organisation that is exquisitely selective for behaviourally relevant sounds. Within a cluttered habitat, this allows the bats to maintain echolocation to avoid obstacles at the same time as detecting prey through the sounds of their movements. It is unknown if other gleaners possess such extreme segregation of auditory inputs. For Australian bats, there exists no such characterisation for R. megaphyllus, and under laboratory conditions Nyctophilus were reported to glean in absence of echolocation altogether (Grant 1991; Cronin and Sanderson 1994) but these bats were apparently spatially acclimatised to an open space without obstructions. Other species demonstrate a reduction in intensity, but not absence, during approach (Russo et al., 2007), or a silent period immediately before
capture (Faure and Barclay 1994; Arlettaz et al., 2001) where proximity to the prey probably alleviates the need for echoic navigation. The dynamic manner in which acoustic strategies are concurrently used by all of these bats highlights the acoustic flexibility of this guild. Whilst it is beyond the scope of this dissertation to determine the functional purpose of echoic and non-echoic strategies in the focal animals, the use of naïve individuals (untrained and held for a minimal amount of time; Geipel et al., 2013) may further elucidate their acoustic strategies during substrate foraging tasks.

1.2.4 Opportunities with Aerial Hawkers Near the Ground

Although aerial and terrestrial contexts are traditionally treated separately in ecological investigations (Lima and Dill 1990), it is important to consider the overlap between contexts and the likelihood of opportunistic predation. For example, *Austronomous australis*, which appears to inhabit the field study site (Table 1.2), is considered an Interceptor and Air-superiority bat of fast and direct flight (Norberg and Rayner 1987), catching and consuming volant insects (moths and small beetles) on the wing (O’Neill and Taylor 1989; Krutzsch and Crichton 1990; Churchill 2008). In addition, dietary evidence demonstrates that *A. australis* preys on Orthoptera (see Table 1.1) but importantly, this particular bat species has been described in pursuit of crickets along the ground (Bullen and McKenzie 2001). Thus, when considering the categorisation of predators based on the majority of their behaviours, it is important to recognise the flexibility that bats may possess within their defined niche, to exploit opportunistic feeding events. Furthermore, the arbitrary divide between aerial and terrestrial context dissolves when considering the case of aerial foragers following flying female crickets to the ground (Fenton 1982; O’Neill and Taylor 1986) or females being attacked close to the ground when coming in to land (Otte and Alexander 1983; Evans 1988). Clearly, aerial foraging species at the field study site that regularly overlap with established cricket populations, have the potential to exert some degree of predation pressure. Given the morphological requirements for feeding on large, hard-bodied prey (crickets) along with the species for whom dietary evidence exists, the (typically) aerial foraging species in Table 1.2 that might reflect potential candidates for predation on crickets include: *Scoteanax rueppelli*, *Chalinolobus* spp., *Scotorepens* spp., *Mormopterus* spp. and *Saccolaimus flaviventris* (Churchill 2008).
1.2.5 Candidate Bat Species for Study

The use of short-duration, low-intensity, broad-band acoustic signals, combined with passive listening strategies and exceptional manoeuvrability enables particular guilds of bats to hunt in acoustically cluttered environments, and minimise their detection by the prey. Such surface guild foragers which are evidently local to the field study site (Table 1.2) and for whom dietary evidence is substantiating, include *R. megaphyllus* and *N. geoffroyi*. In addition, other members of long-eared bats (*N. gouldi* and *N. bifax*) may also be exerting significant predation pressure on crickets, given their described foraging habits and sensitivity to prey-generated sounds. These bats are therefore strong candidates for study as relevant predators of field crickets within a terrestrial context of interaction. Secondary candidates will be primarily dependent on their overlap with crickets by proximity and frequency, but would include aerial hawkers for whom dietary evidence shows predation on crickets (Table 1.1) and other sizeable species that may be capable (e.g. *S. rueppelli*) and in the case of *A. australis*, have been anecdotally observed foraging on crickets. This project aimed to determine their presence, examine implications of how they overlap spatially with any crickets identified, and characterise interactions between predator and prey.

1.3. Implications of Context for Prey Defence

Insects that are able to detect ultrasound, demonstrate a variable suite of behaviours in response to echolocation cues. Documented response include changes in calling pattern or complete song cessation by males (Belwood and Morris, 1987; Hosken et al., 1994; Bailey and Haythornthwaite, 1998; Farris et al., 1998), performing complex movements during flight that involve multiple motor control pathways (Moiseff et al., 1978; May et al., 1988; Miles et al., 1992; Forrest et al., 1995) and freezing (Libersat and Hoy 1991). Some insect orders such as lacewings, display relatively simple escape behaviour in response to bat ultrasound by ceasing flight and plummeting to the ground (Miller 1970). Crickets, katydids and grasshoppers show more complex evasive behaviours displaying obvious directional changes in flight path or walking track (Moiseff et al., 1978; Yager and May 1990). A directed response away from a source of ultrasound is termed negative phonotaxis, and is indicative of evasive
behaviour. During aerial pursuit, this is well-documented in crickets (Moiseff et al., 1978) and katydids (Faure and Hoy 2000b). In contrast, grounded crickets do not demonstrate the behavioural responses seen in the air despite the apparent neural activation that would lead to such behaviour (Nolen and Hoy 1984; Staudacher and Schildberger 1998; Pollack and Martins 2007; ter Hofstede et al., 2009).

1.3.1 Auditory Processing of Ultrasound

Crickets rely on the integration of key acoustic information from bat emissions (frequency, pulse repetition rate and duration, and signal intensity; Nolen and Hoy 1986b; Fullard et al., 2005; Marsat and Pollack 2012) for their identification and subsequent assessment of associated predation risk. The general pathway for sensory-motor processing of sound by insects involves the activation of auditory receptors in the ear, neural transmission to local and ascending interneurons in the thorax, central integration in the brain, and subsequent motor output (Hoy 1992; Fullard and Yack 1993). In Figure 1.1 the neural network in crickets, which is responsible for ultrasound detection and subsequent directed response, is illustrated.

Sound is detected through two pairs of tympana positioned on the anterior and posterior surface of the cricket forelegs (Figure 1.1a). These ‘ears’ comprise 60-70 chordotonal sensilla arranged tonotopically, such that distal structures encode high frequency sound and proximal structures respond to low frequencies (Yack 2004). Primary afferents from the tympana terminate in the ventral Intermediate Tract (vIT) of the prothoracic ganglion, feeding information to local (ON1) and ascending (AN1 and AN2) interneurons (Hedwig 2006; and see Figure 1b).

The most basic correlate of predator detection by crickets is peak hearing sensitivity: sound frequencies that induce a directed behaviour. Across the insect orders, peak sensitivity for evasive responses ranges from 20 – 70 kHz, not surprisingly, across the main energy of most bat echolocation calls (Schnitzler and Kalko 2001). Figure 1.2 illustrates the neural tuning curve of the *T. oceanicus* auditory system.

It is important to note at this point that *T. oceanicus* (the northern congener in Australia) has been the model system for research on the neurobiology of ultrasound responsiveness in *Teleogryllus* crickets. However, the focal species of this dissertation is *T. commodus*, as this was the verified taxon local to the field study site. Nolen and
Figure 1.1. Neural processing of auditory information in the cricket (Gryllidae). Initial detection occurs via the tympana in (a) from which auditory afferents (Tympanal Nerve) carry encoded information to the prothoracic region of the cricket. In the presence of ultrasound (b), summed excitation-inhibition input from auditory afferents and local ON1 interneurons is carried to the brain via the contralateral AN2 interneuron, and leads to negative phonotaxis from activation of contralateral muscles by descending neural pathways (DNs and TNs). Abbreviations explained in text. Image in (a) sourced from Matthias Lenke (http://www.flickr.com/photos/matthias_lenke/6955927373/); cricket in (b) from Moiseff et al., (1978).
Hoy (1986a) examined the behavioural and sensory responses of *T. commodus* and *T. oceanicus*, demonstrating key similarities between these two cricket species in phonotactic behaviour and behavioural thresholds. To date, there have been no further published reports on the neuroethology of *T. commodus*, and it was not possible to generate audiograms for the focal cricket species, *T. commodus*, during this dissertation. All bats examined in this dissertation are sympatric with both *T. commodus* and *T. oceanicus* (Churchill 2008; Atlas of Living Australia 2015) although it is unknown altogether how extensively any bat interacts with either cricket. As the two cricket species are likely to exhibit some neurophysiological differences in ultrasound sensitivity, all extrapolations for *T. commodus* made from experimental data from *T. oceanicus*, are stated explicitly throughout the dissertation, and the limitations this places on the inferences that can be drawn are discussed where relevant.

Directed steering in crickets is achieved via summation of inputs from the excitatory auditory afferents (AA in Figure 1.1b) and inhibitory local ON1 interneurons onto the ascending fibres (in the case of ultrasound, AN2). Auditory afferents provide encoding
for spectral and temporal patterning (frequency, pulse/inter-pulse duration) while the inhibitory inputs from ONs enable processing of signal direction inhibitory inputs from ONs enable processing of signal direction (Hedwig 2006). Thus, the summed input onto AN2 enables the cricket auditory system to forward information about the identity of the signal and its directional source, which is then integrated centrally in the brain for relative assessment of predation risk. At the same time, input from muscles activated during flight, converge with auditory circuits in the brain. The ultimate (negative) steering response is a product of descending interneurons activating contralateral cell bodies in the anterior Ring Tract (aRT; Atkins and Pollack 1987), which then signal neural input to flight muscles in the mesothorax on the side furthest from the sound source. Importantly, this response only occurs when there is mutual excitatory input from ascending auditory and flight motor pathways (Nolen and Hoy 1986a).

1.3.2 Limitations to Detection and Avoidance Behaviour

Within a terrestrial context, this acoustic-mediated evasion behaviour by crickets is absent (Pollack et al., 1984; Fullard et al., 2005; ter Hofstede et al., 2009). To a large degree, this is attributed to a break in the neural circuitry for ultrasound detection and induced behaviour when insects are not flying (Nolen and Hoy 1984; Staudacher and Schildberger 1998; Pollack and Martins 2007). There are currently two main hypotheses in the literature to explain why a context-dependent switch in avoidance behaviour might have evolved. One hypothesis suggests that the risk of crickets being captured by echolocating bats on the ground is so minimal that it poses no evolutionarily consistent threat (Hoy 1992; Pollack and Martins 2007; ter Hofstede et al., 2009), and thus there has been little impetus for the development of active evasive mechanisms. Alternatively, grounded crickets are evading bats by an altogether different paradigm that is not (exclusively) acoustically based; passive defence through environmental crypsis (Hedrick and Kortet 2006; ter Hofstede et al., 2009).

To date, the strategies used by crickets to avoid bats in a terrestrial setting have been difficult to characterise. Whilst male song cessation is repeatedly documented in crickets and tettigoniids (Bailey and Haythornthwaite 1998; Faure and Hoy 2000b; ter Hofstede and Fullard 2008), locomotory displays are not well-defined in walking, silent individuals. Most researchers report inconsistent behaviours and/or non-responsive
individuals (Fullard et al., 2005; ter Hofstede et al., 2009), despite behaviourally relevant neural activation indicative of predator detection (Nolen and Hoy 1986a, b; Yager and May 1990; Hoy 1992; Faure and Hoy 2000a; Schul and Schulze 2001; Pollack and Martins 2007). The purpose for ultrasound sensitivity in crickets in a terrestrial context has therefore been difficult to define.

During flight, pulse repetition rate and signal intensity provide a cricket with information about the proximity of a bat relative to their own position (Hennig et al., 2004). An increase in pulse rate as a bat approaches can trigger early-stage, evasive responses and often well before the bat can detect its prey. For example, the bushcricket Phaneroptera falcata, detects freely flying bats in the wild from up to 30m away based on call rate (Schul et al., 2000). Similarly, Fullard et al (2005) demonstrated detection ranges of 10 – 40 m by the AN2 fibre of T. oceanicus. These distances equate to an escape time frame of 1.5 – 4 s (Schul et al., 2000), sufficient for successful early evasion by the prey. However, at a critical threshold of stimulus rate (> 26 pulses per second, Samson and Pollack 2002) the AN2 fibre ceases to fire at behaviourally relevant rates altogether (Fullard et al., 2005), due to limitations in the rate of mechanical transduction required for processing (Mason and Faure 2004). Consequently, early avoidance strategies are not triggered.

Signal intensity is the critical threshold trigger for eliciting phonotactic behaviour in the first place (Pollack and Hoy 1981; Forrest et al., 1995; Schul et al., 1999; Pollack 2000; Schul and Schulze 2001; Pollack 2003; Deily and Schul 2004; Triblehorn and Yager 2005). Accurate auditory detection by crickets of preying bats is confounded however, by a reduction in the intensity of emissions as they approach the target insect (Schnitzler et al., 2003). This is reflected by a rapid decline in the strength of neural response and an increase in the response latency of the first spike to be generated (Samson and Pollack 2002; Pollack 2003; ter Hofstede et al., 2009; Marsat and Pollack 2012). Eventually, the AN2 fibre fails to match spike generation for each pulse of ultrasound (Fullard et al., 2005; ter Hofstede et al., 2009). Therefore, if signal intensity at the ear is insufficient, the cricket auditory system may cease to reliably encode signals from an approaching bat well before pulse rate debilitates neural activity.
Under terrestrial conditions of interaction, the use of very soft calls by many gleaners in the first place (Pennay et al., 2004; Surlykke and Kalko 2008), and the attenuation of signals over distance and/or through vegetation (Griffin 1971; Londhe et al., 2009; Sofferman 2012), may therefore critically limit the cues available to listening crickets on the ground. This signifies that not only may there be infrequent physical encounters with bats, but an absence of acoustic stimuli detected. Characterisation of the acoustic environment for grounded crickets in the wild is therefore an important consideration in determining the potential significance of bat echolocation in shaping cricket responses in the terrestrial setting.

1.3.3 The Environment as Passive Defence

The physical environment itself may ultimately be a very important extrinsic factor shaping the prey response. Seeking shelter to minimise the risk of exposure (i.e. ‘hide’) is an important generalised strategy for many prey (Domenici et al., 2011; Camp et al., 2012). For crickets, remaining within environmental clutter could reduce the likelihood of acoustic detection by bats in the first place (Boonman et al., 1998). Alternatively, crickets may seek shelter prior to a bat attack, and then remain still. Hidden amongst clutter, the classic avoidance behaviour (negative steering) would be unnecessary and potentially detrimental, as movement may provide the foraging bat with auditory cues for localisation (Goerlitz et al., 2008; Martín et al., 2009). Remaining within clutter could also discourage further pursuit (Rainho et al., 2010). It is therefore important to investigate how features of the terrestrial environment such as shelter, influences interactions between bats and crickets.
1.4. Research Aims and Key Considerations

This dissertation aimed to contribute to the current understanding of terrestrial bat-cricket interactions from an ecological perspective. The central theme in this regard considers how factors of the environment might contribute to the development of the prey’s response (or lack thereof). In terms of the bat predator in this context, despite frequent mentions of gleaning and perch hunting by such Australian bats, characterisation of their capacities (behavioural and acoustic) for ground foraging tasks is incomplete.

In Chapter 2 I describe general methodologies of field work carried out, and one example setting where focal animals were found to overlap.

In Chapters 3 – 5, this dissertation aimed to address the following research questions.

Chapter 3:
What is the acoustic environment within which crickets are living and what might their audibility of foraging bats overhead be like on the ground?

Chapter 4:
How do grounded crickets respond to echolocation calls and are responses different based on the associated risk from a range of bats they are sympatric with?

Does exposure risk due to life habits reflect differences in male and female cricket behaviour in response to bat echolocation?

How does the (simulated) presence of echolocating bats influence the use of shelter by crickets?

Chapter 5:
What is the behavioural and acoustic repertoire of candidate gleaners during ground foraging tasks for different prey, and are these characteristic of predation in a prey-specific or context-dependent manner?

What is the behavioural repertoire of defence (avoidance and escape) in grounded crickets during live interactions and targeted attacks from these bats?
1.5. References


Chapter 2.

General Methodologies and the Context of Association.
2.1. Introduction

This Chapter details fundamental methodologies that are relevant for subsequent Chapters. In addition, it describes the context of association within which focal animals were found to co-exist and which represent important considerations (Oksanen et al., 1992; Miller and Surlykke 2001; Schnitzler et al., 2003) for subsequent Chapters.

There are evidently 20 species of bats inhabiting South East Queensland (Hall 2013), within which the field study site for this project, Enoggera State Reserve, lies. Site-specific confirmation of these bats’ presence is not however, known from this sole reference. For this reason, all bat species encountered at the field site are documented within this dissertation. Of the purported species, *Rhinolophus megaphyllus* and members of the long-eared genus *Nyctophilus* spp., are the most likely terrestrial predators of crickets, based on their diet and foraging capacities in this context (Chapter 1, Section 1.2.5), with a further subset of the documented local bats encompassing aerial hawkers from up to six genera (also described in Section 1.2.5). The predatory relevance of any bat species however, will be dictated by their frequent and close proximity to crickets. Since male crickets are the stable terrestrial prey whose calls draw in flying females (Otte and Alexander 1983), the bats that are ecologically significant at the study site will be those species that regularly forage close to the substrate. Through the field surveys presented here, these key animals are identified and the nature of their association described.

Members of the *Teleogryllus* genus of crickets are known to inhabit South East Queensland (QLD Museum 2013) but their taxonomic profile and distribution are not well-established. Current indications are that only *T. commodus* occurs within the study region (Atlas of Living Australia 2015; pers. comm. Dr Beth Mantle, CSIRO Entomology); however, there is very little reference material (images, acoustic records and natural history) available on these crickets (Evans 1983; Otte and Alexander 1983; Evans 1988), and almost no neuro-ethological understanding (Nolen and Hoy 1986). My field surveys describe one resident cricket population and their habitat, encountered at the study site. Herein, limiting factors influencing any potential terrestrial encounter with nearby bats, are described.
2.2 Field Work Methodologies

2.2.1 The Field Study Site

South D’aguilar encompasses 28,500 ha of the D’aguilar National Park, located on the western boundary of the city of Brisbane, Queensland, Australia (Figure 2.1). The park is managed for both conservation and recreational purposes aimed at catchment protection, fauna and flora rehabilitation and tourism and education. All field based work for this dissertation was carried out within a 36 sq km region of Enoggera State Reserve in the south-east corner of South D’aguilar (Figure 2.1, enlarged image), and centred at Gold Creek Reservoir (Lat: 27.28º S, Long: 152.52.60º E). For clarity, the entire region within which I conducted field based work will henceforth be referred to as “Enoggera State Reserve”. Where specific reference is made to the ecologically relevant site of predator-prey overlap, this will be referred to as “the field study site”, “Gold Creek Reservoir wall”, “Gold Creek Reservoir” or the “Reservoir wall”.

Vegetation at Enoggera State Reserve is dominated by wet and dry sclerophyll forests, with isolated patches of dry rainforest. Enoggera Creek bisects the region, hosting a variety of fringing forest vegetation (e.g. weeping bottle brush, Callistemon viminalis) and open flood plains. Field work ‘headquarters’ were based at the Moggill Creek Catchment Group (MCCG) cottage at Gold Creek Reservoir, from which forestry tracks enabled access to the north, west and eastern regions of the study site.

Due to its semi-tropical climate, Brisbane and its surrounding regions typically experience mild, dry winters and hot, humid and wet summers. I conducted all field based investigations over a period of four field seasons (2006 – 2009), during peak field activity in each season between November and May (the Australian summer – autumn periods). References to a season by a particular year thus indicate that it commenced in (earliest) November of one year, and extended into the early months of the subsequent year. The start and end times of each productive field season were dictated by climatic fluctuations such as rainfall and night-time temperature, as will be evident below in Section 2.3.1.
Figure 2.1. Location of South D’Aguilar National Park (approximately 20 km west of Brisbane, South East Queensland, Australia) and the field study site (Enoggera State Reserve, enlarged image) where field work for this dissertation was carried out.
2.2.2 Assessing Distribution and Diversity of Prey and Predator

To determine the distribution and diversity of *Teleogryllus* crickets and insectivorous bats occurring at Enoggera State Reserve, a combination of acoustic and trapping approaches were used over the duration of the four field seasons. These were carried out synchronously over the years, with the primary focus being the identification of sites where predator and prey were regularly occurring together.

*Crickets - Acoustic Surveying*

Determining the occurrence and range of field crickets was a continuous process during my work in the field, and was predominantly based on listening for calling males which were considered indicators of stable populations. The calls produced by *Teleogryllus* males are easily distinguishable from other Gryllidae (Otte and Alexander 1983) and so the first means of positive identification was simply to listen for these songs throughout the study site.

To determine the taxonomy of local field crickets, I analysed the acoustic profile of calling males in the field. When located, calling individual males were recorded through a Sony directional microphone onto a personal mp3 player in WMA file format (sampling rate: 44.1 kHz; resolution: 16 bit). The files were imported into Cool Edit Pro (V1.2a Syntrilium Software Corporation, Phoenix, Arizona, USA) for analysis of key call parameters such as peak frequency of pulses and song pattern (chirp and trill elements). These acoustic records were then compared to calls recorded from laboratory reared colonies of *T. commodus*, acoustic profiles for *Teleogryllus* species obtained from the CSIRO Australian National Insect Collection database prior to its discontinuation, and with reference to expert advice from Dr Beth Mantle, CSIRO Entomology.

Acoustic methods were also used to characterise the structure of a cricket colony inhabiting a site by marking the position of individually audible males with flag tape and entering their position into a portable GPS device (based on the methods of Campbell and Shipp 1979). The data were then plotted as a distribution map to provide an estimate of the size of the cricket colony, in terms of the number of individuals and their proximity to one another (male spacing distribution). This information provides a relative indication of the size of the local cricket population available to any bats.
foraging nearby, and that it is not simply incidental occurrences of individuals. It is also documented evidence of cricket colony structure that is not known to date. Presumably, a large population of males will attract mobile females as well, indicative that both sexes are present. For future investigations, these are meaningful considerations for the study of context-dependent interactions between bats and crickets, and offer a valuable study site if such a location can be established.

The spacing distribution of calling male field crickets was carried out twice in 2006 and once each in 2007 – 2009 at the single site discovered to host a colony of field crickets (Gold Creek Reservoir, Figure 2.2). On eight overnight observations in January 2006, I also assessed the relative calling activity of resident crickets every hour between 1300 and 0000 hrs, and again between 0300 and 0900 hrs. Peak calling activity is presumed to indicate the time periods when female crickets might aggregate in the greatest numbers at the site, to interact with these males.

Figure 2.2. Overview of the south-east wall of Gold Creek Reservoir, site of a large colony of *Teleogryllus* crickets, as indicated by the presence of calling males.
Crickets - Trapping Techniques

Various trapping approaches were used for visual verification of locally occurring cricket species, as well as for the intended purpose of collecting live individuals for experiments with wild caught bats (Chapter 5).

Six pit fall traps and eight 800 mm x 650 mm sheets of shade cloth were set across the Gold Creek Reservoir wall, during 12 occasions in February 2008. The use of shade cloth with vegetable matter (e.g. carrots, lettuce) placed underneath is an approach successfully used by Dr Paul Cooper (pers. comm. Australian National University) to collect large numbers of wild crickets. Both types of traps were left overnight on each occasion, and checked twice for the presence of crickets, once in the evening and once on the following day.

To attract mobile field crickets, including flying females, I attempted using a light trap and acoustic trap. The use of a mercury vapour light trap was limited to the area immediately surrounding field headquarters (approximately 200 m from Gold Creek Reservoir) as I did not have access to a mobile power supply for the light source. Over 14 nights in February and March 2008, the mercury light was set up against a white board and turned on for up to four hours. In the first hour of trapping I remained by the light to collect any live individuals, then checked the trap up to six times, thereafter. An acoustic trap was set up on eight evenings in February 2008, across four locations around the Gold Creek Reservoir wall. A speaker was used to broadcast a 30 second recording made previously from calling resident male crickets via a Sony nw-hd3 mp3 player (ATRAC3plus file format; 44.1kHz sampling rate) and looped such that the sequence was played for 30 minutes at a time. The specifications of sound files were presumed appropriate for playback experiments as evident in the methodologies of Leonard and Hedrick (2009) and Jang (2011). The acoustic trap was set up during the period of highest calling activity by crickets, between 1800 and 1900 hr each night, but away from the Reservoir wall where the signal may have been indistinguishable next to calls of resident males. A white sheet was placed beneath the speaker on the ground to facilitate visual identification and collection of crickets as they approached the speaker.
Bats - Acoustic Surveying

Acoustic surveying of locally occurring bat species was carried out over 17 sessions in 2006 and 22 sessions in 2007, by recording the echolocation emissions of foraging bats flying overhead. This is advantageous for the detection of species that might otherwise not fly into traps and thus not be visually identifiable. The sites of acoustic recording sessions across Enoggera State Reserve are illustrated in Figure 2.3 (indicated by stars). Ultimately, the general assessment of bat presence and identity was obtained only from easily accessible locations (e.g. forestry tracks), since cricket colonies other than those at Gold Creek Reservoir, were not found elsewhere (described below). Given that a detailed evaluation of the life habits of all bat fauna was also not a focus of this dissertation, any bias from trapping locations is an acknowledged but ultimately negligible aspect of survey approaches.

Figure 2.3. Sites of acoustic (stars) and harp trap (filled circles) surveys carried out to sample for bat species inhabiting Enoggera State Reserve. Acoustic recording sessions were conducted on a total of 39 nights during the 2006 and 2007 field work seasons; harp trapping during 2008 and 2009 encompassed a total of 58 trapping nights. Red-filled circles indicate sites where the members of the target genus Nyctophilus spp. were most reliably captured.
Real-time, direct recordings (Britzke et al., 2013) were made using a Bat Detector (Ultra Sound Advice S-25, London, UK; frequency range: 15-200 kHz; sensitivity: 10 dB SPL at 50 kHz) with direct input via the High-Frequency channel to the ultrasound analysis software program BatSound (Pettersen Elektronic AB) on a Dell Latitude C400 Laptop. A National Instruments (Austin, Texas, USA) analogue to digital converter card (DAQCard 6062E) enabled capture of uncompressed sequences (sample rate: 500 kHz; resolution: 16 bit; WAV file type), five seconds in duration. This recording duration is sufficient to sample full foraging sequences from search to capture. Long-duration sequence sampling also maximised the chance of obtaining high quality signals which are often difficult due to the bat’s movement and changes in proximity relative to the recording equipment.

Bat species identification followed the methods and guidance of Dr Roger B Coles (pers. comm.) from search phase emissions analysed in Cool Edit Pro. The recordings were sorted to isolate sequences containing at least 10 high quality search pulses, which were not saturated, did not have pulse-echo overlap and were of maximal relative amplitude (i.e. pulse amplitude relative to background noise as observed in Cool Edit Pro). Sound variables of relative amplitude (as described, relative to background noise), frequency at peak energy content (Hanning window spectrogram, 2048-point Fast Fourier Transform (FFT)) and frequency range were extracted from these files, and representative pulses were compared to a call library of known species emissions (owned and cross-checked by Dr Roger B. Coles in 2006 - 2007) and with reference to keys to bat calls published in the literature (Cronin and Sanderson 1994; Pennay et al., 2004).

Bats – Trapping Techniques

Harp traps (five 3-bank and one 2-bank, courtesy of Dr Bruce Thomson, Redleaf Projects, Toowoomba) were obtained during 2008 and 2009 field seasons, to visually verify locally occurring bat species. Traps were set at various locations across the study site (see filled circles in Figure 2.3) between 1600 and 1730 hr, over 33 trapping nights in 2008 and 25 nights in 2009. The traps were usually placed beneath overhanging vegetation to funnel flying bats in. Collection bags were checked twice on each trapping night, once between 2000 and 2100 hr, and again between 0330 and 0430 hr on the following morning, at which time the traps were packed up. Trapped
bats were identified in the hand to the species level based on Churchill (2008). Individuals from the target genus *Nyctophilus* spp. used in experimental investigations during the 2008 and 2009 field seasons (Chapter 5) were kept for a maximum of two nights before being released at their site of capture. All other bats were released at the time and site of trapping following their identification. Mist netting was not utilised for field surveys and the capture of focal species. For the majority of field work a second field hand was not available thus mist netting could not be consistently carried out nor was it feasible to do so in conjunction with the time and effort requirements of harp trapping which later also overlapped with experimental work at the field study site (Chapter 5).
2.3. Resident Taxa and their Overlap

2.3.1. Overview of Field Seasons

Monthly rainfall and temperature (max-min) data over the four seasons of field work are illustrated in Figure 2.4, indicating the duration of active work. Active field time in each of the four seasons (2006 – 2009) was dictated in particular, by rainfall and minimum nightly temperatures since these factors impact greatly on insect and bat activity: too wet and the emergence of insect larvae can be delayed; too cold and bat activity levels decrease. Both of these extremes occurred to a notable extent in the 2008 field season. Over the four field seasons, there was much diversity in climactic variables, with the region experiencing severe drought (2006 – 2007) then extreme flooding (2008 – 2009). Night-time temperatures were fairly consistent from year to year, although in the 2008 field season, temperatures significantly dropped after March, and bat numbers were noticeably reduced, cutting short this particular field season.

In the 2006 and 2007 field seasons, field efforts focused primarily on identifying any stable colonies of *Teleogryllus* crickets throughout the study site and assessing the diversity and distribution of foraging bats through acoustic surveying. In 2007, this included focused acoustic recording of foraging bats at Gold Creek Reservoir for the purposes of the study presented in Chapter 3. Over the 2008 – 2009 seasons, I switched to harp trapping for visual verification of locally occurring bats. In addition, field efforts in these seasons were aimed at the capture of target bat species (*Nyctophilus* spp.) for protocol optimisation and subsequent testing of the study presented in Chapter 5. Over the duration of all four seasons, the search for any other cricket colonies, characterisation of the population on the Reservoir wall and general assessment of bats local to the area, were carried out synchronously.
Figure 2.4. Monthly climactic data during active field work months at Enoggera State Reserve (Queensland, Australia) in (a) 2006, (b) 2007, (c) 2008 and (d) 2009. Vertical blue bars indicate monthly mean minimum and maximum temperatures (°C). Red line indicates monthly mean rainfall (mm). Data obtained from the Australian Bureau of Meteorology (http://www.bom.gov.au/climate/).
2.3.2 Summary of Teleogryllus Population at Enoggera State Reserve

From the four seasons of field work carried out for this dissertation, I confirmed the presence of one large, stable colony of field crickets, inhabiting the south-east facing wall of Gold Creek Reservoir (Figure 2.2). This site is likely to be an important habitat for field crickets across Enoggera State Reserve since this population of calling males was the only colony found in the region, it was recurrent over the four field seasons, and which probably attracts a large number of the local females (if not all) for reproductive interaction. This location, and the colony of field crickets it hosts, therefore represents a valuable, stable site for (any) investigations of their interactions with sympatric bat species, especially within a terrestrial context.

The site itself is an open grass field approximately 80 m x 60 m in size. Being council-owned and maintained land that is periodically mown throughout the year, the grass lining the ground level ranges in height from approximately 10 cm to 50 cm. This probably offers crickets a reasonable amount of cover within which they are relatively inconspicuous to flying bats. However, the grass is patchy in some regions (e.g. centre of the wall and around the sewer outlet at the bottom), so individuals may be required to cross a matrix of complex and open space during their activities. Male crickets construct burrows in the soil at the base of grass clumps, calling from just outside these burrows (pers. obs.) to attract potential females for copulation. Female field crickets typically move between burrows visiting multiple males, and lay eggs into the soil (Evans 1983).

The population of calling male field crickets at Gold Creek Reservoir was assessed by listening to singing males and marking the positions of individuals. One example of the population size from this approach is mapped out in Figure 2.5, also illustrating male spacing patterns for general records. In 2006, 82 and 73 male crickets were recorded in January and April, respectively. In subsequent years, these numbers were relatively similar, with 76 males identified in a session in 2007, 60 individuals in 2008 and 87 males in 2009. It is possible that the heavy rainfall during January and February 2008 caused large-scale ruin of the eggs deposited by females at the start of the season, and delayed the emergence of calling adult males until later than usual in the season. This may explain the relatively smaller population size indicated in the 2008 sample. Males tended to form small clusters of 2 - 4 individuals, spaced no more than 1 m
apart, but extended across the whole area of the Reservoir wall. Based on observations of calling activity, crickets generally called sporadically but continuously throughout the day, with activity increasing from 1600 hr. Peak calling levels coincided with nightly scotophase between 1800 and 1900 hrs, with a second period of high calling behaviour between 0300 and 0400 to sunrise on the following morning.

Over 12 sessions in February 2008, daily pitfall trapping at the Reservoir wall yielded a total of 12 crickets, while the use of shade cloths to attract sheltering individuals during the day was completely unsuccessful with none obtained. Attempts to attract field crickets by broadcasting the calls of resident males through speakers also proved unreliable, with only two individuals captured over eight nights. These approaches
were subsequently abandoned with respect to attempts at collecting wild individuals for testing in Chapter 5. From captured crickets, there was some variation in size and colouration (see Figure 2.6), as compared to reference images and records from the literature (AINC database, now discontinued; Otte and Alexander 1983; QLD Museum 2013; Atlas of Living Australia 2015). As compared to the size (body length 3 – 4 cm) and colouration (black) of the laboratory specimen (far right in Figure 2.6), individuals collected from Gold Creek Reservoir (far left in Figure 2.6) tended to be slightly smaller with a body length of 2.5 – 3 cm, and were lighter in colouration, ranging between light and very dark brown. *Gryllus nitidula* (middle specimen in Figure 2.6, but not local to the study site) is included to illustrate the noticeable difference in size as compared to *Teleogryllus* crickets, which is of relevance for handling capability by different sized bats. The ultrasound sensitivity of this smaller species is unknown although other members of the Gryllus genus in Europe and America are known to detect bat emissions (Popov and Markovich 1982; Nolen and Hoy 1986; Imaizumi and Pollack 2001, 2005; Pollack and Martins 2007).

I further determined the taxonomic identity of the resident cricket species at Gold Creek Reservoir based on acoustic parameters of the male song. Analysis of acoustic recordings made in the field reveals that the cricket population at Gold Creek Reservoir is *Teleogryllus commodus*. Figure 2.7 compares the song profiles (pulse pattern and

![Figure 2.6. Cricket specimen representing (from left to right) individuals captured in the field (top: female; bottom: male), *Gryllus nitidula* (male, to show size class difference across species) and *Teleogryllus commodus* (female) obtained from the laboratory colony.](image-url)
peak frequency) of individuals recorded in the field against calls from laboratory reared *T. commodus* males and reference songs for *T. commodus* and *T. oceanicus* obtained from the CSIRO ANIC database.

Figure 2.7. Comparison of song structure (units and peak frequency content) from male *Teleogryllus* crickets. Panels display recordings from (a) male individual at the study site, (b) *T. commodus* from the laboratory colony; (c) reference recording of *T. commodus* and (d) *T. oceanicus* from the CSIRO ANIC database.

Songs from both species are characterised by repeating units consisting of a chirp and multiple trills, but differ in the number of pulses within the trill elements: seven to 10 pulses in each trill for *T. commodus*, paired sets in *T. oceanicus* (Otte and Alexander 1983). Additionally, the species are differentiated by the peak frequency of their calls, with *T. commodus* calling at 1 - 0.5 kHz lower than *T. oceanicus* (Hennig and Weber 1997; and see values for species reference calls in Figure 2.7). Based on this
comparison, and expert advice (as previously described, pers. comm. Dr Beth Mantle),
the song structure and frequency content of calls obtained from male crickets at Gold
Creek Reservoir reflects the signature of calls produced by *Teleogryllus commodus*.

**2.3.3 Summary of Bat Population at Enoggera State Reserve**

Through acoustic surveying in the 2006 and 2007 field seasons, and harp trapping in
the 2008 and 2009 field seasons, I positively identified the presence of 13 bat species
at Enoggera State Reserve (Table 2.1), representing a mixture of foraging guilds. Of
primary relevance for terrestrially bound field crickets are the long-eared bats
(*Nyctophilus* spp.) and the eastern horseshoe bat (*Rhinolophus megaphyllus*), all of
which demonstrate capacities for substrate based foraging. These bats are highly
manoeuvrable and agile, hunting close to the ground (< 5 m) often within or
surrounded by clutter on more than one side (Bullen and McKenzie 2001, 2004;
Churchill 2008). Predation on crickets (or Orthoptera) is evidenced from dietary work
on *R. megaphyllus* but absent for the two *Nyctophilus* species encountered. However,
both are consistently described as gleaners (Duncan et al., 1999; Churchill 2008), and
which has been experimentally demonstrated with comparable prey (cockroaches;
Grant 1991) in *N. gouldi*. Their positive identification in direct proximity to the stable
colony of field crickets at Gold Creek Reservoir thus make these species very relevant
candidate predators in terrestrial encounters. These bats are depicted in Figure 2.8,
along with their respective echolocation identification profiles where available from
acoustic surveying.

From acoustic assessment, seven species were verified based on 742 call sequences
in 2006 and 480 in 2007, including two members of the target genus (*N. gouldi* and *N.
bifax*), but not *N. geoffroyi*. Directly overhead the resident colony of crickets at Gold
Creek Reservoir, *N. gouldi* and the aerial hawker *Scotorepens greyii* were consistently
recorded over the two seasons. The acoustic profile for *S. greyii* is also included in
Figure 2.8. *N. bifax* and *R. megaphyllus* (the other species of interest for terrestrial
interactions) were detected only beside the Reservoir wall. For *R. megaphyllus*, their
presence was confirmed through trapping only.
Table 2.1. Bat fauna composition at Enoggera State Reserve determined from acoustic survey work in 2006 and 2007 field seasons, and from harp trap catches during 2008 and 2009 field seasons. Checks (√) in 2006 and 2007 columns indicate positive detection of bat species through analysis of acoustic recordings. Harp trapping records indicate the number of individuals per species captured each season, and the percentage each species contributes to the total number of captures over the two trapping seasons.

<table>
<thead>
<tr>
<th>Species</th>
<th>Common Name</th>
<th>Acoustic Surveying</th>
<th>Harp Trapping</th>
<th>% Total Captures</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>2006</td>
<td>2007</td>
<td>2008 (n)</td>
</tr>
<tr>
<td>Rhinolophus megaphyllus</td>
<td>Eastern horseshoe bat</td>
<td>2</td>
<td>1</td>
<td>1.9</td>
</tr>
<tr>
<td>Chalinolobus gouldii</td>
<td>Gould’s wattled bat</td>
<td>✓</td>
<td>✓</td>
<td>4</td>
</tr>
<tr>
<td>Chalinolobus morio</td>
<td>Chocolate wattled bat</td>
<td>6</td>
<td>5</td>
<td>6.9</td>
</tr>
<tr>
<td>Chalinolobus nigrogriseus</td>
<td>Hoary wattled bat</td>
<td>1</td>
<td>1</td>
<td>1.3</td>
</tr>
<tr>
<td>Nyctophilus bifax</td>
<td>Eastern long-eared bat</td>
<td>✓</td>
<td>✓</td>
<td>5</td>
</tr>
<tr>
<td>Nyctophilus gouldi</td>
<td>Gould’s long-eared bat</td>
<td>✓</td>
<td>✓</td>
<td>2</td>
</tr>
<tr>
<td>Scototax rueppellii</td>
<td>Greater broad-nosed bat</td>
<td>✓</td>
<td>✓</td>
<td>20</td>
</tr>
<tr>
<td>Scotorepens greyii</td>
<td>Little broad-nosed bat</td>
<td>✓</td>
<td>✓</td>
<td>4</td>
</tr>
<tr>
<td>Vespadelus pumilis</td>
<td>Eastern forest bat</td>
<td>12</td>
<td>15</td>
<td>16.9</td>
</tr>
<tr>
<td>Myotis macropus</td>
<td>Large-footed myotis</td>
<td>✓</td>
<td>✓</td>
<td>10</td>
</tr>
<tr>
<td>Miniopterus australis</td>
<td>Little bentwing bat</td>
<td>✓</td>
<td>✓</td>
<td>1</td>
</tr>
<tr>
<td>Miniopterus oriana oceanensis</td>
<td>Eastern bentwing bat</td>
<td>✓</td>
<td>✓</td>
<td>1</td>
</tr>
<tr>
<td>Mormopterus beccarrii/ridei</td>
<td>Beccarri’s/Eastern freetail bat</td>
<td>✓</td>
<td>✓</td>
<td></td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td></td>
<td>58</td>
<td>102</td>
<td></td>
</tr>
</tbody>
</table>
Figure 2.8 (continued over next pages). Focal bat species at Enoggera State Reserve, as confirmed by acoustic and visual (trapping) surveys carried out between 2006 and 2009. Characteristic call profiles are provided for those bats that were acoustically detected and verified, from 2006 and 2007 surveys.
Figure 2.8 continued

Nyctophilus gouldi
Figure 2.8 continued

Scotorepens greyii

Rhinolophus megaphyllus

Confirmed through trapping only
Harp trapping in 2008 and 2009 confirmed the presence of *N. gouldi* and *N. bifax* in close proximity to the resident colony of field crickets, with their capture at two locations around the Reservoir wall (see red-filled circles in Figure 2.3). *N. geoffroyi*, was again not detected as it was never captured in traps. *Nyctophilus* bats were notoriously difficult to capture on a regular basis, and contributed only 23 individuals to the total number of captured bats (n = 160) across the two seasons. This is similar to the account from Cronin and Sanderson (1994) on trapping success for *N. geoffroyi*. They appeared to be highly sensitive to the presence of unusual obstructions (i.e. harp traps) along their usual flight paths, and after the first night in a particular location, were either exceptionally skilled at avoiding the traps set there on subsequent nights, or were avoiding the area altogether. Despite this, three locations were identified as successful and reliable trapping sites (re-confirmed by continued captures in 2009) as indicated by all three red-filled circles in Figure 2.3. *R. megaphyllus* was also regularly trapped at the location on Scrub Road, suggesting the bats overlapped in their foraging niche in at least two sites. The vegetation structure at these sites consisted of a very small, dense patch of hoop pine and wet sclerophyll, with overhanging branches that created a narrow (~ 4 m) funnel within which the bats were easily observed by the naked eye. For perch hunting and gleaning of stationary prey from vegetation or the ground, these sites appear ideal hunting grounds for this group of bats. Indeed, previous accounts of *N. bifax* and *R. megaphyllus* foraging in the wild describe such behaviours displayed in similar settings (Fenton 1982; Crome and Richards 1988; Pavey and Burwell 2004). At such sites around Gold Creek Reservoir, these bats could encounter flying female field crickets upon their approach to the male colony on the Reservoir wall, or males that reside on the ground along the site fringes. Collectively, the four field seasons of survey work indicate a small but stable population of long-eared bats (and potentially, *R. megaphyllus*) inhabit Enoggera State Reserve. Vitally, they overlap with a historically stable population of ground dwelling field crickets in direct proximity whilst foraging on and around the Gold Creek Reservoir wall. These bats therefore reflect prime candidates as relevant predators of crickets under a terrestrial context.

From the other bat species detected across the study site, *S. greyii* constituted almost half (47.5 %) of the total bat population based on trap catches. These bats were common both in number of individuals captured and frequency of occurrence, their
presence being acoustically and visually confirmed at all survey sites including at Gold Creek Reservoir. Over 11 nights in April – May 2007, I conducted focused recording sessions of these (and any incidental) bats foraging directly above the resident cricket population at Gold Creek Reservoir and formed the data upon which Chapter 3 is based. At the start of these recording sessions, foraging bats were visible to the naked eye and so I also observed these events for as long as there was sufficient light. At the time of these observations, species identity was unknown but subsequent analysis of the recordings determined the emissions were from *S. greyii* and *N. gouldi* only.

Foraging bats during these sessions displayed two main patterns of flight. Most events (39 of 52 passes) involved a bat flying fast and direct, approximately 5 m above the ground, with sudden arced turns to change flight path. On six occasions, I observed a bat flying relatively slower and at lower levels, with numerous sharp directional changes in flight path and dips toward the ground. These respective flight patterns are characteristic of the behaviours described for *S. greyii* and *Nyctophilus* spp. (Duncan et al., 1999; Bullen and McKenzie 2001; Churchill 2008; George et al., 2011). I did not align my observations to specific recording sequences which therefore does not account for variation in flight behaviour within species; however, these were conducted simultaneously until bats were no longer visible in the dark. Since most sequences were identified as belonging to *S. greyii*, it is likely that these were the species exhibiting the flight pattern I observed most often (fast and direct). The second flight pattern then probably correlates with the low number of echolocation sequences obtained from *N. gouldi*. The flight events that involved diving towards the ground suggest that the pursuit of flying prey directed these bats towards the ground. Alternatively, bats could have been responding to the detection of non-volant insects resting on grass/ground. I did not directly observe gleaning and thus cannot conclusively determine the particular nature of foraging events by either species.

The remaining species of bats listed in Table 2.1 include one trawler, and eight aerial hawkers that forage in the open or with minimal (edge) clutter, at mid to high levels (within 10 m above the ground) in the vegetation strata (Churchill 2008). Note that the taxonomic classification of *Mormopterus* bats is unresolved and keys to the species based on their acoustic profile are inconsistent (for example, compare descriptions in Milne 2002 with those cited by Churchill 2008). My identification of the species present at Enoggera State Reserve, and whether both or one of these inhabit the site, is
therefore a conservative estimate at best, based on relevant keys to Australian bat calls, personal communication with Dr Roger Coles, and consideration of the distribution of Mormopterids across Australia. Subsequently, I have indicated both Beccari’s and the eastern freetail bat in Table 2.1 but for records of occurrence these are more appropriately referred to as *Mormopterus* spp. The echolocation profiles for these bats (where recordings were obtained) are provided in Appendix 1, including for *Miniopterus australis*, the species relevant to work presented in Chapter 4.

From the survey work carried out, these bats were consistent in terms of relatively few individuals encountered and often within limited distribution across survey sites. For example, *Myotis macropus* were only ever acoustically detected over the body of water of the Reservoir, or on the northern bank away from the resident colony of male crickets. They may be exerting some predation pressure if crickets are occurring on the northern side however, this was not determined given the obvious value the south-east facing wall provided for directed investigations. *S. rueppelli* and *Chalinolobus* spp. (identified as potentially relevant for cricket predation in Chapter 1) were only acoustically and visually detected along Centre Road (see Figure 2.3). Excepting *M. macropus*, none of the other species were detected anywhere near the resident colony of field crickets at Gold Creek Reservoir. *Austronomous australis*, which was suggested as a flexible forager due to observations of their pursuit of crickets along the ground (Bullen and McKenzie 2001) was not at all detected. For the purposes of this dissertation, these nine bat species are not considered to be significant predators of resident field crickets. For future work, their presence at Enoggera State Reserve demonstrates a valuable site of sympatric predator and prey species, from which much understanding already established for *T. oceanicus*, could be replicated and extended in *T. commodus*. 
2.4. Focal Species and the Context of their Association

The presence and distribution of field crickets (*Teleogryllus commodus*) at Enoggera State Reserve was expected to be a limiting factor in determining which bat species will be the most likely and relevant predator candidates. The south-east facing wall of Gold Creek Reservoir hosts a large, permanent population of calling male field crickets (*Teleogryllus commodus*). From the few pit fall catches I obtained the presence of females at this location was also confirmed. Since this was the sole colony found across the study region of Enoggera State Reserve, this site is likely to be an important area of large aggregation by male and female crickets especially during peak reproductive times (Evans 1983; Otte and Alexander 1983; Evans 1988). Moreover, the colony was recurrent from year to year, so it is probably an ecologically important, well-established zone for the resident *Teleogryllus* crickets in the region.

Identification of the bats that may be relevant predators for these crickets was then dependent on those species that spatially and temporally overlap at Gold Creek Reservoir. Four species of bats were found recurrently and frequently inhabiting the immediate vicinity of this site. Two of these, *S. greyii* and *N. gouldi*, were acoustically detected and visually verified (Section 2.3.2) directly above the resident colony of male *T. commodus*. On the immediate fringes within a small, dense patch of overhanging vegetation, another long-eared bat (*N. bifax*) and *R. megaphyllus* were detected through trapping. These bats represent a mix of foraging guilds (Churchill 2008) to which the resident crickets are exposed, and possibly for many years (at least four).

Any selection pressure exerted on resident (male and female) *T. commodus* by the focal bat species may be most directly elucidated throughout dietary analyses. It is an unfortunate gap in this dissertation that dietary composition of the target (or any) bat species at Gold Creek Reservoir was not determined. This was an initial aim of the dissertation; however, I obtained very few samples from any species trapped to subsequently enable meaningful inferences about prey presence in their diet (for example, see Trites and Joy 2005). For the focal bat species, I obtained 11 samples from *S. greyii*, six from *N. gouldi*, four scats from *N. bifax* and none for the single *R. megaphyllus* individual trapped. *Miniopterus australis* (Chapter 4) were never caught in traps thus samples could not be collected from this species at all. This is an important caveat for future work, and molecular techniques may provide particularly
meaningful inferences for context-dependent associations (Murphy et al., 2003; Beveridge and Simmons 2005; Hall et al., 2010; Clare 2014). Indicators of the possible extent of association between these focal bat species and field crickets at Gold Creek Reservoir may come from the context of any likely encounters.

A large number of male crickets occupy the grass field at Gold Creek Reservoir (Section 2.3.2). Male crickets remain generally substrate-bound and within cover, calling from burrows and moving over short distances to ambush neighbouring males (Evans 1983; Otte and Alexander 1983; Evans 1988). Given the grass height that can occur at this site (10 – 50 cm), males are probably well-concealed amongst a good density of clutter. In contrast, females seek calling mates over long distances, by first flying through open air then coming to the ground and navigating towards the advertising males terrestrially (Otte and Alexander 1983). The sexes are therefore mobile to a variable extent and across a matrix of space, factors that could have ecologically relevant implications for their association with foraging bats.

I did not directly observe or test predation on field crickets (either flying females or grounded males) by any bat at the study site. However, the foraging habits of focal bats provide important considerations for any potential predatory association with resident crickets on the ground.

Those bats that do not come to the ground to forage but are flying overhead, will not represent a direct threat to substrate bound crickets, but may be so for approaching flying female crickets. Alternatively, if the emissions from such bats are audible to crickets on the ground because they are sufficiently close (Fullard et al., 2005), they may exert some indirect predatory influence on these crickets. This encompasses the potential risk that S. greyii could represent for T. commodus at Gold Creek Reservoir, given their observed foraging height (Churchill 2008; George et al., 2011). Based on source intensity levels for their foraging guild, their emissions may be sufficiently loud for acoustic detection by crickets over this range (Boonman and Jones 2002; Fullard et al., 2005; Holderied et al., 2005; Surlykke and Kalko 2008; Denzinger and Schnitzler 2013; Jakobsen et al., 2013).

Where terrestrial foraging by a bat is possible, this achievable proximity to grounded crickets represents a direct predation risk (Lima and Dill 1990). Herein, N. bifax and R. megaphyllus may well be capable of preying on the crickets at Gold Creek.
Reservoir, based on their behavioural and acoustic (for horseshoe bats) repertoire (Duncan et al., 1999; Pavey and Burwell 2004; Pavey and Young 2008). Based solely on their limited distribution beside the Reservoir wall (Figure 2.3) however, they are not of immediate threat to ground dwelling male *T. commodus* unless individuals on the fringes (see yellow-filled circles on far-right of Figure 2.5) move into this space. These bats may be relevant however, for any female crickets approaching the site as they fly through this space or potentially, rest on substrates within (Fenton 1982). In the case of *N. gouldi*, these bats could represent a very relevant and high risk of predation on crickets: they were detected recurrently foraging overhead the resident colony, possess the behavioural attributes necessary for terrestrial captures (Grant 1991; Churchill 2008) and the auditory sensitivity to exploit prey-generated sounds (Guppy and Coles 1988).

Within the setting at Gold Creek Reservoir, a number of limiting factors exist that may be shaping any potential terrestrial association between *T. commodus* and the focal bat species: (1) the potential to meet due to physical barriers; (2) acoustic detectability due to distance; and, (3) acoustic detectability due to vegetation impedance. Physical interactions within vegetation (e.g. shrubs) beside the Reservoir wall or at the grass base, may be a very limiting task for any bat (Sleep and Brigham 2003) altogether. Subsequently whilst predatory attempts may occur, their relative rate of success would be low if prey recede into inaccessible vegetation. Acoustically, emissions from bats flying overhead may be diminished through impedance by the substrate (Craddock and White 1992; Londhe et al., 2009), if these cues are at all audible over distance to crickets on the ground (Miller and Surlykke 2001; Fullard et al., 2005). In closer proximity either on the ground or in vegetation beside the Reservoir wall calls may be audible; however, impedance could still be a factor in the case of the surface foraging species (Fenton 1982; Duncan et al., 1999; Pavey and Burwell 2004; Churchill 2008), especially if any of these emit only the very soft calls such bats are described to use in clutter (Milne 2002; Pennay et al., 2004; Jakobsen et al., 2013). The prey’s defence response may therefore be very closely associated with the environment here (crypsis) (ter Hofstede et al., 2009; Domenici et al., 2011). Similarly, acoustic detection by bats of prey within vegetation could be very limited due to the density of this clutter (Arlettaz et al., 2001; Jones et al., 2003; Rainho et al., 2010).
In the ensuing Chapters (3 – 5), I present a series of investigations aimed at addressing some of the points of consideration raised in this section. Specifically, I examined in further detail the relevance of echolocation audibility for the crickets at Gold Creek Reservoir listening to *S. greyii* and *N. gouldi* foraging overhead (Chapter 3); the role of echolocation design and habitat structure in bat avoidance behaviour for field crickets on the ground (Chapter 4), and; the behavioural nature of terrestrial encounters between crickets and wild caught *N. bifax* and *N. gouldi* and grounded field crickets (Chapter 5). For the purposes of clarity and conciseness throughout the dissertation, references to the focal long-eared bats by the genus name (but not spp.) is used to refer to these two species only.
2.5. References


Milne, D. J. (2002). "Key to the bat calls of the Top End of the Northern Territory.". Territory, P. a. W. C. o. N. 71.


Chapter 3.

Estimation of the Audibility of Echolocation Calls for

*Teleogryllus commodus* on the Ground.
3.1. Introduction

During aerial encounters, successful evasion of bats by insects is dependent on the early detection of the predator’s echolocation calls dictated largely by the intensity of signals perceived (Miller and Surlykke 2001; Hennig et al., 2004). In a terrestrial context however, the echolocation cues available to grounded field crickets will depend on their attenuation over distance and impedance through the physical strata (e.g. grass). This will therefore have ecological significance for the prey if escape from bat predators relies solely on acoustic drive. To date, the acoustic (echolocation) environment for grounded field crickets has not been characterised. In this Chapter, I therefore examined the emissions from two bat species – the aerial hawker *Scotorepens greyii* and gleaning *Nyctophilus gouldi* – which live in sympathy with field crickets (*Teleogryllus commodus*) at Gold Creek Reservoir (Chapter 2, Section 2.3) to assess their relative (theoretical) audibility for crickets on the ground.

There exists no published characterisation of AN2 sensitivity in *T. commodus* and it was not possible here to generate audiograms from these crickets. Direct comparison between *T. commodus* and *T. oceanicus* of their phonotactic behaviour does however, exists and which shows some similarity in behavioural sensitivity across a range of high frequency signals (Nolen and Hoy 1986). This certainly does not enable direct inferences from one species on another however, characterisations from *T. oceanicus* may provide some indication of patterns in *T. commodus*. All interpretations about the relative audibility of emissions from different bats for *T. commodus* are therefore made cautiously. Since *T. commodus* and the focal bats in this study were found to live in close proximity over recurring years (Chapter 2), echolocation emissions from these bats could represent ecologically relevant sounds to resident crickets. Whether or not they are detectable then, and any differences due to the species of origin, are only theoretically estimated, based on collective implications from research to date on *T. oceanicus*.

A number of factors will determine the audibility of bat emissions for substrate bound crickets and thereby, their capacity to assess the location and proximity of a bat (Faure et al., 1990; Hennig et al., 2004). First, during an attack lasting only a few seconds, bats attenuate their signals to obtain an increasingly more precise image of their target in space, resulting in shorter, faster and softer calls as proximity to prey increases.
(Schnitzler et al., 2003). These adjustments will diminish the accuracy of processing by insects due to limitations in their sensitivity to, and transduction of, acoustic cues (Imaizumi and Pollack 2001; Hennig et al., 2004; ter Hofstede et al., 2009). Then, since attenuation of a signal over distance is dependent largely on the inherent properties of the emitted sound (frequency, energy content, source intensity; Neuweiler 1983; Sofferman 2012), the emissions of bats from particular guilds may be altogether differentially detectable based on their niche- and task-specific call design. Preferential tuning for aerial hawkers but not gleaners has been demonstrated for T. oceanicus (Fullard et al., 2005; ter Hofstede et al., 2009), signifying divergent selection pressures on crickets across bat foraging guilds. Herein, signal intensity was a major limiting factor for activating AN2 to behaviourally relevant thresholds, with required call amplitudes from gleaners being unrealistic (Schnitzler et al., 2003; Pennay et al., 2004; Fullard et al., 2005). Finally, the physical environment on the ground (grass) could greatly limit the cues available due to impedance (Parsons 1996; Pritz 2004; Londhe et al., 2009; Sofferman 2012). Indeed, this might also be limiting for the bats that encroach this space (Boonman and Jones 2002; Marimuthu et al., 2002; Goerlitz et al., 2008), and where a subsequent switch to passive localisation would entirely eliminate ultrasonic cues for the prey.

On the ground then, field crickets may not hear echolocating bats flying overhead if they are too far away. However, when faced with a relevant threat from a gleaner that may be already acoustically cryptic (soft calls), the collective implications of changes in call structure over a bat's approach, species-specific signal design, and attenuation of such signals over distance and through physical strata, suggest crickets may well be ‘deaf’ during crucial stages (e.g. approach) when early, evasive tactics would normally be possible. If this is true, it highlights the inefficiency of acoustic input for the prey response in a terrestrial setting, and that crickets may in fact need to rely on alternative strategies of defence.

In this Chapter, I evaluate the relative audibility of echolocation calls to crickets emitted by S. greyi and N. gouldi, bats that were found regularly flying directly above the colony of T. commodus at Gold Creek Reservoir. Foraging sequences were recorded from positions occupied by resident male crickets on the ground in the field, providing an approximation of the signals to which these insects were frequently exposed. Estimates of relative sound intensity at the point of listening crickets are presented, and provide
an indication of what these crickets might hear. Further extrapolation to determine the degree of attenuation of echolocation calls over distance was then used to estimate the distances at which resident crickets can detect these foraging bats, based on thresholds of *T. oceanicus* AN2 responsiveness. Again, these extrapolations and subsequent inferences, are presented as cautious estimates only. Source intensities of signals emitted by the bats were not measured here, which is a critical requirement for accurate extrapolations (Jacobs et al., 2008; Stilz and Schnitzler 2012; Jakobsen et al., 2013). This issue is addressed throughout the ensuing Sections, and in Chapter 6. It is also an important future direction of inquiry, in order to determine whether *Nyctophilus* bats at Gold Creek Reservoir reflect cryptic predators that crickets cannot reliably detect acoustically. Based on predictions of acoustic detectability by crickets and the height at which the bats were observed foraging, it was expected that search and approach phase calls from both species should be theoretically, sufficiently loud for detection by crickets. From previously suggested preferential tuning by crickets (e.g. Fullard et al., 2005; ter Hofstede et al., 2009) the approximated audibility of echolocation calls should differ between bats, such that emissions from the aerial hawker *S. greyii* would be generally more detectible to grounded crickets than the calls from the gleaner *N. gouldi*. 
3.2. Methods

3.2.1 Field Recordings of Bat Echolocation Foraging Sequences

From 11 sessions between April and May 2007, echolocation emissions were obtained from bats foraging within 5 m directly above a colony of field crickets at Gold Creek Reservoir. A detailed description of the methodology for acoustic recordings and analysis of echolocation sequences for species identification purposes, is provided in Chapter 2; further details on acoustic analyses relevant to this Chapter are described below. Echolocation sequences were collected from all bat species intercepted while flying overhead. From previous acoustic recording around the Reservoir wall and subsequent harp trap catches, at least four taxa were present in the immediate vicinity (*Scotorepens greyii*, *Myotis macropus*, *Rhinolophus megaphyllus* and *Nyctophilus* spp.). All recordings for investigations in this Chapter were made from the centre of the wall with the microphone on the ground and pointing upward. During the time of recordings, grass height was at its lowest (recent council mowing of the field) protruding approximately 10cm above the ground. Bats were observed to arrive at this location around 1820 hr each night and were visible for a further 20 – 30 minutes. Foraging activity lasted approximately one hour as emissions were no longer detected after this.

My primary aim during these recording sessions was to obtain maximum quality sequences defined by high intensity, low signal-to-noise ratio and complete capture cycles. The quality of recordings from real-time monitoring of foraging bats is inherently unpredictable, because: (1) the bat is visually obscure; (2) during flight, the bat changes course and thus direction and proximity relative to the recording device; (3) bat emissions fluctuate in intensity due to side-to-side head movements for navigational scanning, and in response to the acoustic task at hand; and (4) detection of individual pulses at any one time may not eventuate into a full capture sequence. The recording system was thus automated for a looped delay that obtained 5-second recordings (i.e. recording began five seconds prior to triggering), allowing for the delay between hearing a sequence (via acoustic monitoring with headphones) and determining if it was a valuable sequence. The delayed mode of the recording system thus allowed a degree of selection in the field of the sequences that were recorded.
3.2.2 Calibrations to Determine Relative Peak Equivalent Intensity of Echolocation Calls

To correct for variation in the gain setting of the bat detector during field recordings, a measure of the embedded Noise Level (i.e. background noise from the environment and not the echolocation signals) was obtained from the Min RMS Power analysis parameter in Cool Edit Pro, which was used to analyse sequences. Recordings were then categorised into one of four obtained mean Min RMS Power increments (within ±2 dB for each of -36 dB, -41 dB, -44 dB and -48 dB) to account for variation in background noise levels. To calibrate for signal attenuation over distance at these gain settings, a reference signal consisting of a 40 kHz pure tone (similar to the peak frequency used by the target bat species) was recorded over distances of 3 – 10 m. These recordings were made through the bat detector directly into Cool Edit Pro in the same manner as in the field. The gain setting on a bat detector does not have interval indicators, so for each category of noise level, ambient noise was first recorded through the bat detector and the gain adjusted until the input signal matched the specified (category of) noise level. Following this, the calibration tone was recorded at this gain setting over increasing distances. This process enabled validation that the signals recorded at the gain settings used during field recordings were not distorted, and for reference levels of intensity (in % in Cool Edit Pro) for the 40 kHz reference tone at each gain setting.

To determine the peak equivalent SPL of signal intensity (peSPL: conversion of intensity from % values displayed in Cool Edit Pro to dB), the reference 40 kHz tone was broadcast toward a ¼ inch Brüel & Kjaer microphone connected to a Brüel & Kjaer sound pressure meter, and the SPL input of the tone over set distances from 1 – 20 m was recorded. This procedure was replicated twice to determine mean SPL (dB re20μPa) of the calibration reference signal over distance (see Appendix 1 for calibration response plot). The relative peak intensity of echolocation calls was then determined from the reference signal SPL measured at 10 m, plus the ratio of the maximum % intensity of echolocation calls relative to the % intensity of the reference signal at the same distance, according to Equation 1:

$$\text{Rel } dB \text{ peSPL}_{\text{peak } f_{\text{req}}} = \text{Ref } dB \text{ SPL} + 20 \times \log_{10}\left(\frac{\text{Peak Amp } \%}{\text{Ref Amp } \%}\right)$$  \hspace{1cm} \text{(Equation 1)}
3.2.3 Extrapolation of Threshold Sound Pressure Levels for Field Crickets

Since direct recording of the AN2 cell in response to particular frequencies (i.e. those found from analysis of echolocation sequences) was not possible, the auditory sensitivity of field crickets to frequencies from 1 – 100 kHz was extracted from data published by Fullard et al. (2005) on the AN2 inter-neuron response in *T. oceanicus* (Figure 3.1).

![Audiogram of the Australian field cricket (*Teleogryllus oceanicus*), presented as the median (bold line) thresholds of response of the AN2 ultrasound sensitive auditory interneuron, with lower and upper ranges (25th and 75th Quartile, lighter lines), for sound frequencies in the ultrasonic range (20 – 100 kHz) (adapted from Fullard et al., 2005). Dashed vertical lines represent mean peak frequencies for search (S), approach (A) and terminal buzz (B) echolocation call phases, depicted here for *S. greyii*. Circles indicate the values extrapolated from the lower quartile threshold of intensity (y axis) at these mean peak frequencies. This process was also applied to extract cricket threshold values at the mean peak frequency of call phases from *N. gouldi*.

The minimum relative threshold of response, indicating detection of acoustic stimuli by the cell, was extracted from the lower threshold values in the cricket audiogram (25th Quartile, bottom light line in Figure 3.1). The 25th Quartile range provides inferences about the minimum intensity at which ultrasound will induce relevant AN2 activity in the field cricket (i.e. levels consistent with predator recognition rates). Since auditory threshold values are dependent on the frequency of peak energy of the sound signal, minimum threshold values for crickets were extracted based on sensitivity at the mean
peak frequency of bat emissions for each call phase (see Figure 3.1, vertical dashed lines for example). The median threshold, indicated by the bold line in Figure 3.1, represents behaviourally relevant sound intensities that will induce escape behaviours established for aerial contexts. Higher thresholds of activation imply a greater predatory threat due to proximity. My primary focus was to quantify those sounds that are just detectable by the crickets (i.e. minimum thresholds), but have included data on median and upper thresholds for comparative purposes. The methodology described henceforth thus applies to extractions at these higher thresholds as well. To determine the relative audibility then of bat emissions to crickets, the effect of sound attenuation (described in the next section) was applied to the mean relative dB peSPL obtained from Equation 1 for each phase, and compared to the respective threshold value as illustrated in Figure 3.1.

3.2.4 Data Transformation to Account for Sound Attenuation

What is heard by crickets on the ground is a diminished version of the source signal emitted by the bat. As sound moves through air, the amplitude emitted from the source, \( p_o \), is attenuated. Again, it is important to note that source intensity levels were not obtained at the time of recording emissions from echolocating bats. Extrapolations in this Chapter are therefore theoretical and made tentatively, based on the available data and key literature of modelling on how bat acoustics are attenuated. At the very least, these provide the first estimated insight on what these sounds might be like on the ground.

The sound level \( p(d) \), at a distance \( d \) (in m), is decreased due to spherical and atmospheric losses, the latter of which is dependent on frequency (Griffin 1971; Lawrence and Simmons 1982; Clare et al., 2011) and climatic variables, in particular temperature and humidity (Clare et al., 2011). Spherical loss can be calculated as:

\[
p(d) = \frac{p_o}{d^2}
\]  
(Equation 2)

Atmospheric loss is defined as:

\[
p(d) = p_o \times 10^{-\frac{m \times d}{10}}
\]
where $m$ (in dB/m) is the atmospheric linear attenuation coefficient, which is a sum of classical and molecular contributions:

$$m = m_{\text{class}} + m_{\text{molec}}$$  \hspace{1cm} \text{(Equation 3)}

with:

$$m_{\text{class}} = (287 + 1.74 \times T) \times f^2 \times 10^{-12} \text{dB/m}$$

$$m_{\text{molec}} = \frac{1.09 \times f \times 10^{-4}}{2 \times \pi \times \frac{f}{k} + k/2 \times \pi \times f} \text{dB/m}$$

where $T$ is the temperature [$^\circ\text{C}$], $f$ is the frequency [Hz], $k = 1.92 \times 10^5$, and $h$ is the % water vapour content of the air.

Relative humidity values were not measured during the recording sessions so I have used the best approximation available from data published by the Bureau of Meteorology (Australian Government, [http://www.bom.gov.au](http://www.bom.gov.au)) for mean monthly values at 1500 hr (53.5%, but likely to be slightly lower at time of recordings at night). Mean temperature for the nights from which data are presented here was 16.7$^\circ\text{C}$. These values are comparable to the conditions Clare et al. (2011) cite when discussing attenuation of the emissions by the big brown bat, *Eptesicus fuscus* (RH = 50%, $T = 18^\circ\text{C}$).

For the ultrasonic emissions of echolocating bats, this means that sound intensity decreases according to the peak frequency of the calls, spreading loss over the distance between the recorder (target, prey) and the bat, and the relative humidity and temperature levels on the night of recording. Taking these conditions together as per Figure 3 in Griffin (1971), the total attenuation of sound is expressed as linear attenuation in dB (LDB) according to Equation 4:

$$L_{\text{DB}} = 10 \times \log_{10}\left(\frac{m \times d/10}{d^2}\right)$$  \hspace{1cm} \text{(Equation 4)}

Equation 4 was then used to determine for each echolocation call phase how much closer from the arbitrary (recording) position, a cricket would need to be (rearranging Equation 4 to yield $d$), so that the sound obtained at the recorder is at an amplitude above the AN2 inter-neuron threshold. To do this, $L_{\text{DB}}$ is determined from the difference
between two known values: the relative intensity of signals at the point of the recording device and the AN2 intensity threshold values from the cricket audiogram (Figure 3.1). Values for \( d \) from Equation 4 were then obtained for each echolocation call phase, for the two bat species.

### 3.2.5 Data Analysis

Suitable foraging sequences obtained from field recordings were categorised into stereotypical phases based on inter-pulse duration as exemplified by Figure 3.2. Search phase signals were characterized based on established criteria: inter-pulse durations greater than 50 ms, the approach phase by intervals of 10 – 50 ms, and the terminal buzz phase of the capture sequence was defined by inter-pulse durations less than 10 ms (Griffin et al., 1960; Fenton 1982; Kalko 1995; Moss and Sinha 2003).

Figure 3.2. Example echolocation pulse pattern from a foraging sequence recorded from *Scotorepens greyii*, illustrating the search, approach and terminal buzz phases as defined by mean inter-pulse duration (ms).

Echolocation calls were analysed in Cool Edit Pro (specifications previously described in Chapter 2, Section 2.2.2) to obtain key characteristics of pulse design, as illustrated in Figure 3.3. The acoustic signature of each bat was defined by six call parameters: start frequency (kHz), end frequency (kHz), pulse bandwidth (start – end frequency, kHz), peak frequency (kHz) at peak energy content of the dominant harmonic, pulse...
duration (in ms), and inter-pulse duration (in ms). Extraction of spectral data was obtained as previously described in Chapter 2 (2048-point FFT power spectrum with Hanning window). Means for each parameter were extracted from the spectral and waveform views for search, approach and terminal buzz call phases, for each species. Then, mean signal amplitude (in %) was used to extrapolate relative dB SPL for each call phase, for the two bat species.

Figure 3.3. Echolocation call parameter analysis in Cool Edit Pro included measuring temporal pulse pattern (top image, inset at left), % amplitude for conversion of intensity values to peak equivalent dB SPL (top, dashed lines to vertical axis), and spectral content (bottom image).
It is well established that acoustic repertoire is related to foraging strategy in bats and there are significant differences in call parameters between aerial hawkers and gleaners (Kalko 1995; Jones and Holderied 2007). Therefore, I confirmed whether there were statistically significant differences between calls recorded from S. greyii and N. gouldi based on the six defining call characteristics sampled, described above. Peak frequency and peak equivalent intensity (i.e. call amplitude, the 7th call parameter quantified from recordings) were used to determine how (theoretically) audible these signals are to field crickets on the ground and thereby any differences in audibility of the two bats to crickets.

The D'Agostino & Pearson omnibus normality test was applied to each data set for the seven key call parameters to verify Gaussian distribution. Data sets that were not normally distributed were transformed for nonlinear regression and outliers automatically detected via the Polynomial: first order analysis (Slope = 0, Q = 1 %), and the normality test reapplied to the data without outliers. Since there was an unequal number of sufficient quality sequences from the two bat species (S. greyii, 14 sequences; N. gouldi, 2 sequences), the sample size between data sets (for the seven call parameters from two bat species at each call phase) were similarly unequal. Statistical analysis was therefore applied to the weighted means, S.D. and n values of the six temporal call parameters for each call phase. Subsequently, a two-way ANOVA with Sidak’s multiple comparison test was applied to determine, for all call parameters, significant differences between bat species and across the three call phases. Statistical analysis was carried out in GraphPad Prism 5.0 (GraphPad Software Inc., La Jolla, CA, USA).
3.3. Results

Acoustic identification of recorded bat species at Gold Creek Reservoir was based on peak frequency, bandwidth and pulse shape (in the spectral view of Cool Edit Pro) of search calls, as compared to a call library and available keys (Dr Roger B Coles; Milne 2002; Pennay et al., 2004) previously described in Chapter 2. Representative pulse patterns and frequency spectra of the two bats identified foraging over the colony of crickets at Gold Creek Reservoir, are presented in Figure 3.4.

![Figure 3.4](image)

Figure 3.4. Representative search phase pulse patterns and frequency spectra from (a) the little broad-nosed bat *Scotorepens greyii*, and (b) Gould’s long-eared bat *Nyctophilus gouldi*.

A total of 243 echolocation sequences were recorded from the little broad-nosed bat (Figure 3.4a), of which 14 (5.65 %) sequences were of sufficient quality for analysis. This set constituted 235 search phase pulses, 123 approach phase pulses, and 221 terminal buzz phase pulses for echolocation call analysis. Only five sequences were obtained from additional bat taxa, all of which came from *Nyctophilus gouldi*. From these, two sequences were of sufficient quality for analysis. Both sequences included search and approach phases (total of 17 and 18 calls, respectively), and one of the
sequences included the terminal buzz phase (a further 19 pulses). The low number of sequences collected from long-eared bats limits the power of statistical analyses presented hereafter, since at best this reflects emissions from only two individual animals. Descriptive statistics on the call parameters for sequences from *S. greyii* and *N. gouldi* (excluding amplitude) are summarised in Appendices 3 and 4, respectively. Differences in these call parameters between species are then further illustrated in Figure 3.5a-f.

### 3.3.1 Within-Species Differences Across Call Phase

All four frequency parameters for calls produced by *S. greyii* (Appendix 3) differ significantly between search, approach and terminal buzz call phases (*p* < 0.0001). Peak frequency and call bandwidth was found to differ significantly across all call phases for *N. gouldi* (Peak Frequency: *p* < 0.0001; Bandwidth: *p* < 0.05 for Search vs Approach, *p* < 0.0001 for all other comparisons; Appendix 4). However, only during the buzz phase did these bats alter the Start and End frequency of their calls significantly (*p* < 0.0001).

Inter-pulse duration in both bats follows the expected ranges of values for search (>50 ms), approach (10 – 50 ms) and terminal buzz phases (<10 ms), with significant differences in mean values between all phases (*p* < 0.0001, see Appendices 3 and 4). Pulse duration decreased significantly from phase to phase for *S. greyii* as they approached targets (*p* < 0.0001). Similarly, *N. gouldi* reduced pulse duration significantly upon approach (*p* < 0.0001 for Search vs Approach) but thereafter there was no difference detected from approach to the terminal buzz phase.

### 3.3.2 Between-Species Differences Across Call Phase

During search phase emissions, *S. greyii* and *N. gouldi* differed significantly in all six call parameters (first set of bars in Figure 3.5a-f). Compared to the little broad-nosed bat, the peak frequency of search emissions produced by Gould’s long-eared bat was significantly higher (*p* < 0.0001, Figure 3.5c). These search emissions from *N. gouldi* were also characterised by longer bandwidth (*p* < 0.0001, Figure 3.5d), and an associated higher start frequency (*p* < 0.001, Figure 3.5a) and lower end frequency (*p* < 0.0001, Figure 3.5b).
Figure 3.5. Comparison of echolocation call parameters between *Scotorepens greyii* (green bars) and *Nyctophilus gouldi* (blue bars) in search, approach and terminal buzz phase emissions recorded in the field. Sample sizes for the number of high quality sequences selected, and number of calls within these, are provided in text. Data plotted are the mean ±S.D. values for (a) Start Frequency, (b) End Frequency, (c) Peak Frequency, (d) Bandwidth (Start – End) Frequency, (e) Inter-pulse Duration, and (f) Pulse Duration. Significant differences between bat species for each call phase are indicated at $p < 0.05$ (*), $p < 0.01$ (**), $p < 0.001$ (***), and $p < 0.0001$ levels (****).
Both inter-pulse and pulse duration of search calls from *N. gouldi* were significantly shorter than those produced by *S. greyii* (*p < 0.0001*, Figure 3.5e,f). These differences are consistent with adaptations in echolocation call design for particular foraging habits; for example, broad bandwidth, higher peak frequency and short-duration search calls in many gleaners (Schnitzler et al., 2003; Jones and Holderied 2007). In terms of AN2 sensitivity in field cricket *T. oceanicus*, the peak frequency of search calls in both bats are very close to the auditory threshold of best sensitivity (around 46 kHz for median threshold levels; Fullard et al., 2005).

Data on the approach phase emissions of these bats also demonstrate significant differences between the species for some call parameters (second set of bars in Figure 3.5b-e). The same trends were detected between the bats as during search phase comparisons. During approach, *N. gouldi* continued to produce broader bandwidth calls (*p < 0.01*) than *S. greyii*, characterised by lower end frequency (*p < 0.0001*) and higher peak frequency (*p < 0.01*). Both species increased the start frequency of their emissions during approach to similar values (~ 72 and 78 kHz, respectively, n.s., Figure 3.5a). Despite pulse duration not differing between the bats (Figure 3.5f), *N. gouldi* produced these calls at a significantly higher rate during this approach phase (significantly lower inter-pulse duration, *p < 0.01*, Figure 3.5e). This may be indicative of long-eared bats adjusting their emissions to avoid echo overlap as has been suggested for other gleaners (Neuweiler 1990; Schnitzler et al., 2003; Russo et al., 2007; Melcon et al., 2009). Based on peak frequency, the approach signals of both bats are again within close-range of the best sensitivity level in the cricket AN2 fibre (compare mean peak frequency values to bold line in Figure 3.1).

Comparisons in the terminal buzz phase yielded very little difference in call design between bats. Call bandwidth and the end frequency of buzz phase emissions from long-eared bats remained significantly different as compared to buzz calls from *S. greyii* (*p < 0.05*, Figure 3.5d), but otherwise there were no differences detected between these bats. Peak frequency was very similar between the bats, reducing to approximately 32 kHz, and pulse duration had also decreased in both bats to < 2 ms. Peak frequency in this case, for both bats, intersects with higher threshold levels in the cricket AN2 audiogram (compare intersection at 32 kHz with bold line in Figure 3.1) and so may be less detectable than preceding phases of foraging sequences based on frequency alone. Additionally, the cricket neural system may fail to reliably encode these very short
bursts of sound based on pulse duration (Nolen and Hoy, 1986; Triblehorn and Yager, 2002; ter Hofstede et al., 2008).

### 3.3.3 Audibility of Bat Emissions – Call Phase and Signal Intensity at the Ground

As previously outlined, source intensity of signals emitted by bats was not obtained. The following description on calling amplitude and inferences of audibility by grounded crickets, is therefore presented with emphasis that these are best approximations given the resources at hand.

Mean relative call amplitude (peak equivalent intensity, conversion from % to relative dB in Cool Edit Pro) for search, approach and terminal buzz phase emissions from *S. greyii* and *N. gouldi* are presented in Figure 3.6 and 3.7, respectively. For the little broad-nosed bat, overall mean call amplitude was calculated (solid black line in Figure 3.6) with sequence means for call amplitude plotted as the spread around this mean (filled circles in Figure 3.6). Because only two sequences were obtained from *N. gouldi*, the bold lines in Figure 3.7 show the overall mean call amplitudes from these two sequences, but filled circles indicate the estimated intensity of individual pulses. Based on these data, there was no significant difference between the bats in call amplitude, at any phase of emissions. However, there was no interaction effect ($F_{2, 83} = 0.28, p = 0.7549$) indicating that the trends observed between these bats are unique to each species. There is thus a possibility that a larger data set for *N. gouldi* may have reflected significant outcomes.

In both bats, there was a significant decrease in call amplitude from the search to approach phase (*S. greyii*: $P = 0.0007$, Figure 3.6; *N. gouldi*: $p < 0.0001$, Figure 3.7). Thereafter, the bats maintained a consistently lower signal intensity that did not differ between the approach and terminal buzz phases.

The calls from the little broad-nosed bat were all below the minimum (25th Quartile) AN2 threshold in the cricket by 6.46, 14.68 and 13.69 dB peSPL for the search, approach and buzz phases respectively. In two sequences that were analysed however, mean call amplitude of search phase signals matched the minimum threshold level of neural response in crickets (compare top two data points in Search phase with value above red dashed line in Figure 3.6).
Figure 3.6. Comparison of estimated sound intensity (dB peSPL) at the ground of search, approach and terminal buzz phase echolocation calls produced by the little broad-nosed bat (S. greyii) during foraging, and the minimum hearing threshold (indicated by the red dashed line with values above) in the field cricket, T. oceanicus. Data points represent mean intensity of calls from recordings made in the field that included 14 search, 12 approach and 8 terminal buzz phases, with overall mean intensity for call phase indicated by the solid black line. The threshold of minimum hearing in crickets is dependent on the peak frequency of the stimulus which in this case was: search = 41.93 kHz, approach = 46.99 kHz, and terminal buzz = 32.08 kHz. *** indicates significant difference (p < 0.001) in the relative sound intensity of search phase calls as compared to other call phases.
Figure 3.7. Comparison of estimated sound intensity (dB peSPL) at the ground of search, approach and terminal buzz phase echolocation calls produced by Gould’s long-eared bat (*N. gouldi*) during foraging, and the minimum hearing threshold (indicated by the red dashed line with values above) in the field cricket *T. oceanicus*. Data points represent the intensity of calls from recordings made in the field that included 2 search and approach phase sequences, and 1 terminal buzz phase sequence, with mean intensity for call phase type indicated by solid black line. The threshold of minimum hearing in crickets is dependent on the peak frequency of the stimulus which in this case was: search = 44.22 kHz; approach = 48.56 kHz; terminal buzz = 31.66 kHz. *** indicates significant difference (p < 0.001) in the relative sound intensity of search phase calls as compared to the other phases.
Overall, based on these recordings obtained at the position of field crickets on the ground, the signals from foraging *S. greyii* flying overhead appear to be largely undetectable by crickets in the wild.

Although at all phases, call amplitude from *N. gouldi* was lower than minimum threshold intensities for AN2 activation, the difference was smaller in these bats than in *S. greyii*. This is because the higher peak frequency of emissions from *N. gouldi* reflects lower response thresholds in the cricket AN2 fibre. Subsequently, signal intensities differed less as compared to *S. greyii*, by 1.62, 12.38 and 8.18 dB peSPL for search, approach and terminal buzz phases, respectively. Importantly, although the overall patterns are similar between the two species, there is a higher proportion of search phase pulses from *N. gouldi* that are above threshold. Nonetheless, as with *S. greyii*, most emissions from long-eared bats flying above grounded crickets would most likely be undetectable from the ground. This however, is based on AN2 recordings from flying female crickets. Since auditory responsiveness is thought to be diminished in walking individuals (Orida and Josephson 1978; Staudacher and Schildberger 1998; Triblehorn and Yager 2006) the threshold levels may potentially be even higher, and thus bat emissions even less detectable, when crickets are grounded.

### 3.3.4 Audibility of Bat Emissions – Distances Required for Detection

For signals to be of an amplitude sufficient to match the minimum (25\(^{th}\) Quartile) sensitivity threshold of AN2 fibres in *T. oceanicus*, both species of bats had to be closer to the microphone at the time of recording. In Figure 3.8, the change in distance between the arbitrary position of a cricket (*d*\(_0\)) at the time of recording and the echolocating bat (*d*\(_i\)) which would yield signal amplitudes to be at threshold levels, is illustrated for the three call phases with respect to the sensitivity threshold levels of the cricket AN2 fibre.

For calls emitted by *S. greyii*, a listening cricket on the ground would need to be at least 1.37 m, 2.37 m and 2.6 m closer to the bat for the minimum threshold of AN2 response (line at Q25 in each box for *S. greyii*) to be activated by search, approach and terminal buzz phase signals, respectively. Extending on this, values for the median (Q50) and upper (Q75) quartile ranges of AN2 response are also indicated at each call phase. The median range represents the behaviourally relevant threshold;
Figure 3.8. Proximity (distance closer to bat, m) required for the estimated amplitude of calls from an echolocating bat (at $d_i$) to activate AN2 auditory fibres in $T. oceanicus$ crickets ($d_0$) at different auditory sensitivity thresholds (25th – 75th Quartile ranges, as published in Fullard et al., 2005). **Top panel:** a listening cricket ($d_0$, far left) represents ground position where recordings were obtained in the field, relative to foraging bats flying overhead at an arbitrary distance ($d_i$, far right). **Middle** (*S. greyii*) and **Bottom** (*N. gouldi*) Plots: Calculated distances grouped by call phase (Search, Approach, Buzz), with vertical lines within boxes (Q25, Q50, Q75) representing distances at which bat call amplitude for each call phase would activate the cricket AN2 fibre at 25th, 50th and 75th Quartile sensitivity thresholds.
that which induces evasive steering from bats (Hennig et al., 2004; Fullard et al., 2005). At these higher threshold values, the distance to a bat becomes increasingly closer: 1.86 – 3.51 m closer based on call phase at the median threshold level, and 2.53 – 4.09 m closer for Q75 thresholds.

The corresponding values of distance closer to a bat determined from the emissions produced by *N. gouldi* are lower at all threshold levels. A cricket positioned closer to the bat by 0.9 m (search), 2.01 m (approach) and 1.71 m (buzz) would theoretically enable the emissions of *N. gouldi* to be detectable at the 25th Quartile range of AN2 sensitivity (see lines for Q25 at each call phase in bottom plot of Figure 3.8). For the median and upper thresholds, proximity of a cricket to the echolocating bat for the three call phases ranges from 1.26 – 2.75 m (Q50) and 1.98 – 3.33 m (Q75) closer. These trends indicate that the signals from *N. gouldi* were louder and thus may be more detectable than those from *S. greyii*. However, in light of observations of the respective bats’ foraging in the field (*S. greyii* at higher levels than *N. gouldi*), it is possible that the quantified intensities of emissions from these bats are indicative of their proximity to the recording microphone. Again, this is suggested tentatively. If indeed this is true, then the small range of distance over which signals by long-eared bats become detectable (i.e. 0.9 m at best for early avoidance typically elicited by search phase emissions) reflect that these predators were in fact foraging closer to the ground at the time of recording, than *S. greyii*. Ultimately, the distances from bats under the best case scenario (detection of search phase signals within proximity of 1.37 m for *S. greyii* and 0.9 m for *N. gouldi*) may imply notable differences in the crickets’ capacity for long-range detection of these two bats.
3.4. Discussion

This Chapter describes the acoustic repertoire of emissions (search, approach and terminal buzz phases, Figure 3.5 and Appendix 2-3) for two bat species, Scotorepens greyii and Nyctophilus gouldi, that were observed foraging in the wild overhead a population of field crickets at Gold Creek Reservoir. Their call design aligns with characterisations for their respective foraging guilds (Schnitzler et al., 2003; Pennay et al., 2004) and provides new records for the South East Queensland region. Although based on only two sequences for N. gouldi, differences between the species were consistent for all identifying call features from the search phase emissions. Gould’s long-eared bat (a gleaner) emits calls of shorter duration, higher peak frequency and longer bandwidth than those from the aerial hawker, S. greyii.

The (conservatively estimated) amplitude of calls recorded from bats appears to suggest that neither species is detectable by grounded crickets at Gold Creek Reservoir, at any call phase, despite expectations that at least search and approach emissions would be so. All calls were estimated to be below cricket (T. oceanicus) AN2 threshold levels irrespective of emission phase (Figure 3.6 and 3.7). For emissions to be potentially audible to crickets, both bat species would need to be closer to crickets (the microphone) by at least 0.9 – 1.37 m under the most stringent conditions (Figure 3.8, distances at Q25 for search phase emissions from N. gouldi and S. greyii, respectively).

3.4.1 Implications of Estimated Audibility on Cricket Detection Ranges

Inferences about the relative amplitude of bat calls and their audibility to grounded crickets, are indicative only in light of limitations in methodology. In contrast to expectations, calls from S. greyii appear to be generally softer than those from N. gouldi (Figure 3.6 and 3.7); however, these differences in relative amplitude are likely due to the proximity of bats at the time of recording. Verification of this would come from measurement of source intensity levels at the time of foraging and direct measurement of bat distance from the microphone(s) (Holderied et al., 2005; Berger-Tal et al., 2008; Surlykke et al., 2009; Brinkløv et al., 2011; Stilz and Schnitzler 2012). From my observations S. greyii generally foraged higher than N. gouldi (within 5 m and 3 m above the ground, respectively) which fits within foraging heights described
for these species (Churchill et al., 1984; O'Neill and Taylor 1986; Lumsden and Bennett 1995; Brigham et al., 1997; Lloyd et al., 2006). Nevertheless, at the (unknown) distances over which echolocation was captured my estimates suggest that neither species’ emissions are likely to be of sufficient amplitude (> 70 dB peSPL at the microphone) to be detectable by grounded crickets let alone activate predator avoidance behaviours (Fullard et al., 2005).

These extrapolations on echolocation audibility are based on published AN2 sensitivity in *T. oceanicus* but may be similar for the focal cricket species here *T. commodus*, at least from behavioural indicators. Nolen and Hoy (1986) found that negative phonotaxis was elicited in both species over 30 – 60 kHz (frequencies that overlap with bat echolocation here) at intensities of 55 – 60 dB SPL; thresholds were slightly higher in *T. commodus* than *T. oceanicus* by approximately 5 dB at 40 kHz, but consistent with *T. oceanicus* at 50 kHz (closest ranges for comparison to peak frequency of search calls from *S. greyii* and *N. gouldi*). These measurements are comparable but slightly lower than the behaviourally relevant AN2 thresholds in *T. oceanicus* (bold line (Q50 values) in Figure 3.1) characterised by Fullard et al (2005). A conservative estimate then may be that *T. commodus* are comparably but slightly less sensitive than *T. oceanicus* to the bats foraging overhead at Gold Creek Reservoir, meaning their calls are even less audible. This of course requires verification from detailed characterisation of the auditory response properties of *T. commodus*, and is an important caveat for future work.

Since signal source intensity was not determined and such information for *S. greyii* and *N. gouldi* is not available in literature, a reasonable estimate of intensity ranges may be indicated by species from comparable foraging guilds. Holderied et al. (2005) reported echolocation call intensities from the aerial hawker *Eptesicus bottae* in the range of 105 – 115 dB peSPL with the bat at 2 – 3 m away, while at standard levels (10 cm from the bat’s mouth) values range from 100 – 115 dB peSPL for some *Myotis* spp. and pipistrelles (Surlykke et al., 1993; Waters and Jones 1995; Richards et al., 2004) and up to 121 – 137 dB peSPL from the most recent assessment of a range of aerial insectivores by Surlykke and Kalko (2008). In contrast, documented levels from gleaners such as *Myotis evotis*, *M. septenriionalis*, *Plecotus auritus*, *P. townsendii*, range between 60 – 80 dB peSPL (Faure et al., 1990; Faure et al., 1993; Waters and Jones 1995; Fenton 2000) with upper limits of 100 – 110 dB peSPL (Miller and Treat
Under conditions of the lowest source levels therefore, crickets at the study site may detect signals if they were originally emitted at approximately 100 dB peSPL from *S. greyii* and 80 dB peSPL from *N. gouldi*, with upper limits in the range of 130 and 110 dB, respectively. Values around 80 – 90 dB SPL are consistent with “realistic estimates” of source emissions from *N. geoffroyi* by Fullard et al (2005) and ter Hofstede et al (2009). These signals may then continue to reduce in intensity as a gleaner adjusts calls to suit sonar range in a cluttered environment (Miller and Treat 1993; Jones 1999; Russo et al., 2007; Jakobsen et al., 2013; Weinbeer et al., 2013).

The critical detection range in crickets (the distance over which initial detection and avoidance is elicited) appears to be greater for aerial hawking bats than gleaners (Fullard et al., 2005). In that study *T. oceanicus* preparations were tested with calls from *Nyctophilus geoffroyi*, a gleaner purported to inhabit Enoggera State Reserve, but which I did not detect during field work. Emissions from these bats were characterised by a peak frequency of 66.5 kHz, which is more than 20 kHz higher than values quantified for *N. gouldi* in the current study. Based on peak frequency, bandwidth and pulse duration, calls from *N. gouldi* are more comparable to the emissions of another bat tested by Fullard et al (2005), *Chalinolobus gouldii*. AN2 was first stimulated by calls from *C. gouldii* at a source level of 95 dB peSPL, and by *N. geoffroyi* at 105 dB peSPL, equating to approximated distances of < 1.5 m and < 2 m, respectively, and up to 10 m and 5 m respectively, at higher intensities (Fullard et al., 2005). Critical thresholds that would evoke behaviourally relevant responses before the distance at which the bat would detect the cricket (3.5 – 10 m), required calls to be at 125 dB peSPL for both species and equated to detection distances of 5 m for calls from *C. gouldii* and 3.5 m for *N. geoffroyi*. However, such intense calls are unlikely for *Nyctophilus* spp. (Acharya and Fenton 1992; Pennay et al., 2004; Fullard et al., 2005).

A theoretical estimate of the initial distance of recorded bats at the study site, based on search phase emissions and lower estimates of source intensity, would equate to 7 m between the aerially hawking *S. greyii* and a grounded cricket, and 2.12 m for *N. gouldi*. Bats were proposed to be detectable at behaviourally relevant AN2 thresholds (Q50 values in Figure 3.8) if they were closer by 1.86 m (*S. greyii*) and 1.26 m (*N. gouldi*). Within these conditions, the critical distance of detection by crickets for *S. greyii* may thus be about 5 m, which would be beyond the target detection range of
the bat (Cronin and Sanderson 1994; Kalko 1995; Fullard et al., 2005; Comer and Baba 2011; Stilz and Schnitzler 2012). In contrast, *T. commodus* would have a critical distance of only 0.86 m with *N. gouldi*. The collective implications from Fullard et al (2005) and ter Hofstede et al (2009) based on *N. geoffroyi* and *T. oceanicus* suggest an initial detection estimate of only 2 m, reducing the potential detection range even further. Importantly, both of these estimates equate to distances within the bat’s detection range of the prey (Schnitzler et al., 2003; Stilz and Schnitzler 2012; Pollack 2015), and when the predator is already approaching. For the grounded crickets at the study site then, these short distances for initial detection would provide very little time to effectively respond and evade a bat predator.

With respect to the most relevant predator for grounded crickets (*N. gouldi* as a gleaner), if signal intensity is further decreased during approach (Miller and Treat 1993; Jakobsen et al., 2013), acoustic information would be altogether absent or redundant for influencing any avoidance behaviour. Indeed, walking and singing field crickets do not demonstrate any response indicative of detection of *N. geoffroyi* when emission intensities are below 82 dB peSPL (ter Hofstede et al., 2009). Dynamic adjustments in signal intensity on a task-specific basis may also limit the acoustic cues available to crickets: intensity compensation rates up to 30 dB occur in some bats over a range of 7 m to 2 m from detected targets (Norum et al., 2012). Detection ranges by crickets for both bat species are likely to be even lower than my estimates if impedance of these signals through grass is also taken into account (Parsons 1996; Pritz 2004; Londhe et al., 2009). At the time of recordings, grass height was at its lowest (~ 10 cm) but it can reach levels up to 50 cm throughout the year. The true extent of ultrasound impedance across this range of clutter is unknown, but its limitations on acoustic detection of bats by *Teleogryllus* crickets is further doubtful. Given the passive role the ground vegetation might serve for cricket defence however, a key question is whether these sounds are behaviourally relevant at all even at audible levels on the ground. Specifically, do crickets ‘choose’ to not respond even if they can hear these signals?

At least two bat species are foraging in close proximity (< 5 m) directly overhead grounded field crickets at Gold Creek Reservoir however, estimates of their audibility suggest they may be undetectable by crickets on the ground. Any encounter (acoustically or directly) between these crickets and bats will be in close proximity such
that both detection and evasion will likely occur within 2 m of the predator. Those calls that crickets may be most sensitive to, as inferred from neural, behavioural and extrapolated findings on detection distances, originate from aerial hawking bat species that are not going to forage for prey on the ground. However, echolocation calls from gleaning specialists such as *Nyctophilus* spp. may not be detectable over critical distances (> 2 m). Verification of these first estimates and further detailed characterisation of the bats foraging at this site, could reveal highly relevant insight on the range of detectable signals available to crickets on the ground.
3.5. References


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Chapter 4.

Responses of Walking *Teleogryllus commodus* to Bat Echolocation: Differences Between the Sexes and the Relevance of Shelter.
4.1 Introduction

Chapter 2 describes one example setting where terrestrial interactions between *Teleogryllus commodus* and three bat species (*Nyctophilus gouldi*, *N. bifax* and *Rhinolophus megaphyllus*) may be occurring. A fourth bat was detected, the aerial hawker *Scotorepens greyii*, directly above crickets, who may prey on females as they fly toward calling males. In Chapter 3, the acoustic environment for these crickets was examined since along with *S. greyii*, the gleaner *N. gouldi* was also detected foraging in close proximity. The cautious estimates there suggest neither of these bats are likely to be audible to crickets on the ground, probably because they are too far away. In this Chapter, I remove the distance factor by exposing walking male and female crickets to bat echolocation presented in close proximity. Then, I begin to examine the relevance of the ground environment in prey defence, presenting calls to crickets when cover is available.

Ultrasound-induced behaviour in crickets is context-dependent since silent, walking individuals do not display evasive responses (Pollack et al., 1984; Nolen and Hoy 1986; ter Hofstede et al., 2009). However, only calls from gleaning bats have been presented (ter Hofstede et al., 2009), as these represent the most relevant predators on the ground. In this Chapter, I examine how grounded field crickets (male and female *T. commodus*) respond to emissions from a range of bats that represent a mix of predatory risks: a low-risk aerial hawker (*Miniopterus australis*), a possible-risk aerial hawker (*S. greyii*) and a high-risk gleaner (*N. bifax*). All of these bats are sympatric with *T. commodus* across Australia (Churchill 2008; Atlas of Living Australia 2015), and two species co-exist in close proximity at Gold Creek Reservoir. However, the extent to which they directly interact with crickets (Chapter 2, Section 2.3.3), and models of neural sensitivity in *T. oceanicus* across foraging guilds (Miller and Surlykke 2001; Agosta et al., 2003; Fullard et al., 2005; ter Hofstede et al., 2009; ter Hofstede et al., 2013; Pollack 2015), suggest they may exert different selection pressures. To examine if proximity of a predator, as encoded from the rate of arriving signals, alters cricket behaviour, echolocation calls were also presented to crickets at increasing pulse repetition rates.
Emissions from *M. australis* were presented to field crickets because evidence implies they will be unlikely predators of crickets (Chapter 1, Section 1.2: despite dietary evidence for Orthoptera, unsuitable morphological and foraging characteristics for focal prey) and they were not detected anywhere near *T. commodus* at Gold Creek Reservoir (Chapter 2, Section 2.3.3). The possible risk *S. greyii* poses was discussed in Chapter 1 and 2; briefly, apart from dietary and morphological attributes (Section 1.2) they forage in close proximity to the ground (within 5 m; pers. obs.; Churchill 2008) and so may encounter approaching, aerial females. I was therefore interested in how walking crickets would respond to their calls, which in the field appeared to be inaudible (Chapter 3). Tests with these bat species would confirm that grounded crickets do not respond to the emissions of aerial hawkers. Calls from *N. bifax* (rather than *N. gouldi*, Chapter 3) were presented to crickets to represent the most relevant bat predator in the terrestrial setting. This was the species from which emissions were available at the time of testing, and upon subsequent discovery of *N. gouldi* in the field it was not possible to re-examine cricket behaviour to their emissions. However, the bats may be equally relevant and similar terrestrial predators. *N. bifax* inhabits the immediate edges of Gold Creek Reservoir and although not acoustically detected directly above crickets, could be foraging over this landscape as well (Fenton 1982; Churchill et al., 1984; Duncan et al., 1999; Churchill 2008). They are morphologically, behaviourally and acoustically well-equipped to glean prey (Fenton 1982; Churchill et al., 1984; Crome and Richards 1988; Duncan et al., 1999; Pennay et al., 2004; Churchill 2008) and so are also capable for preying on ground dwelling field crickets at the site. Indeed, Chapter 5 brings both *Nyctophilus* species together with *T. commodus* to examine their live interactions.

If any of the three bat species induce avoidance-like behaviour in walking crickets, I expected this to be with calls from *S. greyii*. Whilst this is contrary to context-dependent associated risks, these bats may be the species that females at least, are best tuned to. This prediction is based on *T. oceanicus* sensitivity to aerial hawkers (Fullard et al., 2005) and how closely *S. greyii* occurred at the study site. The echolocation profile of *N. bifax* is comparable to the signals from *N. geoffroyi* used by ter Hofstede et al (2009), and these species are acoustically highly overlapping (Pennay et al., 2004). Therefore, if walking crickets are particularly insensitive to calls from long-eared bats
and generally to such gleaners (Fullard et al., 2005; ter Hofstede et al., 2009), evasive behaviour should be absent. Emissions from *M. australis* were hypothesised to not elicit any evasive behaviour if they are not relevant natural predators either in the air or on the ground. For tests on predator proximity (pulse repetition rate), if crickets respond to any particular bat, I expected avoidance behaviour to be more pronounced at rates consistent with approach and terminal buzz phase emissions.

To date, there exists just one investigation on the responses of walking, rather than calling, male crickets exposed to bat echolocation (ter Hofstede et al., 2009) and here, the sexes were equally unresponsive. This is important since assumptions on relative exposure risk suggest the divergent life habits of crickets should lead to sex-specific differences in sensitivity to bats (Pollack 1982; Pollack and Plourde 1982; Otte and Alexander 1983; Cardone and Fullard 1988; Yager 1990; Stumpner and Heller 1992; Acharya 1995; Mason and Bailey 1998; Pollack and Martins 2007). Based on these predictive indices (discussed further below), I expected female *T. commodus* to display avoidance behaviour more consistently than males.

If bat echolocation is difficult or not at all reliably detected by crickets due to vegetation clutter, it seemingly represents an unreliable cue to base behavioural decisions upon (Nolen and Hoy 1986; Marsat and Pollack 2012; Ostrowski and Stumpner 2013). Behavioural decisions may therefore stem from the environment as a passive source of defence. Some moths for example remain close to or within vegetation to minimise encounters with foraging bats (Andersson et al., 1998; Rydell 1998; Svensson et al., 2002). Such mechanisms have also been recognised in crickets (ter Hofstede et al., 2009) but not investigated further despite the importance as a generalised avoidance strategy in many insects (Wallin and Ekbom 1988; Larsson et al., 1997; Hedrick and Kortet 2006; Abarca et al., 2014). Here, shelter (cover) is defined as any space in contrast to the open.

Seeking shelter from an exposed position requires decisions about moving at all, and then the direction of movement (towards or away; Ydenberg and Dill 1986; Bonenfant and Kramer 1996). Sex-specific differences may be evident here, due to their relative risk of exposure to bats. Since male crickets are largely non-volant and generally well hidden within vegetation (Campbell and Shipp 1979; Evans 1983), covered space
should be a recognised and preferred habitat; open space reflects a starkly different physical zone where they are highly exposed to predation (Sakaluk and Belwood 1984; Hedrick and Dill 1993). Seeking shelter should thus be a strong trait in male crickets. For females, seeking shelter may be an important strategy because they are more mobile and conspicuous to predation through their movements (Hedrick and Dill 1993). Moving into shelter would be important when they first land on the ground (Hedrick 2000), and then across a matrix of space when seeking calling mates. For both sexes, there would be conflicting implications on shelter seeking when presented with a predator in the direction of refuge. Not moving at all reduces the cues available to a predator but leaves the prey exposed (Brodie 1977). Moving away will maximise distance attained, but at the cost of exposure and being easier to track along the line of path that localisation initially occurred (Shifferman and Eilam 2004; Ghose et al., 2006). Moving towards shelter, a high-risk decision, could disrupt this initial spatial map for the predator (Domenici et al., 2011) and yield the high reward of crypsis for the prey when shelter is reached (Brodie 1977; Kramer and Bonenfant 1997).

The relative ecological importance of shelter and how it used was investigated by testing whether male and female *T. commodus* recognise, and preferentially move to cover or remain in the open. Playback trials to simulate the presence of a bat predator within this covered zone were then carried out to evaluate how any shelter seeking behaviour is impacted by a bat’s presence. Crickets here were presented with calls from the gleaner *N. bifax*, since of the three species tested, this bat would represent the most ecologically relevant sounds (if emitted and detectable) on the ground.

I expected crickets to recognise and preferentially move to closed space, reflected by repeated localisation of cover and moving to it sooner over successive trials, and for males to more readily find and move to covered space. If shelter is an important and preferred space for any cricket, the presence of an echolocating bat within should set up a conflict of choice: move into cover but toward the predator, or stay away. Given it is unknown altogether how the terrestrial environment impacts on the behaviour of walking crickets, these experiments offer important and novel insight. As a first step therefore, determining any change in shelter seeking behaviour by crickets in the presence of bat echolocation was important to assess.
4.2 Methods

4.2.1 Animals

Colonies of *Teleogryllus commodus*, obtained from Dr Paul Cooper (Australian National University, ACT, Australia), were maintained in the laboratory on a 12:12 hr day:night light cycle at 20 – 24 ºC, and fed on carrots and water *ad libitum*. Males and females were kept separate as soon as their sex was identifiable (indicated by the appearance of the ovipositor in adult females) and individuals up to 21 days after the final moult were used in experiments. Each insect was tested once in individual experiments. To examine the responses of walking crickets to different bat species and call designs that simulate proximity of the predator, 30 male and 30 female field crickets were tested. In subsequent experiments investigating how bat echolocation impacts on shelter use by crickets, 10 males and 21 females were used (10 males and females in two experiences during control (-Bat Calls) trials, 11 females in two experiences during experimental (+Bat Calls) trials). Full description of experimental conditions and number of animals that completed the trials, is described in Section 4.2.5.

4.2.2 Experimental Setup

All experiments were carried out under near-dark conditions (illumination from 8W fluorescent emergency exit sign in laboratory) within a trapezoid arena (H50 cm; base dimensions: L56 cm x W40 cm; top dimensions: L72 cm x W56 cm) enclosed with fly screen. Acoustic stimuli were amplified (NAD Monitor Series Stereo Amplifier, Model 3100) and delivered through a Fountek speaker at one end of the arena. The speaker was placed 45 cm from and pointed toward the centre of the arena floor at a downward angle of 56.3º. This produced the maximum intensity of any sound in the middle of the floor, as determined during the calibration process (described below). A Bat Detector (Ultra Sound Advice S-25, London, UK) on the opposite end of the arena was used to register and record acoustic stimuli via direct stereo feed into a Sony Digital Handycam (DCR-TRV520E PAL) mounted directly above the middle of the arena floor, at a height that provided maximum field of view. All experiments were recorded onto digital Hi-8 film under Nightshot mode. Black photography cloth lined with sound-attenuating foam
was suspended around the arena to minimise sound leakage and any disturbance from observer presence.

4.2.3 Acoustic Stimuli

Single pulses of bat echolocation calls were obtained from real-time recordings made at Enoggera State Reserve via the methodology detailed in Chapter 2 (Section 2.2.2). Calls were collected from three species of Australian bats sympatric with T. commodus at Enoggera State Reserve that represented a range of predation risks to crickets as outlined in Section 3.1 above: High Risk – eastern long-eared bat (Nyctophilus bifax); Possible Risk – the little broad-nosed bat (Scotorepens greyii); and, Minimal Risk – the little bent-wing bat (Miniopterus australis). Calls from the High and Minimal Risk bats could reflect allotonic frequencies if tuning in T. commodus is similar to published accounts on the congener T. oceanicus (Fullard et al., 2005).

Individual, high quality pulses from each bat (Figure 4.1) were imported into an Arbitrary Waveform Generator (AWG, Agilent E1441A) via Agilent Intuillink Waveform Editor software. This program was also used to generate the first of two controls, an amplitude-modulated 5 kHz cosine wave (30 ms duration) to elicit positive phonotaxis (Pollack and Plourde 1982; Pollack and El-Feghaly 1993). The second experimental control, white noise, was included to account for all frequencies to which crickets were exposed, and was generated from the built-in noise function of the AWG.

For each stimulus, the speaker was calibrated with reference to a pure tone equivalent to the peak frequency of the signal type. Using a ¼ inch condenser microphone (Brüel and Kjær) the speaker and amplifier were attenuated to provide an intensity range of 83.5 dB peak equivalent sound pressure level (peSPL re. 20 µPa) for the 5 kHz pure tone burst, and 78.5 – 81.5 dB peSPL for the bat pulses, as detected at the centre and furthest end of the arena floor (45 – 100 cm from speaker). Since white noise consists of all frequencies at the same intensity, this signal was attenuated within the AWG to the same relative amplitude as the bat echolocation calls and the pure tone-burst (150 mVpp). These signal intensities are all higher than those estimated from echolocating bats foraging in the wild (see Chapter 3) and above the behaviourally relevant threshold for the respective peak frequency of each signal and known to induce negative phonotaxis in flying females or interrupted calling behaviour in singing males.
(Moiseff et al., 1978; Moiseff and Hoy 1983; Miles et al., 1992; Pollack and El-Feghaly 1993; Fullard et al., 2005; ter Hofstede et al., 2009).

Eastern long-eared bat
*Nyctophilus bifax*

Little broad-nosed bat
*Scotorepens greyii*

Little bent-wing bat
*Miniopterus australis*

Figure 4.1. Pulse patterns and frequency spectra of echolocation calls presented during playback trials to grounded, freely moving male and female *Teleogryllus commodus*. 
Table 4.1 summarises the signal characteristics that a total of 11 stimuli crickets were presented with during the series of open space (without cover), playback trials. To simulate search, approach and terminal buzz phase calls (Schnitzler and Kalko 2001), signals were delivered at repetition rates of 2, 40 and 100 pulses per second respectively, manipulated via the AWG. All of these pulse rates are consistent with the emission phases analysed from wild foraging bats in Chapter 3. These are pre-set rates in the AWG, thus for the calls from S. greyii (11.95 ms) approximately 83 pulses were delivered over the duration of one second. This rate is still however consistent with terminal buzz phase calls for these bats and well above the rate at which neural processing fails (Samson and Pollack 2002). For ease of reference, this call condition is listed as “100 pps” henceforth. In the open arena experiments (see below), male and female crickets (n = 30 of each sex) were exposed to all signals to test for sex-based differences in responsiveness and if any particular echolocation call design (bat species and pulse repetition rate) was more effective at inducing evasive behaviour.

<table>
<thead>
<tr>
<th>Stimulus</th>
<th>Peak Frequency (kHz)</th>
<th>Pulse Duration (ms)</th>
<th>Repetition Rate (pps)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pure Tone</td>
<td>5</td>
<td>30</td>
<td>16</td>
</tr>
<tr>
<td>White Noise</td>
<td>1 - 100</td>
<td>*</td>
<td>*</td>
</tr>
<tr>
<td>Nyctophilus bifax</td>
<td>64.2</td>
<td>6.28</td>
<td>2 40 100</td>
</tr>
<tr>
<td>Scotorepens greyii</td>
<td>38.4</td>
<td>11.95</td>
<td>2 40 100</td>
</tr>
<tr>
<td>Miniopterus australis</td>
<td>59.2</td>
<td>6.48</td>
<td>2 40 100</td>
</tr>
</tbody>
</table>

I was unable to determine any one call that induced consistent bat avoidance behaviour in walking crickets (see Results) so in the second series of experiments (cover available) I exposed crickets (n = 11 females) to emissions from N. bifax (40 pps, 10 second pulse train), based on the higher risk that gleaning Nyctophilus spp. are described to represent in this context. These tests were used to investigate the significance of shelter in performing predator avoidance behaviours. Only female crickets were tested because males did not demonstrate consistent recognition of
shelter and so would not reliably demonstrate preferential movements between shelter and open space (see Results).

4.2.4 Open Space Experiments: Effect of Call Design between Sexes

In the first series of experiments, *T. commodus* males and females were exposed individually to each of the stimuli in Table 4.1, delivered in random order. A cricket was placed into the centre of the testing arena and allowed two minutes to become accustomed to its surrounds. Each stimulus was then broadcast for 10 seconds, with 30 seconds of silence before and after stimulation (total time per trial = 70 seconds), allowing at least 60 seconds of silence between each signal presented to avoid habituation to the sound by crickets (Wyttenbach and Hoy 1997). During testing, the cricket’s movement was uninhibited, and since the timing of stimulation was predetermined, the insect may or may not have been moving when the signal was presented. I accounted for variation in behaviour across individual insects before and after stimulation by maximising the total number of individuals tested (n = 30 for each sex). If a cricket did not move after five minutes in the arena (two minutes pre-stimuli time + 11 x 10 second trials) it was removed from the experimental pool altogether. To avoid habituation by crickets to the direction of the sound source, the speaker position was alternated between the two ends of the testing arena, once during the experiment (at trial 5 or 6).

A conservative range of criteria were defined to determine what sort of behavioural response a stimulus elicited in *T. commodus*. Unlike neural recordings of acoustic detection and motor response generation, behavioural observations have shown to not return reliably consistent outcomes (Fullard et al., 2005; ter Hofstede et al., 2009). Any behaviour that was ambiguous or was the same after stimulation as before was scored as ‘No Response’. To demonstrate ‘Evasion’, a cricket had to respond to the stimulus by moving or turning away from the sound source (if the insect had been still or moving prior to stimulation) or stopping and freezing (if moving prior to stimulation). There were insufficient observation counts of each of these behavioural subcategories and so all such responses were subsequently scored as ‘Evasion’. A cricket that moved or turned toward the sound source was deemed to have shown ‘Attraction’ to that stimulus. Thus, there were three cricket behaviours scored from video recordings.
of the trials: No Response, Evasion and Attraction. These behaviours were determined from responses performed in the first second of stimulation.

4.2.5 Cover Experiments: Significance of Shelter in Response to Echolocation

The second series of experiments tested how the behaviour of seeking shelter (cover) is affected by bat echolocation, and if there are differences in these responses between the sexes. To simulate shelter, fly screen was placed over 25% of one end of the arena, 15 cm above the floor (see methods of Hedrick and Dill 1993). The covered end of the arena was randomly assigned between individual crickets, and the floor wiped with a clean wet cloth to minimise odour cues from previous individuals.

To establish how shelter seeking behaviour is demonstrated by both sexes (control condition, -Bat Call), and then affected by bat echolocation calls (experimental condition, +Bat Call), individual crickets were tested in the arena with 25% cover, over successive experiences as follows. In the first trial (1st Experience), a cricket was placed on the centre of the arena floor (separated from the cover by the same amount (25%) of open space). It was then allowed five minutes to find the covered end, and to explore and ‘learn’ the spatial layout, before being removed. The time taken by a cricket to find cover was recorded. After a five minute resting period, the same cricket was placed back into the arena (2nd Experience), and the time to find cover again recorded. During control testing (-Bat Call), crickets (n = 10 males and females) were tested over both Experiences. In the experimental series of tests, crickets (n = 11 females) were given five minutes to find cover in their 1st Experience, in silence. During their 2nd Experience, the stimulus from *N. bifax* (detailed in Section 4.2.3) was played from the covered end 10 seconds after the cricket was placed into the arena, and the time taken to find cover recorded again. Control experiments indicated that this delay time before stimulation was sufficient for crickets to begin moving, but less than the shortest time taken to move to cover during their 2nd Experience. These experiments therefore set up a conflict of choice for crickets to investigate whether they will move into shelter despite the predator’s simulated presence, or stay away and thus remain in the open.

If a cricket did not find cover in the 1st Experience (two of 10 males in control condition, one of 11 females in experimental condition), it was not put into a 2nd Experience. If a
cricket did not find cover within five minutes during its 2nd Experience (three of 11 females in experimental condition), rather than scoring 300 seconds which would skew data by inflating mean values, I removed these crickets from the data set for both 1st and 2nd Experiences. Data were therefore a conservative estimate of the effect of bat call because no single female failed to move to cover during the 2nd Experience under the control trials (-Bat Call). In contrast, even after 300 seconds, three males failed to move to cover during the 2nd Experience under control trials (-Bat Call). I interpreted crickets that found cover sooner in their 2nd Experience, as demonstration of shelter seeking behaviour and preference for closed, rather than open space.

4.2.6 Data Analysis

For the open space experiments, I determined the frequency of each response observed (evasion, attraction, non-responsive) for each stimulus, and for male and female crickets. I then used a multinomial model to test whether responses differed in relation to the sex of crickets or to the call design (species and repetition rate), and if there was an interaction between the two variables such that the sexes responded differently to the various stimuli. This involved two separate analyses: one to test the effect of stimulus type (5 KHz, white noise, or the three bat species' calls pooled by repetition rate) on the crickets' response, and another to test the effect of varying repetition rate of the bat species' calls. The analysis of stimulus type and cricket sex was conducted as an among-subjects (crickets) analysis because there was no within-subjects replication of the 5 KHz and white noise treatments. Hence, only one treatment combination was used from each cricket. Call repetition rate and cricket sex was conducted as a within-subjects analysis, with tested individuals (cricket ID) as a random factor. This latter test allowed me to test for variation in the responses of crickets that were not associated with the treatment effects. The among-subjects analysis was performed using the 'multinom' function from the 'nnet' package for R (Venables and Ripley 2002; R Development Core Team 2010). The mixed-effects (within-subjects) analysis was performed using the 'clmm' and 'clm' functions from the 'ordinal' package for R (Christensen 2010).

From video recording of cover experiments, the time (sec) taken by crickets to find cover was extracted for both Experiences in the two series of experiments. Then, time
to cover in the 2nd Experience was calculated as a proportion of time in 1st Experience and differences in this change, referred to as normalised time to cover, tested for. These experiments aimed to determine whether males and females differ in the change in time to find cover. In the second series of experiments where data were compared for females between -Bat Call and +Bat Call conditions, I aimed to determine if responses differed between conditions. To test differences between the sexes, a one-tailed, paired t-test was applied to the original data on 1st and 2nd Experience time to cover in male and female crickets. Data from the second series of experiments testing females with and without bat echolocation were analysed using a one-tailed, unpaired t-test. Statistical analysis was carried out using GraphPad Prism 5.0 software (GraphPad Software Inc., La Jolla, CA, USA).
4.3. Results

4.3.1 Open Space Experiments

Sex Effects and Stimulus Type

The predicted mean probabilities for each response category that crickets demonstrated in open space experiments are given in Table 2. There was no interaction between sex and stimulus type (Likelihood ratio $\chi^2 = 10.464$, df = 8, p = 0.234), and there was also no main effect of sex (LR $\chi^2 = 1.168$, df = 2, p = 0.558). This implies that sex did not contribute to any differences in behaviour, and males and females were not responding differently to any stimulus type (controls and bat species). The results in Table 2 therefore represent the statistical output following pooling for sex. There was a significant effect of cricket individual ID (LR $\chi^2 = 6.306$, df = 1, p = 0.012) indicative of a large inter-individual variability but small intra-individual variability. However, a significant effect of stimulus type was detected (LR $\chi^2 = 17.642$, df = 8, p = 0.024).

Table 4.2. Mean response probabilities of field crickets (T. commodus) compared for stimulus type (controls and bat species), derived from the most parsimonious among-subject multinomial model and pooling for sex.

<table>
<thead>
<tr>
<th>Behaviour</th>
<th>5 kHz</th>
<th>White Noise</th>
<th>N. bifax</th>
<th>S. greyii</th>
<th>M. australis</th>
</tr>
</thead>
<tbody>
<tr>
<td>No Response</td>
<td>0.33</td>
<td>0.83</td>
<td>0.5</td>
<td>0.5</td>
<td>0.67</td>
</tr>
<tr>
<td>Evasion</td>
<td>0</td>
<td>0.17</td>
<td>0.5</td>
<td>0.33</td>
<td>0.33</td>
</tr>
<tr>
<td>Attraction</td>
<td>0.67</td>
<td>0</td>
<td>0</td>
<td>0.17</td>
<td>0</td>
</tr>
</tbody>
</table>

Table 4.3. Mean response probabilities of field crickets (T. commodus) compared for echolocation pulse repetition rate (in pulses per second), derived from the most parsimonious among-subject multinomial model and pooling for bat species.

<table>
<thead>
<tr>
<th>Behaviour</th>
<th>2 pps</th>
<th>40 pps</th>
<th>100 pps</th>
</tr>
</thead>
<tbody>
<tr>
<td>No Response</td>
<td>0.59</td>
<td>0.64</td>
<td>0.64</td>
</tr>
<tr>
<td>Evasion</td>
<td>0.31</td>
<td>0.29</td>
<td>0.27</td>
</tr>
<tr>
<td>Attraction</td>
<td>0.10</td>
<td>0.07</td>
<td>0.09</td>
</tr>
</tbody>
</table>

For effects of bat species and control noises, crickets showed the highest probability of responding positively (‘Attraction’, 0.67) to the control stimulus intended to simulate
the conspecific call (5 kHz), with no likelihood of evasive behaviour in the presence of this signal. Similarly, white noise elicited the expected behaviour in both male and female crickets, with a mean probability of 0.83 for ‘No Response’. When comparing the effect of bat call origin (species), ‘Attraction’ was the least likely response (mean probabilities range: 0 – 0.17, see Table 1), but this analysis did not yield convincing data for eliciting ‘Evasion’ (mean probabilities range: 0.33 – 0.5). Unreplicated stimulus treatments (5 kHz and white noise) were subsequently removed from the analysis, and the analysis re-applied as a mixed-effects model, comparing just the bat calls. Again, there was no significant interaction between sex and stimulus type (LR \( \chi^2 = 0.991, df = 4, p = 0.911 \)), nor was there a main effect of sex (LR \( \chi^2 = 1.121, df = 2, p = 0.571 \)) or stimulus type (LR \( \chi^2 = 1.24519, df=4, p= 0.871 \)). The pooled probabilities from the most parsimonious model were ‘No Response’ = 0.64, ‘Evasion’ = 0.29 and ‘Attraction’ = 0.07. The significant effect of stimulus type in the among-subject analysis prior to removing the 5 kHz and white noise treatments from analysis was largely a consequence of the effects of these control treatments. Overall, when presented with the nine bat calls above threshold, male and female crickets show no response.

**Echolocation Pulse Repetition Rate**

The effect of call repetition rate on cricket behaviour was determined from trials using the bat call signals only (i.e. excluding controls), again comparing responses between the sexes. No significant interaction was detected between sex and Repetition rate (LR \( \chi^2 = 0.066, df = 2, p = 0.968 \)), and no effect of sex alone was evident (LR \( \chi^2=1.186, df = 2, p = 0.553 \)). Data from male and female crickets were therefore pooled to determine the predicted mean probabilities for responses based on call rate (Table 3). There was no significant effect of repetition rate (LR \( \chi^2 = 0.728, df = 2, p = 0.695 \)) with the pooled probabilities from the most parsimonious model being: ‘No Response’ = 0.65, ‘Evasion’ = 0.25 and ‘Attraction’ = 0.09. ‘Evasion’ by crickets was more probable than ‘Attraction’ (Table 3, compare at all repetition rates), but crickets in general did not distinguish between bat echolocation call patterns. Again, there was also significant variability in the crickets’ responses that was not explained by the experimental treatments (LR \( \chi^2 = 9.271, df = 1, p = 0.002 \)). Together with the outcome of the first analysis on stimulus type, these experiments indicate that no particular bat echolocation call design is more potent in influencing the behaviour of crickets than
another and that the most likely response of walking crickets to bat echolocation is ‘No Response’.

4.3.2 Cover Experiments

Male and Female Shelter Seeking Behaviour

A significant difference was detected between the sexes in their ability to locate cover (Figure 4.2), with only females showing evidence of the ability to ‘learn’ where covered space was available. As a proportion of 1st Experience times, females moved to cover in their 2nd Experience significantly faster than males (one-tailed unpaired t-test, \( p = 0.0121 \)) and varied in the individual normalised values significantly less than males (\( F(7,9) = 56.2, p < 0.0001 \)).

Females moved to cover in about half the time during their 2nd Experience in the arena (normalised mean ± SEM 2nd/1st Experience: 41.7 ± 10.6 %), while male time to cover increased two-fold (239.7 ± 88.6 %). All 10 females tested found cover the first time, and all of them moved to cover faster during their 2nd Experience (mean ± SEM time...
(sec) to cover: 1st Experience = 124.4 ± 28.7; 2nd Experience = 40.9 ± 9.7; unpaired t-test; F(9,9) = 8.781, p = 0.0047). Whereas eight of the ten males found cover in the 1st Experience, only three males moved to cover sooner during their 2nd Experience. Subsequently, there was no significant difference in the change in time to cover between Experiences for males (mean ± SEM time (sec) to cover: 1st Experience = 86.8 ± 26.5, 2nd Experience = 121.1 ± 42.2; unpaired t-test, variance – n.s., p = 0.5012). Since *T. commodus* males failed to demonstrate a preference for cover they were excluded from the second series of cover experiments which were focused on determining how preference for cover in the first place is altered by predatory stimuli.

Figure 4.3 illustrates normalised 2nd Experience time to cover as a proportion of 1st Experience times demonstrated by females during silence (-Bat Call, n = 10) and in the presence of bat echolocation (+Bat Call, n = 7). Of the 10 females that found cover during their 1st Experience, three failed to find cover at all when presented with calls from *N. bifax* during their 2nd Experience. Based on the remaining seven females seeking cover in the presence of bat echolocation, these did not move to covered space any sooner than during the 1st Experience (Figure 3, +Bat Call, mean ± SEM 2nd/1st Exp % = 103.1 ± 35.5). Thus, compared to silent conditions, the mean proportional time to cover from these seven females was significantly greater and variance significantly higher (Figure 3, -Bat Call vs +Bat Call, one-tailed, unpaired t-test, F(6,9) = 7.876, p = 0.0367). The shelter seeking behaviour females demonstrated in silence appeared to have been disrupted by the acoustically simulated presence of a bat within the covered region of the arena.
Figure 4.3. Mean ± SEM time taken by female crickets to move to cover in silence (-Bat Call, n = 10) and in the presence of echolocation calls (+Bat Call, n = 7), following two experiences in the testing arena with cover. Data represents 2nd Experience time taken to move to cover as a proportion of the time taken during 1st Experience (Normalised time to cover, %). * denotes significant difference to -Bat Call (p < 0.05).
4.4. Discussion

This Chapter aimed to characterise avoidance behaviour by grounded field crickets (*Teleogryllus commodus*) in response to echolocation calls from bats. These signals did not elicit any obvious change in behaviour by walking male or female crickets, regardless of bat species (Table 4.2) or predator proximity (repetition rate, Table 4.3). The sexes did not differ in their responses, both being unresponsive to the stimuli and displaying ambiguous behaviours. The chapter also aimed to examine the relevance of one physical feature of the terrestrial environment in the behavioural defence repertoire of grounded crickets: the presence of shelter. Only female *T. commodus* show preferential seeking of covered space (Figure 4.2) but this behaviour appeared to be disrupted by echolocation calls from *N. bifax* (Figure 4.3), suggesting recognition of predatory risk. To my knowledge this is the first demonstration of some degree of ultrasound-induced change in behaviour in freely moving field crickets on the ground.

4.4.1 Absence of Cricket Response to Echolocation in Open Terrestrial Settings

Since there was no consistently demonstrated avoidance behaviour from walking male or female crickets irrespective of echolocation call design, it was not surprising that the sexes did not differ. Some extent of variation was expected however, because of the relative exposure risk implied by the life habits of male and female crickets (largely substrate bound and comparatively cryptic males; Evans 1983; Otte and Alexander 1983; Evans 1988). For example, flight incapable (and therefore less exposed to bats) male *Gryllus texensis* demonstrate markedly reduced behavioural and AN2 sensitivity to ultrasound as compared to flight capable morphs (Pollack and Martins 2007). Sex-specific differences based on risk of exposure to bats have also been implicated in other insects (e.g. in moths: Cardone and Fullard 1988; praying mantis: Yager 1990; bushcrickets: Stumpner and Heller 1992; Acharya 1995; katydids: Mason and Bailey 1998). Despite this, the most recent characterisation of neural sensitivity to bat echolocation by male and female *T. oceanicus* suggests little dissimilarity, and behaviourally, they are equally inconsistent (ter Hofstede et al., 2009). The results of the current study align with these conclusions for the southern congener of Australian *Teleogryllus*, and that neither sex recognised the tested bat signals as a predatory
threat. This suggests context, rather than relative exposure risk, is a determining factor for cricket behaviour to ultrasound.

The absence of a clear, consistent avoidance behaviour in walking field crickets was evident irrespective of the bat species of origin or call repetition rate. Differential tuning for bats (Fullard et al., 2005; ter Hofstede et al., 2009) and graded responsiveness to predator proximity (Schul and Sheridan 2006; Marsat and Pollack 2012), are therefore not indicated from these results. Further, the signals from *N. bifax* are similar to emissions from *N. geoffroyi* presented to *T. oceanicus* (based on frequency, and previous characterisations; Milne 2002; Pennay et al., 2004; ter Hofstede et al., 2009). Thus *T. commodus* crickets were also unresponsive to a potential gleaner, but equally so for the calls of other bat species that previous predictions suggest crickets may be better tuned to.

Acoustic proximity also does not appear to be a relevant factor. The intensity of all calls presented to crickets (81.5 dB peSPL) was within behaviourally relevant AN2 thresholds for *T. oceanicus* (Moiseff et al., 1978; Moiseff and Hoy 1983; Miles et al., 1992; Pollack and El-Feghaly 1993; Fullard et al., 2005) and just slightly higher than the most intense signal from a gleaner these crickets were exposed to by ter Hofstede et al (2009). The intensity of the three bat calls is also higher than the behavioural thresholds at which negative phonotaxis is elicited in *T. commodus* (albeit during flight; Nolen and Hoy 1986). The crickets in the current study should have been capable therefore, of detecting the bat signals presented to them yet they did not respond. For responses to *S. greyii*, the species whose emissions were estimated to be inaudible to grounded crickets in the field (Chapter 3), even when these signals should be audible, crickets did not demonstrate avoidance behaviour. These results therefore raise the question if crickets are simply ‘choosing’ to not respond even to detectible bat echolocation, when they are within a terrestrial setting.

These findings highlight further that the terrestrial context may diminish the responsiveness of crickets to (any) bat signals. However, if the passive strategy of environmental crypsis is sufficient to reduce the detectability of crickets by bats (Svensson et al., 2002; ter Hofstede et al., 2009), this classic, acoustically-mediated avoidance behaviour may not be necessary anyway. This is particularly so if any
assessments of an approaching bat, especially those that can achieve close distances on the ground, can be obtained through alternative sensory modalities (Tauber and Camhi 1995; Jacobs et al., 2008; Hartbauer et al., 2010). Under these conditions then, any active behaviour by crickets would probably involve late-stage emergency responses only.

4.4.2 Shelter Elicits Changes in Behaviour in the Presence of Ultrasound

In the absence of bat echolocation, when crickets were presented with the choice to move under cover or remain in the open, there was a significant dichotomy in shelter seeking behaviour between the sexes, in contrast to predictions; only *T. commodus* females reliably displayed this preference for cover over successive trials. The divergent lifestyles of the sexes as a function of adaptive significance may be an important factor in this. Higher conspicuousness of some male lizards due to their colouration has been linked to greater predation risk and flight to shelter being initiated earlier than in females (Martín and López 1999; Lailvaux et al., 2003). Male *Gryllus integer* seek cover more frequently and remain within it longer than females as an adaptation to being in a high-predation environment from arachnids and reptiles (Hedrick and Kortet 2006). Moreover, adult females demonstrate a greater extent of “boldness” through risk-taking behaviours (e.g. exploration of novel environments) and males ontogenetically become shyer over their life (Hedrick and Kortet 2012). The cautious tendency of males has been extensively demonstrated for *G. integer* in terms of calling behaviour, refuge use and emergence from shelter (Hedrick 2000; Hedrick and Kortet 2012) and ascribed to their relatively sedentary, cryptic life where exposure to predators is lower than for the mobile females. Such sex-specific differences may also apply to *T. commodus* given their similarly dichotomous life habits and use of space. The usual cluttered microhabitat of male *T.commodus* crickets on the ground (Evans 1983) would reflect a habitat of low/minimal risk from bat predation, since it provides a consistent means of remaining relatively inconspicuous (Rainho et al., 2010). They are also less mobile than female crickets and across a relatively short, stable matrix of space (Otte and Alexander 1983; Evans 1988). Male *T. commodus* are therefore less likely to move out of their sheltered habitat into an unfamiliar setting, and thus shelter seeking behaviour when they are in the open may be diminished in comparison to females (Hedrick and Kortet 2006). This could then indicate why males
that did eventually find cover within the allotted time of testing took longer than female crickets. I did not explore this outcome further as my aims were to assess the relevance of cover use in a predator-prey setting (i.e. requiring recognition of cover in the first place), which hereafter concerns *T. commodus* females only.

Seeking shelter, rather than remaining in the open, was a consistent behaviour displayed by female field crickets in the absence of bat echolocation, suggesting these crickets recognise open and closed space, and preferentially move to be within shelter. Whilst a far larger sample size would be required to generalise that female crickets have better spatial learning and recognition than males, their repeated performance of this behaviour is indicative of a consistent difference in choices made by the sexes (Hedrick and Kortet 2012). This cover seeking behaviour by females appeared to be subsequently disrupted by the presentation of echolocation calls from *N. bifax* (Figure 4.3) from within this shelter, and crickets stayed away for longer. This was the only sound that crickets were tested with and so it is also possible that any signal (other than conspecific songs that would attract them; Moiseff et al., 1978; Nolen and Hoy 1986) could elicit this response. However, whilst these tests may not definitively indicate that crickets recognised the source of the sound as *N. bifax*, their consistent display of staying away suggests the sound is not attractive (Karlsen et al., 2004) and thus avoidance of an undesirable stimulus.

Predator induced changes in shelter seeking behaviour have been demonstrated in a number of other animals (Balakrishnan and Pollack 1996; Kramer and Bonenfant 1997; Stankowich and Coss 2006; Cooper and Frederick 2007) and is an obvious outcome when the preferred microhabitat of the prey is compromised by the presence of a predator (e.g. Savino and Stein 1989). This is especially the case if seeking shelter is a key mechanism by which prey can avoid predators altogether (e.g. mice: Dickman 1992; snails: Turner 1996; gobies: Schofield 2003; field crickets: Hedrick and Kortet 2006). Indeed, by remaining in the open, female crickets tested here appeared to be choosing to stay in what constitutes a relatively high risk, conspicuous position, especially given their recurrent movement into the preferred region of cover during control experiments (Hedrick and Kortet 2012). This is a limited conclusion however, since it excludes many complex factors that drive prey escape responses such as the availability of alternative refuges (Domenici et al., 2011). Indeed, shelter is available
to *T. commodus* in all directions and in very close proximity at Gold Creek Reservoir (Chapter 2, Section 2.3.2) in which case staying in the open might not necessarily be the demonstrated behaviour. In other animals such as cockroaches, crabs and lizards moving into shelter in the presence of a predator appears to be the primary goal irrespective of the cues such activity elicits, because of the cryptic value a refuge ultimately provides if reached in time (Brodie 1977; Woodbury 1986; Bonenfant and Kramer 1996; Domenici et al., 2009; Zani et al., 2009). The absolute significance of behavioural decisions to move into cover or not, could therefore be further elucidated where the responses of grounded crickets to bat echolocation are tested with shelter available over a range of escape angles.

Without the presence of additional refuge in the current study, staying away from shelter but from which echolocation calls were broadcast, may then reflect decisions by crickets to maximise their distance from the perceived threat (Domenici and Batty 1997; Cooper and Hawlena 2007; Stankowich and Coss 2007; Domenici et al., 2009). Further, the longer time it took for most individuals to move into cover (three failed to do so at all) in the presence of echolocation, suggests these females may have been delaying their response. Such a strategy would be advantageous to crickets on the ground. Generally, delayed reactions will minimise unnecessary energy expenditure induced by fleeing and maximise time for other biologically important tasks such as feeding and mate interaction (Ydenberg and Dill 1986; Cooper and Frederick 2007); delaying will also enhance the prey’s ability to monitor a predator (Hall et al., 1986; Cooper 2008; Martin et al., 2010) and thus initiate the most appropriate response when it is truly necessary and/or most cost-effective. This latter model has been demonstrated in the arctiine moth *Bertholdia trigona* in the presence of echolocating bats (Corcoran et al., 2013). Here, the defensive tactic of sonar-jamming is selectively deployed by moths in response to approach phase emissions only, stages of bat detection that signify a “legitimate threat”. The delayed movement to cover by *T. commodus* in the presence of echolocation, could similarly reflect an assessment period of the potential threat; their subsequent movement into shelter sometime after the cessation of these signals may then imply evaluation that the threat is gone.

The delayed response exhibited by crickets in this study would also be effective if refuges are readily available and in close proximity, but prey immobility hinders the
predator’s capacity to locate them amongst clutter in the first place (Nunes et al., 2015). Indeed, the density of pond vegetation within which prey are hidden greatly scatters, and thus masks, returning prey echoes for foraging *Myotis daubentonii* (Boonman et al., 1998). Predation success is also greatly reduced in *Myotis myotis*, a typically adept ground gleaner, when crickets are offered amongst high density clutter (93 – 100 % of vegetation); bats wait longer (up to 10 minutes) to initiate an attack, taking up to 12 minutes after landing in their vicinity to capture prey, and ultimately capturing only 40% of prey, a marked reduction from the near-complete success rate during foraging tasks in sparser clutter (Rainho et al., 2010). This study highlighted the economic efficiency for bats searching for hidden crickets within dense vegetation.

Based on these bats’ body mass (25 g; Rainho et al., 2010) *M. myotis* would need to capture a cricket every 15 minutes over a typical foraging time of 3 hours. For their comparable mass, *N. bifax* and *N. gouldi* (8.6 g and 8.0 g respectively; Churchill 2008) would need half the energy requirements in a single night (Speakman 2003); this equates to six crickets which still seems a significant amount. When amongst vegetation, remaining temporarily immobile could therefore be a significantly effective and sufficient strategy for *T. commodus* to discourage further attack by terrestrially foraging bats. This delay model may then explain why investigations to date, which have only examined cricket responses in context of playback trials in the (relative) open, have observed relatively non-responsive individuals (although, see conditions for male crickets in ter Hofstede et al., 2009). Delayed escape behaviours would also align with assumptions that selection pressure for predation in a terrestrial context is relatively infrequent (i.e. only respond when a directed attack actually ensues), or occurs with predators that have circumvented the cricket’s ability to acoustically detect them over long distances (and thus demonstrate early-stage evasion).

The results from this Chapter re-inforce previous models of context-dependent prey behaviour, and provide some further insight on the responses elicited in field crickets when exposed to terrestrial encounters with echolocating bats. Neither male nor female *T. commodus* respond (or seem to choose) to echolocation from a range of sympatric bat species. Herein, the influence of the terrestrial environment (shelter availability) on cricket defence mechanisms is important, since at least female *T. commodus* seemed to preferentially choose cover over open space but did not do so,
or delayed in moving toward cover, in the presence of emissions from *N. bifax*. The cryptic value of environmental clutter in the ground setting may ultimately represent an initially sufficient source of passive avoidance of bats whereby active evasive tactics are not needed or are delayed; thereafter, only in close proximity with such a predator would a response be necessary and executed, in which case crickets may only demonstrate emergency escape behaviours.
4.5. References


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Chapter 5.

Live Interactions Between Naïve *Nyctophilus* Bats and *Teleogryllus commodus*. 
5.1. Introduction

The collective body of understanding on Australian long-eared bats describes a genus whose members are evidently quite flexible in their foraging habits, feeding on both volant and ground dwelling insect prey (O’Neill and Taylor 1986; O’Neill and Taylor 1989; Milne 2006) and within a diverse range of vegetation structures (O’Neill and Taylor 1989; Fullard et al., 1991; Lumsden and Bennett 1995; Young and Ford 2000). Despite the generalist hunting approach this might suggest, all members of *Nyctophilus* spp. are consistently described as gleaners with the capacity for passive localisation of prey (Fenton 1982; Duncan et al., 1999; McKenzie et al., 2002; Churchill 2008). These habits are characterised in more detail for four members of the genus (including *N. gouldi*) from just a few laboratory investigations (Grant 1991; Cronin and Sanderson 1994; Hosken et al., 1994; Bailey and Haythornthwaite 1998). This Chapter aimed to extend on these investigations.

From the previous chapters, the Australian field cricket (*T. commodus*) may not hear echolocating bats from the ground (Chapter 3) as they forage overhead, and is not responsive to their emissions even when these are presented in close proximity (Chapter 4) at presumably detectable levels (Moiseff et al., 1978; Pollack et al., 1984; Fullard et al., 2005; ter Hofstede et al., 2009). This suggests crickets simply choose not to respond, or at least that active avoidance behaviours are not displayed possibly because they are not necessary in the terrestrial context (Cooper 2008; Ratcliffe et al., 2008; ter Hofstede et al., 2009). The recognition by female crickets of covered (vs open) space and subsequent disruption to moving into this space in the simulated presence of *N. bifax* (Chapter 4), suggests that the physical environment (refuges) may be an important element in their repertoire of general predator avoidance (Domenici et al., 2011). Within the clutter of vegetation, long-range acoustic detection of bats by crickets may be diminished (Londhe et al., 2009; Pollack 2015) and active avoidance behaviours not necessary until very late when a predator is close. In this Chapter, I place potential predator (*N. gouldi* and *N. bifax*) and prey (female *T. commodus*) in close proximity, to examine how they interact.

Experiments were carried out under controlled conditions within a confined space to facilitate close characterisation of behaviours. Within this, I considered the naivety of the tested bats critical. I define naivety by the minimal time bats were held in captivity,
and the absence of prior training of prey localisation and capture. These criteria are highly comparable to the conditions of testing carried out by Geipel et al (2013). If from their sympatric distribution at the study site and across Australia (Atlas of Living Australia 2015) there is a historical association with one another (or at least with cricket-like prey), then capture of grounded *T. commodus* by naïve *Nyctophilus* bats should not be a novel task.

With respect to the bats, my key questions were: (1) whether substrate foraging on field crickets is a familiar task in naïve individuals; and, (2) whether these behaviours are consistently associated with a specific acoustic strategy (echoic or passive, or a combination of both).

If gleaning is a preferred strategy of hunting in the wild, then this should be associated with regular foraging on those types of prey that are typically found on the ground (Denzinger and Schnitzler 2013). If this is true for *Nyctophilus* spp., then the individuals tested here should demonstrate a specific set of behaviours when hunting crickets as compared to typically aerial insects (moths). However, if gleaning is used opportunistically, then context (terrestrial setting) is the main influencing factor. In this regard, *Nyctophilus* bats should employ a consistent set of behaviours to glean all insects they encounter, simply because they are encountered on surfaces. Because evidence to date suggests these bats exploit a wide range of habitats reflected by a diversity of insects in their diet (reviewed in Chapter 1 and outlined above), I expected the bats to display context-dependent foraging irrespective of prey type.

Acoustically, previous research on *Nyctophilus* bats implies that gleaning is accompanied exclusively by passive listening for prey-generated sounds (from their movement and the calls of males; Grant 1991; Cronin and Sanderson 1994; Hosken et al., 1994; Bailey and Haythornthwaite 1998). In this study, possible cues from crickets that bats could detect include crickets walking on the artificial grass floor or the fly mesh walls of the testing arena (Grant 1991; Arlettaz et al., 2001; Marimuthu et al., 2002; Goerlitz et al., 2008; Holderied et al., 2011). The auditory sensitivity of *N. gouldi* certainly indicates high sensitivity to the frequency and intensity of such sounds (Guppy and Coles 1988). How exclusively passive localisation is relied upon during prey capture by *Nyctophilus* spp. is however, variably reflected from past research and lacks empirical characterisation: complete absence in *N. gouldi* and *N. geoffroyi* (Grant
1991), switched off by *N. geoffroyi* at some (undefined) point prior capture (Cronin and Sanderson 1994). In other gleaners, the silent period (when echolocation is switched off prior to contact) ranges from 50 ms to over 1 second (Faure et al., 1990; Faure and Barclay 1994; Arlettaz et al., 2001; Ratcliffe and Dawson 2003), highlighting the flexible manner in which echoic and passive strategies may in fact be utilised (Faure et al., 1990; Faure and Barclay 1994).

The cues available to bats from field crickets were altered by offering live and intact individuals, deafened, and dead crickets. If any echolocation is detectable by field crickets during their interactions with long-eared bats, these cues would be eliminated for deafened crickets and these ‘unaware’ crickets may be more active than hearing individuals providing relatively more audible cues for bats. Dead crickets would provide no auditory cues for the bats and they should not be able to locate these prey if passive localisation is relied on exclusively during terrestrial foraging tasks. Given the evidence to date about the use of echoic and non-echoic strategies for terrestrial foraging by *Nyctophilus* bats, I expected echolocation to be absent during capture of live (intact) and deaf crickets.

For field crickets, this investigation aimed to address the following key questions: (1) do grounded crickets show early-stage responses to *Nyctophilus* bats, including patterns indicative of recognition and early avoidance; and, (2) do they demonstrate a consistent (final-stage) escape response during predatory encounters with bats.

These experiments aimed to elucidate what (if any) responses crickets produce in the presence of a live bat. I did not measure the intensity of bat signals but within the small confines of the testing space most emissions were expected to be detectable by crickets (Imaizumi and Pollack 2001; Pollack 2003; Fullard et al., 2005). If field crickets are detecting the bats and the primary strategy is to minimise conspicuousness in general, avoidance behaviours like freezing and remaining spatially distant from bats should be evident. Should bats attack field crickets, emergency tactics will be the most obvious response. This probably erratic display, should be defined by speed, direction and magnitude to maximises the distance of escape and hinder pursuit attempts by the predator (Shifferman and Eilam 2004; Eilam 2005).
5.2. Methods

5.2.1 Study Site

The experiments for this chapter were carried out within a storage room beneath the Moggill Creek Catchment Group (MCCG) Headquarters building at Gold Creek Reservoir, Enoggera State Reserve (Queensland, Australia, 27S 27' 35.44', 152E 52' 55.69'). All tests on animals were conducted at night between 1800 hr and 0100 hr, in the dark.

5.2.2 Animals

*Nyctophilus* bats were targeted for testing. Based on their common distribution across Australia, hardiness in captivity, adept flying capacity in close confines and gleaning behaviour, these bats were the only suitable candidates for study from the species consistently observed at Enoggera State Reserve (Chapter 2). All bats were captured by harp trapping, and released at their site of capture after testing. At no time during their holding in captivity did any bat show signs of distress. Additional to the insects they consumed during experiments, bats fed on mealworm and were housed in cloth bags in a dark room during the day. Bats were identified in the hand, to the species level with reference to Churchill (2008).

Relatively few *Nyctophilus* spp. were trapped. Of 58 bats captured over 33 trapping nights in 2008, only seven (12%) represented members of this genus. From the 102 bats trapped in 2009, just 15 individuals (15%) were long-eared bats. The 2008 field season served as a pilot study for subsequent controlled testing of animals in this Chapter. Of the 15 long-eared bats caught in 2009, a very disappointing small number of individuals (two *N. bifax* and three *N. gouldi*) completed the full experiment. Ethical constraints meant that bats could be held for no more than two nights. Together with the overall duration of testing time for each of four trials (described below), a maximum of two animals could be tested and held over the two nights. The 15 *Nyctophilus* captured in 2009 were obtained from just five of the total number of trapping nights. On four of these occasions, more than two individuals were found in traps and so excess animals had to be released, leaving seven animals to test. Of this subject pool, one individual never moved from the onset of testing and another failed to complete the full experiment due to inactivity on the second night. These individuals were
therefore discarded from the testing cohort, leaving five bats upon which this study is based. Whilst a larger number of animals would have been desirable, my sample size is comparable to previous studies of terrestrial foraging by captive bats (e.g. Arlettaz et al., 2001; Stamper et al., 2008; Holderied et al., 2011; Geipel et al., 2013; Ubernickel et al., 2013). At the very least, these bats provide an assay for their interactions with crickets, and some important future directions of research.

Since trapping attempts in the field failed to yield a sufficient number of wild *Teleogryllus commodus* (described in Chapter 2), bats were tested with individuals from the established laboratory colony (second and third generation offspring of individuals obtained from Dr Paul Cooper, Australian National University, ACT, Australia). However, tested species of bats are sympatric in distribution with *T. commodus* across some parts of Australia, and at the field study site (as determined from acoustic and trapping records around Gold Creek Reservoir, see Chapter 2). In each of the three trials where crickets were the target prey (live and intact, deaf and dead), bats were presented with five females. Crickets were deafened by piercing the tympana on both forelegs with a surgical (2 mm) needle and scrambling the ascending auditory fibres within the tympanal canals. Pilot work validated this procedure through phonotaxis trials with calling males, to which they will normally move if auditory capacity is intact, but consistently failed to do so once deafened. Phonotaxis trials were carried out on all deafened females used for the experiments in this Chapter as well.

To test the behaviour of bats with an alternative insect prey, moths were used and this served as the fourth prey condition for foraging trials. Moths were light trapped near the MCCG headquarters building using a mercury vapour light suspended in front of a white poster board, and individuals caught by hand when they approached the light. Moths were chosen based on size (body length < 2 cm) to contrast the large size of field crickets (~ 4 cm). These were not identified to the species level since their selection was simply to offer bats morphologically different, and typically volant, prey. A total of 60 individuals were tested with each bat in these experiments (12 moths per bat).
5.2.3 Experimental Setup

All interactions between bats and insects occurred in a 1 m\(^3\) arena enclosed with fly mesh which is comparable to some previous work (Geipel et al., 2013) and was a necessary requirement for optimal resolution of recording (see below). A trap door on one side allowed access into the arena. The arena was raised 50 cm above the ground, and the arena floor lined with artificial grass (approximately 0.5 cm in height) into which crickets could not burrow. The walls of the testing room were lined with sound-attenuating foam to reduce signal echo. Experiments were conducted in complete darkness; however, the arena was covered with black photography fabric to exclude any possibility of incidental light.

Interactions between bats and insects were recorded onto Hi-8 film through an infrared camera head facing the front of the arena, with direct input into a Sony Digital Handycam (DCR-TRV520E PAL; 25 frames/sec, 29.8 kbps bitrate). The infrared camera head was positioned to provide the best depth and field of view for maximal resolution (optimised during pilot tests), with the Handycam and observer positioned outside the room housing the testing arena. Acoustic recording of audible and high frequency (echolocation) sounds was obtained via a Bat Detector (Ultrasound Advice S-25, London, UK; frequency range: 15-200 kHz; sensitivity: 10 dB SPL at 50 kHz, same device described in previous Chapters) with input through the Audio/Video ID2 socket on the camera (audio sampled at 32 kHz, 1024 kbps bitrate). Pilot testing demonstrated this setup would provide detectable sounds, although it does not enable sophisticated analysis of bat echolocation since the recording setup leads to down-sampled data.

The recording apparatus described here was the best quality available to me. A more sophisticated set up would enable a higher resolution of video capture and acoustic examination of the interaction between bats and crickets. Detailed cricket behaviour was not subsequently possible to consistently track because of poor resolution in the video footage of these black insects under the dark conditions of testing. However, human observation (watching through the Handycam monitor) accompanied the full duration of all trials at the time of their recording and from these records, crickets demonstrated very little activity in general (see Data Analysis section below). Close inspection of video recordings was carried out from five minutes prior to capture of a
cricket until consumption by the bat concluded, thereby providing some indication of the prey's behaviour (and relative level of activity) before a directed attack. The acoustic setup allowed the best possible quantification of the extent of echolocation used by bats during foraging tasks, and whether this changed over the duration of approach to capture of prey. If *Nyctophilus* were using exceptionally soft calls, these would not be obtainable from the down-sampled recordings. The use of a single detector could also lead to softer emissions produced from a bat facing away from the microphone being undetected (although, see Geipel et al., 2013).

**5.2.4 Interactions Between Bats and Insects**

Upon initial introduction into the testing arena, a bat was allowed 30 minutes to acclimatise to the spatial confines (sufficient amount of time as determined from pilot investigations in 2008). In order to prevent bats from knowing the positions of insects ahead of time, they were re-captured with minimal physical disruption (bats readily moved under a bat bag), insects introduced into the arena and after some time (~10 mins) the bat was re-introduced. Prey were placed randomly on the floor and walls of the arena. Interactions between predator and prey were tested individually for each bat; each bat was exposed once, to each of the four prey condition trials (live and intact crickets, deaf crickets, dead crickets (five individuals in each case); and 12 live moths). Experiments were carried out over two nights (two prey trials per night, each trial lasting one hour). The order of trials for each bat was randomised.

**5.2.5 Data Analysis**

To characterise the behaviour of bats with each prey condition, the focal animal sampling technique (Altmann 1974) was applied to video recordings, as optimised during pilot work. This method provides an appropriate estimate of the typical range of behaviours demonstrated by animals at any time as long as the sampling windows are frequent and long enough to represent all behaviours. The number of samples from each animal also needs to be equal to avoid bias toward highly active individuals (Altmann 1974). Video recordings were sampled every minute for 20 seconds, counting the number of times the a bat exhibited a behaviour: head scanning, crawling on the floor, crawling on the wall, flying, and echolocation emissions alone (i.e. when a bat is perched, still and echolocating). Only behaviours that commenced within the sampling period were scored; events already underway were omitted. An example
record of focal sampling is provided in Appendix 5, yielding 45 sampling periods per trial. Each period could include the same behaviour being demonstrated multiple times. I considered an event (behaviour) ending when another event commenced.

In the lead-up to prey capture, echolocation during these tasks was examined from the spectral view of audio recordings in Cool Edit Pro, aligned with the behavioural sequence of capture in video footage. Echolocation activity as a proportionate behaviour of total activity during a trial was verified from the spectrogram of trials, and is described further, below. The silent period, the time between last-detected emission (as was possible to determine by the recording equipment sensitivity) and first-time attack on an insect (Faure and Barclay 1994; Arlettaz et al., 2001; Ratcliffe and Dawson 2003), was measured from the sonogram view of audio recordings. Data here were not conducive to statistical analyses because of the combined effect of a low sample size of animals and of total capture events per insect condition across bats, and high variability within individuals. Additionally, I did not have confidence in some cases (8 out of the total of 37 capture events) in the quality of recording and that emissions were indeed absent. It is acknowledge that even in quantified events, very soft emissions may have been present but undetected by the recording system. This may be because bats were facing away from the microphone. To account for this skew, data are thus described in terms of median and range values for *N. gouldi* and *N. bifax*.

The total count of each event (behaviour) exhibited by a bat was transformed into the percentage proportion of all events scored for that bat in that test. These data (frequency of behaviours as a proportion of total activity) were used to derive descriptive statistics on the relative frequency of behaviours. I found no significant difference between individual bats in the proportional frequency of behaviours they exhibited (two-way RM ANOVA, $F_{(3, 16)} = 1.000$). Matching within subjects did not have a significant effect on the frequency of behaviours demonstrated across testing conditions (two-way RM ANOVA. $F_{(20, 60)} = 0.43, p = 0.9817$). Given the very low sample size within species (only two *N. bifax*, three *N. gouldi*), data from all five bats were therefore pooled (and see Grant 1991; Bailey and Haythornthwaite 1998; Arlettaz et al., 2001). Individual data for each species is provided for additional reference in Appendix 6. Differences between behavioural frequencies across prey type for all bats was subsequently tested using a regular two-way ANOVA with Bonferroni’s post test.
The duration of all flight bouts was also recorded to determine the amount of time bats spent in flight when interacting with different prey (typically-aerial moths and grounded field crickets). Mean flight duration was compared across the four types of prey using a one-way ANOVA with Tukey’s post test. Individual data for the two species are also included in Appendix 6.

For capture events I examined the video footage from five minutes prior to capture in close detail, to determined patterns of behaviours by both predator and prey in the sequence of events leading up to capture. Capture success, defined as the number of insects caught and consumed as a proportion of the total offered, was determined across prey type. Within this, I also determined what proportion of captures were a result of first attack attempts or multiple attacks. The duration of consumption was also recorded since this would be expected to reflect requirements dictated by prey type (size and hardness). For this, I pooled data from live and deaf crickets and compared consumption time to the mean duration obtained for moths using an unpaired, one-tailed t-test. Dead crickets were never eaten in full and so were excluded from this comparison. Individual species data for number of captures and consumption time are shown in Appendix 6. All statistical analyses were carried out using GraphPad Prism 5.0 (GraphPad Software Inc., La Jolla, CA, USA).

Insect behaviours are qualitatively described since these animals were generally inactive throughout trials. For example, analysis of their behaviours during pilot work showed live and deaf crickets were active only 15.35 % (14 mins) and 18.70 % (17 mins) respectively, of time during their interactions with bats, and moths even less so (13.80%; 12 mins). This level of inactivity was similarly observed in subsequent experiments presented in this Chapter. Categorically, crickets were observed to display only terrestrial, locomotory (walking on the arena floor and walls) and predator escape behaviours (leaping away). Flight was never performed by tested crickets. In addition to crawling, moths flew, fluttered their wings when stationary, and plummeted to the floor when attacked by a bat. The behaviour of insects are described in detail over the five minute period of time prior to their capture, any subsequent attempt to escape following attack by a bat, and where incidental behaviours are of specific interest to describe.
5.3. Results.

5.3.1 General Acoustic and Behavioural Activity across Prey Conditions

The relative extent that echolocation was detected over the duration of one hour trials between bats and insects is exemplified in Figure 5.1. Echolocation accounted for 88% of the active time in this example (as determined from focal sampling), with all five bats tested demonstrating a similar pattern of extensive echolocation throughout their trials (behaviourally active on average 80 % of time, range 51 – 99 %, n = 5 bats and 20 trials). This included echolocating while performing active behaviours as well as echolocation alone when the bat was stationary (defined in Methods). Whilst this indicates that bats were generally actively scanning their surrounds, the frequency of detected emissions may also be inflated by the small confines of space since the walls and floor of the arena would also be detected by the bats. During the remaining sampled activity (in the example case, 12% of time), bats made small movements only (crawling over short distances).

Figure 5.1. Exemplary frequency of echolocation behaviour recorded from *Nyctophilus* bats during interactions with insect prey.

The proportional frequency of each behaviour displayed by bats under each condition of prey is displayed in Figure 5.2. Echolocation was detected in conjunction with all
behaviours the bats performed (HS, CW, F and CF bars in Figure 5.2) during trials with all insects. Echolocation alone (Figure 5.2, black bars) represented a further 5 – 15 % of observed events.

Behaviourally, the most frequent event displayed by bats was head scanning, followed by crawling on the arena walls and then flight, representative of continuous monitoring and exploratory behaviours. Head scanning accounted for 44 – 68 % of the total activity by bats (grey bars in each row in Figure 5.2), and was displayed significantly more than any other behaviour within and across prey types (two-way ANOVA, $F_{4,80} = 75.23$, $p<0.0001$). The frequency of this behaviour was not significantly different during interactions with prey type (HS + E between rows in Figure 5.2), and the other behaviours did not differ between one another (two-way ANOVA, $F_{12, 80} = 1.56$, $P = 0.1199$). Prey type had no significant effect on the frequency that any behaviour was performed (two-way ANOVA, $F_{3, 80} = 0.00$, $P = 1.0000$). These results indicate that bats were behaving consistently throughout testing and that prey type does not induce any different pattern of behaviour. Bat behaviour therefore appeared to be

![Figure 5.2. Proportional frequency of behaviours exhibited by naïve, wild Nyctophilus bats (n = 5) during interactions with crickets (live, deafened and dead T. commodus) and wild caught moths. Individual behaviours within each prey type are presented as the proportion (%) of total behaviours scored in that series of trials. Echolocation was detected with all other behaviours and is indicated in each row as Head Scanning (HS + E), Crawling on Walls (CW + E), Crawling on Floor (CF + E) and Flight (F + E). Echolocation alone (E) was exhibited when bats were perched but not scanning. *** indicates a significant difference ($p<0.001$) in observed frequency of HS + E behaviour between behaviours performed in all prey condition trials.](image)
independent of prey type. As described previously, echolocation always accompanied these events and when displayed as a behaviour on its own (black bars in Figure 5.2), was not used any differently across prey conditions.

The mean duration of individual flight bouts performed by *Nyctophilus* during interactions with crickets and moths is displayed in Figure 5.3. Flight bouts were significantly longer when bats were tested with live field crickets than with any other prey (one-way ANOVA, $F_{(3, 214)} = 5.13, p < 0.0001$). This is despite there being no difference in the proportional frequency of flight events across treatments (striped bars in Figure 5.2). Thus, while *Nyctophilus* bats did not fly more frequently in the presence of any particular prey type, they did spend more time in the air when presented with live crickets.

![Flight Duration Bar Chart](image)

**Figure 5.3.** Mean ± SEM duration (sec) of flight bouts exhibited by naïve, wild *Nyctophilus* bats (n = 5) during interactions in an arena with insect prey. * indicates significant difference in flight duration during testing with live crickets (*T. commodus*, n = 5, p < 0.0001) as compared to testing with other insect treatments.

### 5.3.2 Echolocation Patterns During Prey Capture

An example capture sequence for a bat during capture of a live, intact cricket is illustrated in Figure 5.4, with the spectrogram for this in Figure 5.5. A further two example spectrograms during capture sequences are depicted in Figure 5.6, illustrating the differences in last detectable emissions prior to initial contact with prey. As previously highlighted, recording was down-sampled thus detailed spectral content of signals cannot be inferred from the sonogram. Based on the quantifiable data (see
Data Analysis above) median and range time from last detected emission to first contact (silent period) across the four prey conditions are presented in Table 5.1.

Table 5.1. Median and range (minimum and maximum) time (seconds) between last detected echolocation emission and point of first contact with prey by naïve Nyctophilus bats during their live interactions. # Captures indicates the number of sequences from all captures where acoustics could be quantified with confidence (see Data Analysis).

<table>
<thead>
<tr>
<th>Prey Condition</th>
<th>Species</th>
<th># Captures</th>
<th>Median (range, sec)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Live Crickets</td>
<td>N. bifax</td>
<td>4</td>
<td>0.832 (0.291 – 1.940)</td>
</tr>
<tr>
<td></td>
<td>N. gouldi</td>
<td>5</td>
<td>1.295 (0.398 – 3.000)</td>
</tr>
<tr>
<td>Deaf Crickets</td>
<td>N. bifax</td>
<td>3</td>
<td>1.163 (0.428 – 1.564)</td>
</tr>
<tr>
<td></td>
<td>N. gouldi</td>
<td>5</td>
<td>1.539 (0.830 – 3.520)</td>
</tr>
<tr>
<td>Dead Crickets</td>
<td>N. bifax</td>
<td>1</td>
<td>0.789</td>
</tr>
<tr>
<td></td>
<td>N. gouldi</td>
<td>3</td>
<td>1.263 (0.136 – 3.073)</td>
</tr>
<tr>
<td>Moths</td>
<td>N. bifax</td>
<td>6</td>
<td>0.441 (0.242 – 0.948)</td>
</tr>
<tr>
<td></td>
<td>N. gouldi</td>
<td>2</td>
<td>0.576 – 1.020</td>
</tr>
</tbody>
</table>

Detailed inferences about trends and differences in the silent period are cautiously presented due to the high inter-individual variability and low sample sizes. There appears to be a trend of echolocation being maintained for longer during capture of moths (lower median values and smaller variability of ranges) but switched off earlier in the capture of crickets. However, some minimum range values are comparable so the absence (undetected) of echolocation was also quite late during capture of some crickets. Similarly, some moths were approached with maximum silent periods closer to 1 second prior to contact. Any consistent difference between the conditions of live and deaf crickets cannot be deduced from this data, based on the similar variability in median and range values. Moreover, time from last detected emission is equally variable in the dead cricket trials as (at least) other cricket conditions. Minimum values for last detected emission were also comparable in a few cases of immobile prey.
Figure 5.4. Example echolocation repertoire during one capture sequence from naïve *Nyctophilus* bats (*N. gouldi* in this case) during interactions with insect prey. Displayed is the pattern of emissions mapped to a capture event involving one live, wholly intact field cricket (*T. commodus*), initially detected (hover events at left) and localised (head scan and crawl wall events) on a vertical wall of the testing arena, before pursuit and capture on the floor and transport to an elevated position (flight with cricket to wall at right) for consumption.
Figure 5.5. Spectrogram of echolocation behavioural sequence depicted in Figure 5.4, for the period just prior to attack up to capture and take-off flight to wall. Time between last detected emission and capture in this example was 3 seconds.
Figure 5.6. Spectrogram of Nyctophilus echolocation behaviour during captures of T. commodus. Top panel: capture of dead cricket by N. gouldi where last detected emission prior to contact = 0.136 seconds. Bottom panel: capture of live, wholly intact cricket by N. bifax where last detected emission prior to contact = 0.651 seconds.
1 dead cricket, 5 alive (live/deaf) crickets and 3 moths). Given the small confines of the arena space, it is likely that some of these emission patterns were induced by the projections against the arena walls as bats approached the prey. From these data therefore, it cannot be conclusively determined how cricket conditions influenced the use of passive localisation. The strategy appears to be consistently used (at some point) for all prey captures however, indicating bats were switching to non-echoic strategies in a dynamic manner in accordance with any prey detected. These patterns are considered further, below.

Echolocation only appeared to be consistently absent (undetected) once a bat was locked in on pursuit of an attacked prey. Following initial attack, bats pursued fleeing prey (which leapt to the floor) through rapid flight or jumping, with echolocation sometimes still detectable. It appeared to however, be switched off when the bats were on the ground and chasing an insect. Over these moments, the erratic movement of insects could certainly provide sufficient acoustic cues for their pursuit by passive, non-echoic means.

5.3.2 Behavioural Patterns During Prey Capture

Two exemplary sequences of still frames from video footage of prey capture by *Nyctophilus* are included in Appendix 7 and 8, illustrating their behavioural handling of large, hard-bodied crickets and small, soft-bodied moths. There was no notable difference in the pattern of behaviours exhibited by bats in the lead-up to capture of crickets or moths, or within different cricket types. Unless an insect moved obviously and whilst a bat was looking at it directly, bats were generally alternating between scanning the surroundings, crawling along the arena walls and short flight bouts, proceeding to an attack as a result of (usually) an opportunistic encounter with any insect prey. For capture, insects were always gleaned from surfaces, although given their tendency to monitor the arena from an elevated position (walls), *Nyctophilus* bats were also displaying perch hunting. Behavioural differences were however, evident across prey type for the mode of capture, prey restraint and consumption.

Whilst the size of the arena may have influenced the foraging behaviour of bats, they demonstrated great ease in successfully catching prey in a context-dependent manner. They were highly competent during gleaning/perch hunting, with accurate and
effective attacks on substrate bound prey. Bats also displayed exceptional agility within the small confines during flight, including rapid and sharp directional changes, avoiding the boundaries of the walls and, circling and hovering over ground dwelling prey and in front of individuals on the vertical walls. These observations highlight that *Nyctophilus* bats are very capable of moving and hunting within a small space. How this translates to settings in nature requires direct verification from observation of wild individuals (Faure et al., 1993).

**Capture Success**

The percentage of prey caught by *Nyctophilus* was generally low for all prey types (Table 5.2). Only 18% of moths (11 out of 60), 44% of live crickets (11 out of 25), and 40% of deafened crickets (10 out of 25) offered were consumed by bats. Although 20% of dead crickets (5 out of 25) were attacked, these were only partially consumed and all were spat out, suggesting they may have been unpalatable. The fact that some were attacked and consumption attempted at all, indicates *Nyctophilus* may have recognised them as food. However, *N. geoffroyi* will also attack and ‘taste’ paper moths (Cronin and Sanderson 1994) and similarly discard them.

<table>
<thead>
<tr>
<th>Prey Condition</th>
<th>No. Available</th>
<th>Total Captured</th>
<th>Attack Location</th>
<th>Capture Location</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Wall</td>
<td>Floor</td>
</tr>
<tr>
<td>Live Crickets</td>
<td>25</td>
<td>11</td>
<td>6</td>
<td>5</td>
</tr>
<tr>
<td>Deaf Crickets</td>
<td>25</td>
<td>10</td>
<td>6</td>
<td>4</td>
</tr>
<tr>
<td>Dead Crickets</td>
<td>25</td>
<td>5</td>
<td>0</td>
<td>5</td>
</tr>
<tr>
<td>Live Moths</td>
<td>60</td>
<td>11</td>
<td>8</td>
<td>3</td>
</tr>
</tbody>
</table>

The location of initial attack and final capture of insects is also presented in Table 5.2. Ground based captures were most commonly performed by bats, irrespective of where prey was initially attacked. This was a direct consequence of the tendency for live insects to perform an emergency leap upon attack, which landed them on the arena floor and bats pursued them here. During pursuit of escaping prey, bats were extremely quick, agile and precise in successfully catching and restraining an insect. Dead crickets were only ever found on the floor, where they were subsequently
attacked, despite individuals being available for attack on the arena walls. Those insects that were captured by a bat on the arena wall, were always there to start with. All crickets responded to such attacks with escape manoeuvres when the bat touched them, while most moths on the wall simply did not escape the initial attack.

Crickets that were on the arena wall at the time of attack were generally still (all 6 live crickets and 5 of the deafened crickets in Table 5.2) and seem to have been detected by chance because their attack by a bat was not preceded by any behaviour from the predator that indicated prior recognition of the prey. Captures of dead crickets, which offered no audible cues for detection also appeared to be opportunistic encounters. In contrast, crickets on the floor were more active than crickets on the walls and elicited noticeable directed attention from a bat. Attacks on grounded (Floor attack location in Table 5.2) live and deaf crickets were elicited by the prey moving on seven out of nine occasions. Indeed, this was a very strong indicator of passive localisation since longer silence periods (1 – 3 seconds) were observed in six of these events. The movement of crickets along the artificial grass floor may have thus provided audible cues to bats. Moths were predominantly still on both arena walls and the floor prior to an attack by *Nyctophilus* (7 out of 11 captures). At most, they only fluttered their wings. Flying moths were not taken by *Nyctophilus* except in one out of 11 capture events (described below).

*Capture Precision*

The success from first attacks by *Nyctophilus* was high. Figure 5.7 depicts the success rate of capture by bats from first-time attacks, and multiple attempts at capture of live prey. Dead crickets are not included since these prey cannot escape and therefore will not influence the number of attempts for successful capture by a bat. Dead crickets were attacked only once and which always resulted in their successful capture but never consumed in full. *Nyctophilus* successfully captured live prey between 63 and 81 % of the time from first-time attacks (Figure 5.7, black bars). This reflects high capture precision for bats once prey were detected. In the remaining capture events (white bars up to 100 % in Figure 5.7), prey escaped the initial attack; bats then pursued them, often attacking and failing multiple times before finally succeeding.
Figure 5.7. Capture Success Rate (% of all captures) for naive, wild *Nyctophilus* bats offered live crickets, deaf crickets and moths, as a product of first-time attacks (black bars) and subsequent attacks following missed attempts (white bars up to 100%). Data are based on the capture of 11 out of 25 live crickets, 10 out of 25 deaf crickets and 11 out of 60 moths.

**Restraint, Manipulation and Consumption of Captured Insect Prey**

When manipulating the relatively large *T. commodus*, bats enveloped their prey by folding the wings to form a canopy, biting down on the head and folding the uropatagium under the insect. Bats spent 1 – 5 seconds manipulating and restraining captured insects on the ground before most often, flying to a wall for consumption. Take-off from the ground occurred with ease since it involved near-vertical propulsion from a stationary position rather than for instance, a run-up to take-off. Crickets were carried to a wall within the folded tail membrane. Upon landing, *Nyctophilus* bats again used the wings to form a canopy over the cricket and commenced to eat it, always from the head down. The wings and numerous legs were dropped to the arena floor. In the case of moths, the wing and tail membranes were not used; bats landed on a moth and were able to immediately overpower it by mouth alone. However, moths were always carried in the mouth if bats flew to a wall for their consumption, during which time echolocation was sometimes detected. Since *Nyctophilus* bats emit echolocation from the mouth, the ability to maintain acoustic navigation while carrying a prey item in the mouth is notable. Bats consuming moths always discarded the wings.

Bats took significantly longer to consume the large, hard-bodied *T. commodus* (229.7 ± 22.4 sec, 95 % C.I. 182.5 – 276.8 sec, pooled for live and deaf crickets) than the
softer moths (50.55 ± 9.4 sec, 95 % C.I. 29.6 – 71.5 sec; unpaired, one-tailed t-test; t(28) = 5.867, p < 0.0001). As previously described, dead crickets were always tasted but never consumed in full and were spat out. The consumption of all live insects occurred most often on the arena walls (range: 73 – 90 % of captures). In contrast, only one dead cricket was carried to a wall for (partial) consumption.

**Incidental Behaviours Exhibited by Nyctophilus**

In three capture events, *Nyctophilus* hovered in front of or above the targeted prey, which were always moths. In another three capture events, this time involving walking crickets on the arena floor, *Nyctophilus* circled the targeted prey multiple times, before landing on top of or very nearly on the insect. Echolocation was detected in all of these six capture events and involved both *Nyctophilus* species.

On one occasion during testing, a male field cricket (not part of the testing cohort) was heard to be calling sporadically and loudly beside the testing arena for about 10 minutes. Each time it called, the bat under testing turned toward the direction of sound and raised its ears. Echolocation was not detected during this time. This was the only obvious behaviour that indicated *Nyctophilus* was responding to prey-generated sounds by passive listening.

**5.3.3 Observations on the Responses of Insect Prey**

No indication was discernible that *T. commodus* (either live or deaf) were monitoring *Nyctophilus* bats and thus avoiding detection and encounters. They were on the whole relatively inactive, and in the lead-up to directed attacks by echolocating bats, most individuals were already immobile in the five minutes prior to attack (wall location of initial attack for most crickets, Table 5.2). It is likely that the close proximity of animals in the small confines of the arena meant bats were in fact detected by crickets; thus, their relative inactivity indicates a general avoidance strategy of remaining immobile. However, crickets did not appear to be either staying away from bats in a consistent pattern, or avoiding them when walking in their direction. Those that were moving (floor location of initial attacks), were simply moving along a given path of motion in a manner that gave no indication of appearing to be threatened (e.g. rapidly darting across the floor, quick bursts in a stop-start manner or suddenly ceasing to move). Moreover, when crickets were clearly discernible from the video footage, freezing behaviour was
not evident; this however, requires higher camera resolution to further verify. On some occasions, crickets also walked directly up to a resting bat without any obvious behaviour to suggest they recognised them as a predatory threat. They did not subsequently flee from the bat upon contact. A characteristic, specific avoidance strategy was not therefore apparent from the crickets in these experiments.

A consistent response to bats was only evident when a bat made direct contact (or very nearly) with a cricket during attack. In these cases, crickets always performed an emergency style response involving a powerful, rapid leap away from the bat, usually landing on the ground. If they were not captured upon the first pursuit from *Nyctophilus*, crickets continued to jump erratically around the arena floor as a further attempt at escape. It did not appear that these repetitive leaps were coordinated in any particular directional manner; rather, they were simply aimed in any away direction from the attacking bat. The initial leap from first attack by a bat however, was always in a lateral direction, irrespective of whether the insect was on the wall or the arena floor. They never attempted to burrow into the artificial lawn on the arena floor, which was expected since it was not of a height that would have enabled this behaviour. Collectively, whilst behavioural patterns that would indicate crickets detected bats was not obvious nor quantifiable, their subsequent evasive response upon attack were consistent and clear.

When moths responded to bat attacks (4 of 11 capture events) their behaviour was similar to field crickets; these individuals also performed a powerful emergency response. In three of these events, the moths took off and plummeted to the ground. The fourth case was the only time that *Nyctophilus* was observed to aerially hawk for prey as it pursued a moth that flew off erratically upon attack.
5.4. Discussion

The results of this Chapter demonstrate that *N. gouldi* and *N. bifax* tested here are well-suited behaviourally and acoustically for the localisation, capture and consumption of insects encountered in a terrestrial setting. I did not detect differences between *N. bifax* and *N. gouldi* foraging performance; however a larger sample size of individuals is needed to further verify any species-specific difference. Passive localisation appeared to be utilised by all bats in a dynamic manner during prey capture, based on the point of last detected emissions prior to contact. The bats used surface capture techniques competently independent of prey type. This behaviour has therefore probably developed to exploit a wide range of insects, rather than because of preferential feeding in terrestrial contexts.

During their interaction with *Nyctophilus*, there was no clear indication of a pre-empted avoidance behaviour in field crickets. They were largely inactive throughout trials, suggesting a generalised avoidance strategy of staying still; however, when mobile, crickets were also inconsistent in behaviours that would suggest ‘fearful’ awareness of bats. Once attacked, live and deafened *T. commodus* responded consistently with a well-defined, powerful evasive jump. These tests therefore provide characterisation of a consistent escape response.

5.4.1 Acoustic Strategies of Terrestrial Predation by *Nyctophilus*

When approaching prey, both echolocation and passive listening were detected from *Nyctophilus* bats. The extent to which either strategy was exclusively relied on is unclear given some uncertainty in detecting all emissions with my equipment, especially if bats were emitting very soft calls that I could not detect (Pennay et al., 2004). In drawing inferences about the conservatively quantified data on silent periods these discussions are thus presented with acknowledgement of this study’s detection limitations. Previous characterisations of foraging on silent prey by some members of the genus including *N. gouldi* (Grant 1991; Cronin and Sanderson 1994), suggest passive listening is exclusively used to capture live, substrate bound prey; but herein, acoustic detection was also an acknowledged limitation and possibly more limiting due to the use of zero-crossing period detectors (Fenton et al., 2001; Obrist et al., 2004; Parsons et al., 2010). In the current study, passive localisation was also evident but
only in the final moments to capture of prey. Given the variability of silent periods detected in the current study, it is proposed that acoustic strategies during terrestrial foraging may be more dynamic than previous investigations suggest. This warrants further examination to determine how extensively *Nyctophilus* bats use passive localisation and how this strategy is used in conjunction with echolocation during natural foraging tasks (Barber et al., 2003).

The utility of prey-generated sounds for passive localisation by *N. gouldi* and *N. bifax* was most evident during their capture of walking crickets. Here, the range of silent periods quantified upon approach overlaps with values cited for some other gleaners (Faure et al., 1990; Faure and Barclay 1994; Arlettaz et al., 2001; Ratcliffe and Dawson 2003). I did not measure the intensity of prey locomotion, but these sounds were apparently sufficient enough under the controlled testing conditions to be detected. On fly mesh, as used in the current study, walking cockroaches yield sounds of 6 – 12 kHz (Grant 1991), whilst movement on leaf litter also elicits sounds with high frequency elements detectable by bats (Marimuthu et al., 2002; Goerlitz et al., 2008). On both materials, walking insects generate signals between 40 dB to 65 dB (Marimuthu et al., 2002; Goerlitz et al., 2008; Holderied et al., 2011). To the best of my knowledge, locomotory sounds produced when insects are on artificial grass have not been measured. However, *Myotis myotis* and *M. blythii* are equally capable and effective at passively detecting insects on the same material, with up to 1.5 seconds of silence prior to capture (Arlettaz et al., 2001). Collectively then, the movement of field crickets here may be presenting sufficient audible cues for detection by some bats.

The cited values of prey movement cues are within the peak frequency sensitivity of hearing in *N. gouldi* at least (Guppy and Coles 1988), for both low (8 – 14 kHz) and ultrasonic (22 – 45 kHz) cues. Their large pinnae also amplify audio signals above 10 kHz by 12 – 17 dB (Guppy and Coles, 1988), extending their sensitivity threshold for low frequency sounds down to 5 dB. Since in this study, *N. bifax* also consistently demonstrated silent attacks on grounded insects, their auditory capacity may be similar to *N. gouldi*. Higher order functional determinants of auditory capacity such as those available for *Megaderma lyra*, *Antrozous pallidus* and *Hipposideros speris* (Rubsamen et al., 1988; Barber et al., 2003) are yet to be described for *Nyctophilus* spp. This would be very relevant for application of current understanding to nature: whilst they might be able to detect the sounds of walking crickets under controlled
conditions, noises from moving insects would be masked in the acoustically cluttered setting of the wild.

My results cannot conclusively determine or exclude the functional purpose that echolocation served for *Nyctophilus* bats during these trials (e.g. for orientation or prey acquisition; Schnitzler et al., 2003), especially in cases with silent, immobile prey. Echoic navigation was obvious when the bats flew (Figure 5.2), presumably being used to avoid the fly mesh walls (Falk et al., 2015), but is in contrast to previous accounts on *N. gouldi* in the laboratory, where bats flew in silence (Grant 1991). The presence of echolocation during encounters with silent prey may also simply reflect detection of the background (arena walls or floor). Yet, the silent period prior to contact with insects includes events where echolocation was detected very shortly before (within 100 ms), and absent up to 3 seconds prior to capture, and with both immobile and moving prey. In *A. pallidus*, detection and sensitivity for acoustic signals is highly developed, enabling segregated, concurrent streaming of echoic and prey cues (Razak et al., 2007) during foraging. How similarly refined this is in *N. gouldi* and *N. bifax* is unknown, but the variability in when echoic approaches turned silent suggests the bats were able to dynamically adjust their acoustic behaviour in a task-specific manner. During targeted attacks on substrate bound prey echolocation was undetected in most cases for between 1 – 3 seconds prior to contact suggesting echoic navigation was no longer needed. In considering the simultaneous processing of cues by *A. pallidus*, the question then is if these *Nyctophilus* bats were also obtaining information prior to this point of complete silence.

With immobile prey, all approaches by bats occurred on foot (crawling) and with generally longer silences (> 1 second prior to contact), which probably means the bats found insects by chance during general exploratory activity. With some immobile live crickets and one dead individual however, echolocation was maintained until late before contact (down to 0.291 seconds and 0.136 seconds before, respectively). With dead, suspended moths (stationary but aerial prey), Grant (1991) also describes that echolocation is maintained by *N. gouldi* with a final series of emissions at a reduced rate (unquantified) on approach. Whilst the final (undefined) moment to contact may have been made in silence this pattern of reduced (but not absent) echoic activity is similar to *Micronycteris microtis* during detection of immobile, silent dragonflies on vegetation (Geipel et al., 2013). Therein, the final descent involved a reduced (down
to 48 Hz) but consistent series of emissions. Prior to this, *M. microtis* typically assessed prey through multiple hovering approaches (Geipel et al., 2013). Displacement of the insect’s wing by hovering provides reflective echoes that may further resolve prey from background echoes (Kuc and Kuc 2012). In the current study, hovering by *Nyctophilus* was observed on three occasions with stationary moths, and echolocation detected consistently during. On a further three occasions, bats circled in flight over crickets on the floor with echolocation also detected, although here, the crickets were moving. In all cases, the background (wall and floor) would present some extent of clutter (Arlettaz et al., 2001). Although the final approach by *Nyctophilus* here was in absence of echolocation, the probing, echoic inspection of prey in these instances draws comparisons to *M. microtis* (Geipel et al., 2013) and more generally, *N. gouldi* (Grant 1991). Moreover, since the approach toward these immobile prey was on foot, the use of echolocation for steering and landing (e.g. see Rainho et al., 2010) was not relevant. Any possibility that these bats are capable of echoic resolution requires direct and more detailed verification through precise recordings, but which would be a significant extension the sensory capacities described for these species.

### 5.4.2 Foraging Behaviour during Terrestrial Predation by *Nyctophilus*

The collective body of past work on *Nyctophilus* spp., including *N. gouldi*, describes their adeptness in both terrestrial and aerial foraging tasks, with substrate bound prey always captured by gleaning (Grant 1991; Cronin and Sanderson 1994; Hosken et al., 1994; Bailey and Haythornthwaite 1998). The current study extends similar characterisations to *N. bifax* as well, at least for ground captures. Despite the very small confines of space, gleaning/perch hunting was also readily demonstrated by *Nyctophilus* bats tested here, being used in most capture events (excluding incidental events were prey were encountered by a bat on foot). Since aerial events were largely absent (prey generally did not fly and only one capture of a flying moth on the wing observed) I cannot compare across foraging modes. Whilst the confines of the testing arena may have influenced the absence of aerial captures (Ratcliffe et al., 2008), general flight was frequently exhibited by all bats and during which, they were extremely agile and precise (including the one instance where a moth was captured on the wing). From these observations on *Nyctophilus*, foraging mode appeared to be associated with the context of where prey were found rather than prey type.
Bats did not discern between typically aerial (moths) or terrestrial (crickets) insects (Figure 5.2) only adjusting how they handled them for restraint and consumption to suit prey type. Intact and deafened crickets were captured equally as much but, given the general inactivity of all crickets and limited resolution power of recordings, at best this indicates bats recognised any live crickets as food. Indeed, whilst they may not recognise the identity of prey, they do appear to be cognisant of rewarding items since live crickets and moths were interpreted generically as food, while dead crickets were always spat out and abandoned. These bats probably do not therefore, selectively target any one prey type in terrestrial settings, at least not silent individuals (for attraction to calling male insects by other long-eared bats, see Hosken et al., 1994; Bailey and Haythornthwaite 1998). Records across the genus on diet, foraging niche and habits (Vestjens and Hall 1977; Fenton 1982; Brigham et al., 1997; Duncan et al., 1999; Churchill 2008) also suggests these bats are generalist feeders, and that terrestrial foraging has evolved additional to their behavioural repertoire to exploit diverse feeding opportunities.

The duration of flight bouts performed by *Nyctophilus* was the only indication of a change in behaviour with different prey: bats were airborne for significantly longer in the presence of live crickets than any other insect. The relative activity levels of insects during trials could not be effectively characterised (see Methods); moths were somewhat more discernible given the contrast in colouration, but even these appeared generally inactive. If live crickets were the most active prey and bats were aware of their presence due to their movements (Guppy and Coles 1988; Arlettaz et al., 2001; Marimuthu et al., 2002; Goerlitz et al., 2008), long flight bouts may have a functional purpose. Initially, flight could serve to broadly probe an area where activity has been detected; then, remaining airborne would facilitate further assessment to refine the target position and whether to attack (Faure et al., 1990; Schmidt et al., 2000; von Helversen and von Helversen 2003; Russo et al., 2007; Geipel et al., 2013). This probing behaviour during flight is reflected by the hovering and circling by some of the tested bats described previously, and is consistent with observations on *N. geoffroyi* searching for grounded prey (Cronin and Sanderson 1994). Substrate foraging may therefore be performed in a selective manner because if the focused search in the air does not yield a guaranteed catch, the bat will stay airborne and continue to hunt for flying prey.
The localisation by bats of dead crickets at all, differs from Grant (1991) but is comparable with observations from Cronin (1992). Olfaction is the only additional cue that would have been available to bats here given the complete darkness of testing and absence of prey-generated sounds. Whilst olfaction is important in foraging for fruit and nectar eating bats (Altringham and Fenton 2003) and the vampire bat Desmodus rotundus (Schmidt 1973; Bahlman and Kelt 2007) odour cues appear to be variably, or not as extensively, utilised by insectivorous species: 50% - 90% of offered dead prey captured where odour was the only possible source for localisation (Cronin and Sanderson 1994; Jones et al., 2003). Grant (1991) however, argues that odour is of little (or no) relevance to N. gouldi and N. geoffroyi, since in complete darkness these bats captured dead suspended moths as readily as suspended paper moths. In the current study, odour cues may have only be useful over short distances since dead crickets were only found on the ground when the bat itself was there. In this case, odour may serve as an additional cue to other sensory information (e.g. echolocation Thies et al., 1998; Korine and Kalko 2005) but is probably not a primary sense.

My results on the tested bats suggest they would represent a strong threat to grounded crickets if they are encountered in the wild. Both Nyctophilus species demonstrated high capture precision (Figure 5.7) and all insects attacked eventually failed to escape capture. These are consistent to a large extent with observations on N. gouldi and N. geoffroyi by Grant (1991). The confined space in the current study would have limited the possible extent of escape however, bats were extremely fast and agile in their pursuit leaving little time for prey to successfully escape anyway. The large size and hardness of crickets also does not appear to pose limitations on the bats’ capacity to capture them (Freeman 1981; Otte and Alexander 1983; Freeman 1992). Bats easily and quickly (1 – 5 sec) restrained all prey, whether soft-bodied moths or crickets. Following capture of crickets on the ground, bats adeptly took off in a near-vertical direction. The duration that N. bifax and N. gouldi spent on the ground is also within the time observed for other gleaning species foraging on smaller prey (moths, 2 – 8 seconds; Bell 1982; Arlettaz 1996). If chosen, crickets in the wild may therefore be a rewarding food item for these bats despite the associated costs involved, such as a longer search time for cryptic prey (Geipel et al., 2013) and a longer time on the ground for manipulation and restraint, during which the bats themselves might be exposed to terrestrial predators (Clavero and García-Berthou 2005; Pryde et al., 2005). The
efficiency with which *Nyctophilus* overpowered grounded field crickets therefore illustrates a very capable predator and for whom the capture of crickets did not appear to be a novel task.

**5.4.3 Significance of Cricket Emergency Response to Bat Attacks**

This study has described for the first time a consistent late-stage, emergency response of escape in the Australian field cricket (*T. commodus*) from echolocating bats during terrestrial encounters: on all occasions of an attack, crickets produced a powerful, evasive jump away from a bat. Whilst this behaviour is likely to be a general adaptation to any terrestrial predator it would be sufficient and effective to evade gleaning bats.

Pre-emptive avoidance behaviours could not be confidently assayed due collectively to resolution of the video footage and the behavioural inconsistency of crickets. The overall low activity of insects throughout trials may also be a product of their confined proximity to the bats and that in fact, remaining immobile was a general strategy to minimise detection. This is an effective defence demonstrated by some moths in response to bat predation (Ratcliffe et al., 2008), and generally a range of prey (Lopez et al., 2005; Martin et al., 2005; Stankowich and Coss 2006; Martin et al., 2009; Martin et al., 2010). Staying still also allows prey to monitor the approaching predator (Ydenberg and Dill 1986). However, in animals with laterally-positioned eyes (e.g. crickets) continuous, visual monitoring of the predator is mostly, still possible (Cooper 2008) and so obvious behavioural changes indicative of predator detection are not necessarily demonstrated. Even if an approach is from head-on or the rear, additional perceptual information might be obtained from mechanoreceptors and so actively moving the body is not necessary. For example, *Gryllus campestris* (an ultrasound sensitive cricket) guides visual input through antennal tracking of objects, and which can be initiated by sufficiently large (e.g. a bat) objects up to 1.2 m away (Honegger 1981). Indeed, my own presence with crickets would only elicit noticeable movement of their antennae. It is not therefore necessarily surprising that I could not detect a noticeable change in the behaviour of crickets even during discernible encounters. In the wild amongst vegetation clutter however, generally remaining immobile would certainly be a useful initial response to a bat (Martín et al., 2009), whether they are acoustically detectable or only through near-field sensory structures. The relative
immobility of crickets (and moths) in this study could therefore be conducive with an early-stage, avoidance strategy in response to echolocating bats.

As the final, possible attempt at avoiding capture an effective escape response must involve a short latency, directional (away from) and erratic movement (Stierle et al., 1994), and especially so when faced with a fast moving predator (Eilam 2005). This describes the rapid and powerful leap field crickets performed when attacked by bats, and who were subsequently exceptionally quick and precise during prey pursuit. The observed cricket escape response is particularly effective because of its evasive (lateral), rather than fleeing (straight ahead) direction, which can diminish the accuracy of subsequent tracking by a pursuing predator. In barn owls for example, capture success is greatly reduced if prey move rapidly in a lateral direction, rather than straight ahead (Shifferman and Eilam 2004). Lateral dodging by blue tits (Parus caeruleus) also maximises escape probability during high-speed attacks (Lind et al., 2002). Cockroaches respond to repeated threat simulations by fleeing in a different direction each time, presumably so that response patterns are random and a predator cannot learn an expected set of behaviours (Domenici et al., 2008). To my knowledge, the efficiency of prey-tracking by bats when grounded prey are moving laterally (or comparatively in other directions) has not been investigated. In the air however, some bats show exceptional capacity for sustained, accurate pursuit of flying prey. Ghose and colleagues (2006) demonstrated that big brown bats (Eptesicus fuscus) are able to track erratically flying prey with high precision, proposed to be due to sophisticated computation in the bat’s brain to predict the trajectory and flight path of these evading insects. Similarly, Aihara et al (2013) found capture success during aerial prey pursuit by Japanese greater horseshoe bats (Rhinolophus ferrumequinum nippon) was related to dynamic integration of the prey’s and predator’s angles of position with respect to one another. Whether Nyctophilus bats possess such refined capacities for tracking moving prey, and moreover whether these are efficient when hunting on the ground within clutter, are unknown. Under the conditions of testing here, the bats certainly were very effective in pursuit of erratically jumping prey. In the wild however, the presence of vegetation clutter following such a response may significantly impair the bat’s ability to accurately track and capture crickets. In terms of prey survival, lateral escape behaviour would therefore provide a significant advantage for an evading (rather than fleeing) cricket.
The relatively large distances crickets achieved when leaping from an attacking bat (up to 0.5 m) is also effective since it maximises the distance obtained away from a predator more than merely fleeing. Indeed, many of the Orthoptera that some Nyctophilus bats are purported to prey on (Vestjens and Hall 1977; Lumsden and Bennett 1995; Milne 2006; Churchill 2008) demonstrate substantial jump distances mediated by powerful leg muscles. House crickets (Acheta domesticus) and locusts (Locusta migratoria) obtain distances of around 0.5 m (Hustert and Baldus 2010; Snelling et al., 2013), and up to 3 m is achieved by the bushcricket Pholidoptera griseoaptera (Burrows and Morris 2003). All crickets attacked by Nyctophilus in the current study were eventually captured; in the wild however, where vegetation is again a relevant factor, this escape response would be very effective to propel crickets into (or near) cover and limit the subsequent possibility of pursuit by a bat (Sleep and Brigham 2003).

All elicited leaps by crickets were preceded by the bat making contact, or very nearly, with the insect. Here, near-field mechanoreceptors such as the cerci (rearward contact) or the antennae (head-on touch) may be contributing to initiation of the escape response. In fact, caudal structures are capable of detection ranges greater than those perceived by the antennae (up to 120 cm; Honegger 1981) and integration of caudal input with sensori-motor effectors leads to a range of behaviours to a predatory threat including running in cockroaches, flight or jumping in locusts, and all three in crickets (Camhi et al., 1978; Boyan and Ball 1989; Ritzmann et al., 1991; Stierle et al., 1994; Tauber and Camhi 1995; Comer and Baba 2011). The role of caudal perception has in fact been implicated in mediating insect behaviour during a bat’s approach, and when acoustic processing may no longer be effective (Hartbauer et al., 2010). In tettigoniids, activation of Giant Interneurons (GI’s) which receive direct input from the cerci can reliably encode for the position of an approaching bat up to 810 ms (160 cm) before contact, based on the detected wind velocities (Hartbauer et al., 2010). Whilst aerial approaches by a bat might generate sufficient air-borne vibration (e.g. events in the current study where bats landed on prey from flight; Tauber and Camhi 1995; Jacobs et al., 2008; Hartbauer et al., 2010), approaches on foot could also elicit detectable stimuli through substrate-borne vibrations. Either way, 810 ms is an ample amount of time even for last moment, emergency responses (Moiseff and Hoy 1983; Yager and Hoy 1989; May and Hoy 1991; Samson and Pollack 2002;
Tribehorn and Yager 2002; Marsat and Pollack 2005) and is consistent with ranges of last detected emission in some capture events in the current study (Table 5.1). Such integration of information through different sensory modalities would serve a grounded cricket well for any predator interaction. In light of the findings by Hartbauer et al (2010), this direction of inquiry would be a significant step in further elucidating the mechanisms underpinning terrestrial responses to bats by insect prey.

My investigation in this Chapter provides timely extensions to previous characterisations of *Nyctophilus* bats and their terrestrial interactions with grounded crickets. *N. gouldi* and *N. bifax* appear well-suited for terrestrial predation demonstrating agility and adeptness in prey capture with surface capture techniques being readily displayed. Whilst passive localisation was apparent, echolocation was also detected up to very late prior to contact suggesting dynamic and flexible use of acoustic strategies by these bats. Indications of an early-stage avoidance behaviour by *T. commodus* in close proximity to these bats was not obvious; their general immobility suggests this may be the best mechanism on the ground, and would probably be sufficient amongst vegetation in the wild. Upon attack however, *T. commodus* displays a consistent, late-stage escape response involving a powerful, rapid and erratic leap away from a bat. Based on prey escape models, this would be a highly effective behaviour, and which has not been previously described.
5.5. References


Chapter 6.

General Discussion.
6.1 Background and Study Findings

A rich history of investigative work exists on the evolutionary association between echolocating bats and their insect prey. However, the classic repertoire of evasive response that many Orthoptera display (negative phonotaxis) is context-dependent, and absent when insects (crickets) are on the ground (Nolen and Hoy 1984; Pollack et al., 1984; Staudacher and Schildberger 1998; ter Hofstede et al., 2009). The terrestrial setting likely imposes many limitations on the detection of, and engagement between predator and prey, and may therefore serve as a passive source of defence for insects (Svensson et al., 2002; Cooper and Frederick 2007; ter Hofstede et al., 2009). In this case, crickets responding to echolocating bats may possess an entirely different set of behaviours to those elicited in the air, shaped by the environment. This dissertation provides insight on some of the relevant considerations for this context of association.

One poignant model system of context-dependent association includes animals endemic to Australia (*Teleogryllus* crickets and long-eared bats, *Nyctophilus* spp.); yet, few studies have explored their engagements (Grant 1991; Cronin and Sanderson 1994; Hosken et al., 1994; Bailey and Haythornthwaite 1998; Fullard et al., 2005; ter Hofstede et al., 2009). This dissertation provides timely extension on this small but important body of work, particularly for behavioural characterisations of terrestrial interactions between these animals, subsequently offering new animal models for study in future investigations (*N. bifax* and *T. commodus*).

This dissertation provides the following key findings:

1. The emissions of echolocating bats foraging above ground dwelling crickets, appear to be inaudible to the insects unless bats are very close (< 2m).
2. Walking male and female *T. commodus* do not demonstrate avoidance behaviour in response to bat echolocation from aerial hawkers and gleaners.
3. Shelter (cover) is a recognised and preferred space to the open, at least for female crickets; but crickets will stay away from cover when emissions from a gleaning bat are presented from this direction.
4. *N. gouldi* and *N. bifax* use surface capture techniques readily, accompanied by passive localisation of prey to some (dynamic) extent.
5. Female *T. commodus* possess a consistent, effective and powerful emergency response to direct attacks by bats.

### 6.2 Implications, Limitations and Future Directions

My work describes one example setting (Gold Creek Reservoir, Enoggera State Reserve, Figure 2.1) where field crickets (*T. commodus*) are regularly exposed to a number of Australian bat species. At this site, a stable, recurrent population of *T. commodus* males (60 – 80 individuals) vigorously call each night and likely attract a large number of females (*T. commodus* were not found elsewhere across the Reserve). The males reside within the grass layer on the ground, which can extend from between 10 to 50 cm in height. Directly overhead (within 5 m), two species of bats were detected regularly and over successive seasons: the aerial hawker *Scotorepens greyii* and the gleaner *Nyctophilus gouldi*. The gleaner may be a very relevant threat to male crickets if *N. gouldi* are attracted to their calls (Hosken et al., 1994; Bailey and Haythornthwaite 1998), sounds to which these bats demonstrate high auditory sensitivity (Guppy and Coles 1988). Immediately beside this site in a dense pocket of vegetation, two other species described as well-suited for terrestrial interactions were also recurrent: *Nyctophilus bifax* and *Rhinolophus megaphyllus* (Fenton 1982; Crome and Richards 1988; Duncan et al., 1999; Pavey et al., 2004; Pavey and Young 2008). These bats may be particularly relevant for predation on female crickets as these individuals fly past toward the calling males. Gold Creek Reservoir could therefore host frequent aerial and terrestrial associations between these bats and *T. commodus*, and where the extent of predation pressure on resident crickets across bat guilds may be examined closer, in future.

An important opportunity to assay this from dietary analysis unfortunately did not lead to a practical outcome. The very few scat samples collected over the duration of fieldwork (Chapter 2, Section 2.4.2) meant these data were insufficient to reliably quantify selection pressure (Trites and Joy 2005). Molecular approaches to dietary analysis would be a valuable tool for future assessment here, given the high screening capacity, specificity of prey content and direct verification of feeding on terrestrial prey these techniques can offer (Murphy et al., 2003; Beveridge and Simmons 2005; Hall et al., 2010; Bohmann et al., 2011; Clare et al., 2011; Zeale et al., 2011; Burgar et al., 2014; Hope et al., 2014). However, interpretations from such assessment would
require some caution; there is no single standardised approach to suit all objectives and limitations within each of the different techniques available can lead to inappropriate/inaccurate generalisations (Clare 2014; Clarke et al., 2014). To whatever (yet-to-be determined) extent the bats at Gold Creek Reservoir interact with resident field crickets, the extrinsic environment may have a very important role in shaping this association.

The emissions of bats observed flying directly above crickets (S. greyii and N. gouldi) are potentially inaudible to these insects at the ground (Figures 3.6 and 3.7). As emphasised in Chapter 3, these conclusions are cautious and initial approximations only, and require further verification from standardised and direct measurement of source intensity levels and the bats’ proximity at the time of recording. Further, my estimations are based on extrapolations from behavioural and neural sensitivity in T. oceanicus since neural audiograms do not exist, and were not not possible to generate here, for T. commodus. Indeed, Australian and Oceanic populations of T. oceanicus (but not within-Australia populations) are genetically distinct, and demonstrate significant differences in AN2 and behavioural thresholds (Fullard et al., 2010). However, the Oceanic population of crickets exists approximately 9000 km away in a relatively “bat-poor” region which would greatly influence their auditory sensitivity (Fullard et al., 2007; Fullard et al., 2010; Lehmann et al., 2010; Strauss and Stumpner 2015). In contrast, T. commodus and T. oceanicus overlap with an abundance of bat species in Australia, some of which (e.g. N. geoffroyi and N. gouldi) extend across the entire country (Churchill 2008; Atlas of Living Australia 2015). Their distributional limits also overlap in Queensland (Atlas of Living Australia 2015), where the two species could be exposed to the same bats. Variation in their behavioural thresholds also appears to be smaller than across geographical variants of T. oceanicus (Nolen and Hoy 1986); this does not at all provide an accurate and reliable means of inference however, and at most, it would suggest T. commodus is less sensitive to bat echolocation than T. oceanicus. Since signal intensity is a strong determinant of detection and response by both predator and prey (Schnitzler et al., 2003; Hennig et al., 2004), these directions of inquiry are an important caveat for future work on the focal animal species. Based on this project’s initial estimations, a number of key areas of focus would be particularly significant.
With respect to Nyctophilus bats, the species most suited as a relevant threat to grounded crickets (Grant 1991; Cronin and Sanderson 1994; Bailey and Haythornthwaite 1998; Churchill 2008), characterisation of emission source intensities even under laboratory conditions (Faure et al., 1993; Jacobs et al., 2008; Brinkløv et al., 2011) would provide empirical data on exactly how softly they call (Milne 2002; Pennay et al., 2004). A sophisticated suite of acoustic and video techniques (microphone arrays, stereo flash photography and stereo-videogrammetry; Blumstein et al., 2011) would then help describe the diversity, flexibility and adaptive significance of their strategies, and implications for the prey. For example, my estimates on the audibility of emissions on the ground were obtained from a single point; assessment of the same sound over a range of distances across a three-dimensional matrix of space and through variable clutter, would provide crucial detail to determine critical detection ranges of bats for grounded crickets (Schul et al., 2000; Fullard et al., 2005; Londhe et al., 2009). Such spatial mapping would yield valuable insight about the impact of signal adjustment by bats in a guild- and task-specific manner (e.g. Berger-Tal et al., 2008; Brinkløv et al., 2011; Hackett et al., 2014) on the capacity of crickets to initially (or at all) detect these bats. Herein, detailed information may also be gained on any dynamic switching between sensory modalities (echoic and non-echoic prey detection, Chapter 5) during substrate foraging by Nyctophilus.

These techniques would also serve to directly address any correlation between physical strata and acoustic detectability by both predator and prey. Under the least cluttered conditions at Gold Creek Reservoir (10 cm of grass, Chapter 3) the preliminary estimates of echolocation audibility for grounded crickets suggest poor detection; higher grass and thus denser clutter would only further attenuate these sounds (Pritz 2004; Londhe et al., 2009). If clutter is serving a passive source of defence for prey because it reduces their acoustic (or otherwise) detection by bats, crickets may be spatially selective for particular areas similar to that observed in some moths (Andersson et al., 1998; Rydell 1998; Svensson et al., 2002). Cover certainly seems to be a preferred space in contrast to the open for female T. commodus (Chapter 4); but this is abandoned in the simulated presence of N. bifax, tentatively indicating some potential for spatial selection. Exactly how detectable bat signals are for crickets within their natural ground environment, could therefore elucidate whether acoustic monitoring is possible or necessary at all.
For a gleaning bat, sensory specialisations for prey detection against clutter are extensively characterised (Schnitzler et al., 2003; Denzinger and Schnitzler 2013) however, the acoustic and perceptual characteristics of impedance when prey are within clutter is less detailed (Boonman et al., 1998; Rainho et al., 2010). Determining the extent to which hidden prey are detectable by bats, would further elucidate the acoustic correlates and limitations of interactions on the ground. The acoustic characterisation of *N. gouldi* and *N. bifax* during live interactions with grounded crickets (Chapter 5) suggests both echoic and silent strategies may be relevant during terrestrial foraging in unobstructed space at least. The sensitivity of my recordings here is not perfect with some capture events where acoustic information could not be confidently assayed; neither can these experiments conclusively determine what echolocation was being used for (e.g. orientation or prey detection; Schnitzler et al., 2003). However, crickets walking on the arena floor clearly attracted the attention of bats, and these sounds are evidently sufficient cues for passive localisation (Guppy and Coles 1988; Grant 1991; Arlettaz et al., 2001; Marimuthu et al., 2002); in these cases passive listening appeared to be the primary modality for foraging. In a few other events, the acoustic and foraging behaviour of the bats show some similarity to echoic detection of immobile prey by *Micronycteris microtis* (Geipel et al., 2013). This recent account, past suggestions of its possibility (Schmidt et al., 2000; Weinbeer et al., 2013; Simon et al., 2014) and for other task-specific purposes during substrate foraging (Razak et al., 2007; Russo et al., 2007), highlights the functional relevance of active echoic strategies in many gleaning bats. Given some earlier work on the neurobiology of *N. gouldi* (Guppy and Coles 1988), and more recently the functionally specific parallel processing achievable by *A. pallidus* (Barber et al., 2003; Razak et al., 2007), this direction of inquiry could reveal specific insight on the functional relevance of acoustic strategies in these *Nyctophilus* bats.

Characterisation of the acoustic environment from the prey's perspective would help direct future investigations about what (if any) role the physical setting plays in shaping their responses to bat ultrasound and herein, if alternative sensory structures are also involved. My findings in Chapter 4 are consistent with past work in that walking field crickets in the open are not responsive, and inconsistently so, to bat emissions (Tables 4.2 and 4.3; Pollack et al., 1984; ter Hofstede et al., 2009), and to calls from both aerial hawks and a gleaner. Within the physical structure of vegetation however, not only
is acoustic impediment a relevant issue in this absence of behaviour but the manner in which refuge availability influences the prey’s response (Eilam 2005; Cooper and Frederick 2007; Domenici et al., 2011); any display of alternative behaviour is yet to be described.

While spatial recognition and preference may be suggestive from the outcomes of shelter seeking experiments with *T. commodus* females (Figures 4.2 and 4.3; Hedrick and Kortet 2012), the deliberate conflict of choice set up by the absence of alternative ‘refuges’ during *N. bifax* calls, highlights other factors that might be relevant in the decisions prey make. These include: distance and structural complexity of surrounding shelter; speed, direction, size and historical experience with the predator; and even, ontogenetic and individual variation in boldness of risk-taking behaviour (Eilam 2005; Hedrick and Kortet 2006; Cooper and Frederick 2007; Domenici et al., 2011). Indeed, a lack of boldness given their life habits, may explain the failure of male *T. commodus* to meet the criteria of shelter seeking in the current study (Evans 1983; Otte and Alexander 1983; Hedrick 2000; Hedrick and Kortet 2012). In both sexes however, vegetation is likely to be very important as a source of passive defence against predators because of the cryptic value it offers (Svensson et al., 2002; ter Hofstede et al., 2009). Certainly, in the presence of bats *T. oceanicus* males only call when they are within shelter (Bailey and Haythornthwaite 1998), suggesting that the physical barrier serves a sufficient strategy of defence. In this case, active pre-emptive avoidance behaviours such as negative phonotaxis may not be displayed because they are not needed. An alternative classification of the cricket’s behavioural repertoire during terrestrial interactions with bats is therefore, needed but one that is probably a generalised response to predatory risks on the ground. For example, female *T. commodus* could be interpreting echolocation signals simply as ‘generic noise’ to stay away from (Karlsen et al., 2004). Presenting a range of sounds in addition to bat echolocation (e.g. conspecific, other acoustic predator) may reveal behaviourally distinct responses (Hill 1974; Boyan 1979; Schul and Schulze 2001); if these show specificity for ultrasound, they would provide a definitive indication of a terrestrial response to bats.

The outcomes of this dissertation offer some further direction for characterising this alternative repertoire, which may-well still be defined by an early- (delay moving or seek shelter) and late-stage (escape) suite of behaviours, but closely associated with
the terrestrial environment. During the final attempt to survive (escape), ground clutter would certainly maximise the effectiveness of the powerful leap *T. commodus* performed upon attack by *Nyctophilus* (Chapter 5; Burrows and Morris 2003; Hustert and Baldus 2010; Snelling et al., 2013), as well as hinder the predator’s capacity to pursue (Boonman et al., 1998; Edut and Eilam 2004; Shifferman and Eilam 2004; Eilam 2005; Rainho et al., 2010; Domenici et al., 2011). Additionally important for characterising the early-stage (and escape) response however, is the input from alternative sensory structures for detecting echolocating, or silent, bats (Hartbauer et al., 2010). These are important for defining any non-auditory cues utilised by crickets for avoidance on the ground, as well as in driving evasive behaviour (Camhi 1988; Boyan and Ball 1990; Miller et al., 1991; Tauber and Camhi 1995; Dupuy et al., 2012). There is currently little overlap in research addressing cercal- (or antennal) and acoustic-mediated responses in insects (for examples, see Orida and Josephson 1978; Ritzmann et al., 1991; Hartbauer et al., 2010), despite their common purposes in model species with ultrasound sensitivity. This is also poignant since neural inhibition by these sensory structures, not descending motor signalling (Nolen and Hoy 1984, 1986), appears to contribute to diminished early-stage acoustic detection and evasion in some insects (Orida and Josephson 1978). Ecologically, it would be beneficial for crickets to exploit multi-modal sensory perception on the ground, where many predators other than gleaning bats may be present (Comer and Baba 2011). Combined with the passive defence offered by the terrestrial environment, crickets may then be well-armed to detect and evade gleaning bats even if they are acoustically silent.
6.3. References


(Continued over next pages) Bat species diversity at Enoggera State Reserve, as determined through acoustic and trapping surveys but which are not considered of direct threat to resident *T. commodus*. Echolocation call profiles provided for those species that were acoustically detected.

*Myotis macropus*
Appendix 1 Cont’d

Miniopterus australis
Miniopterus orianae oceanensis
Appendix 1 Cont’d

Chalinolobus gouldii
Appendix 1 Cont’d

*Mormopterus beccarrii*

![Graph showing frequency distribution from 0 kHz to 100 kHz]

Note: The graph illustrates the frequency distribution of *Mormopterus beccarrii* ranging from 0 kHz to 100 kHz.
Appendix 1 Cont’d

*Mormopterus ridei*
Appendix 1 Cont’d

Vespadelus pumilis

Scoteanax rueppellii

Chalinolobus morio

Chalinolobus nigrogriseus
Appendix 2

Chapter 3

Calibration response plot of mean sound pressure level (dB SPL re20μPa) measured for a 40 kHz reference signal recorded over distance (1 – 20 m).
Appendix 3

Chapter 3

Descriptive statistics of call parameters recorded from little broad-nosed bats, S. greyii, in April 2007. Data was obtained from 14 sequences recorded in the field. In each column, different subscript letters (a, b, c) denote significant differences between foraging echolocation call phases.

<table>
<thead>
<tr>
<th>Echolocation Call Phase</th>
<th>No. Calls</th>
<th>Start Frequency (kHz) mean ± SD (min - max)</th>
<th>End Frequency (kHz) mean ± SD (min - max)</th>
<th>Peak Frequency (kHz) mean ± SD (min - max)</th>
<th>Bandwidth (kHz) mean ± SD (min - max)</th>
<th>Inter-pulse Duration (ms) mean ± SD (min - max)</th>
<th>Pulse Duration (ms) mean ± SD (min - max)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Search Phase</td>
<td>235</td>
<td>65.14 ± 10.57\textsubscript{a} (47 - 88)</td>
<td>39.34 ± 1.12\textsubscript{a} (37 - 42)</td>
<td>41.93 ± 1.07\textsubscript{a} (39.2 - 44.8)</td>
<td>25.80 ± 10.70\textsubscript{a} (7 - 49)</td>
<td>76.77 ± 11.99\textsubscript{a} (108.1 - 45.6)</td>
<td>6.49 ± 1.67\textsubscript{a} (2 - 10.6)</td>
</tr>
<tr>
<td>Approach Phase</td>
<td>123</td>
<td>72.47 ± 11.28\textsubscript{b} (48 - 95)</td>
<td>40.35 ± 1.71\textsubscript{b} (37 - 45)</td>
<td>46.99 ± 1.84\textsubscript{b} (43.1 - 57.4)</td>
<td>32.12 ± 11.24\textsubscript{b} (8 - 54)</td>
<td>27.19 ± 13.43\textsubscript{b} (10 - 49)</td>
<td>2.58 ± 1.29\textsubscript{b} (1 - 6.8)</td>
</tr>
<tr>
<td>Buzz Phase</td>
<td>238</td>
<td>44.52 ± 8.26\textsubscript{c} (30 - 68)</td>
<td>26.42 ± 1.68\textsubscript{c} (22 - 44)</td>
<td>32.08 ± 1.78\textsubscript{c} (26.8 - 75.4)</td>
<td>17.22 ± 6.84\textsubscript{c} (2 - 40)</td>
<td>4.93 ± 1.63\textsubscript{c} (3 - 9.9)</td>
<td>1.37 ± 0.44\textsubscript{c} (1 - 2.7)</td>
</tr>
</tbody>
</table>
Appendix 4

Chapter 3

Descriptive statistics of call parameters recorded from Gould’s long-eared bats, *N. gouldi*, in April 2007. Data was obtained from two sequences recorded in the field. In each column, different subscript letters (a, b, c) denote significant differences between foraging echolocation call phases.

<table>
<thead>
<tr>
<th>Call Phase</th>
<th>Echolocation Call Phase</th>
<th>No. Calls</th>
<th>Start Frequency (kHz)</th>
<th>mean ± SD</th>
<th>End Frequency (kHz)</th>
<th>mean ± SD</th>
<th>Peak Frequency (kHz)</th>
<th>mean ± SD</th>
<th>Bandwidth (kHz)</th>
<th>mean ± SD</th>
<th>Inter-pulse Duration (ms)</th>
<th>mean ± SD</th>
<th>Pulse Duration (ms)</th>
<th>mean ± SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Search</td>
<td>17</td>
<td></td>
<td>85.69 ± 10.87&lt;sub&gt;a&lt;/sub&gt;</td>
<td>65 - 100</td>
<td>36.06 ± 1.88&lt;sub&gt;a&lt;/sub&gt;</td>
<td>33 - 38</td>
<td>44.22 ± 1.57&lt;sub&gt;a&lt;/sub&gt;</td>
<td>42.3 - 46.6</td>
<td>49.63 ± 12.00&lt;sub&gt;a&lt;/sub&gt;</td>
<td>23 - 65</td>
<td>66.03 ± 12.9&lt;sub&gt;a&lt;/sub&gt;</td>
<td>51.8 - 92.5</td>
<td>4.39 ± 1.08&lt;sub&gt;a&lt;/sub&gt;</td>
<td>2.7 - 6.2</td>
</tr>
<tr>
<td>Approach</td>
<td>18</td>
<td></td>
<td>78.06 ± 9.33&lt;sub&gt;a&lt;/sub&gt;</td>
<td>63 - 94</td>
<td>37.12 ± 2.18&lt;sub&gt;a&lt;/sub&gt;</td>
<td>34 - 41</td>
<td>48.56 ± 3.45&lt;sub&gt;b&lt;/sub&gt;</td>
<td>44.7 - 54.9</td>
<td>40.50 ± 11.42&lt;sub&gt;c&lt;/sub&gt;</td>
<td>18 - 59</td>
<td>19.54 ± 13.10&lt;sub&gt;b&lt;/sub&gt;</td>
<td>7.1 - 46.6</td>
<td>2.55 ± 0.86&lt;sub&gt;b&lt;/sub&gt;</td>
<td>1.1 - 4.4</td>
</tr>
<tr>
<td>Buzz</td>
<td>19</td>
<td></td>
<td>49.74 ± 9.97&lt;sub&gt;b&lt;/sub&gt;</td>
<td>37 - 72</td>
<td>24.56 ± 1.03&lt;sub&gt;b&lt;/sub&gt;</td>
<td>23 - 26</td>
<td>31.66 ± 0.93&lt;sub&gt;c&lt;/sub&gt;</td>
<td>30.1 - 32.9</td>
<td>23.53 ± 6.518&lt;sub&gt;c&lt;/sub&gt;</td>
<td>13 - 36</td>
<td>3.89 ± 0.03&lt;sub&gt;c&lt;/sub&gt;</td>
<td>3.3 - 4.4</td>
<td>1.83 ± 0.22&lt;sub&gt;b&lt;/sub&gt;</td>
<td>1.5 - 2.4</td>
</tr>
</tbody>
</table>
Appendix 5

Chapter 5
Example observation record from focal sampling used in Chapter 5 for characterisation of behaviours (type and frequency) exhibited by wild caught *Nyctophilus* bats during interactions with field crickets, in an arena.

<table>
<thead>
<tr>
<th>Tape</th>
<th>Bat Species</th>
<th>Bat No.</th>
<th>Running Time</th>
<th>Period count</th>
<th>Event</th>
<th>Bat Position</th>
<th>Flight time</th>
</tr>
</thead>
<tbody>
<tr>
<td>11</td>
<td>N. bifax</td>
<td>5</td>
<td>Start at 01.30</td>
<td>1</td>
<td>HS with E train, F with E train, HS with E train, CW with E train, HS with E train, F with E train</td>
<td>mid back corner RH wall, land low RH back wall</td>
<td>1.31 - 1.34, 1.48 - 1.52</td>
</tr>
<tr>
<td></td>
<td>5 x whole cricket</td>
<td>1.30 - 1.50</td>
<td>1</td>
<td>HS with E train, F with E train, HS with E train, CW with E train, HS with E train, F with E train</td>
<td>mid back corner RH wall, land low RH back wall</td>
<td>1.31 - 1.34, 1.48 - 1.52</td>
<td></td>
</tr>
<tr>
<td></td>
<td>ATE 2 CRICKETS</td>
<td>1.58 -</td>
<td>bat low back RH wall, HS with E train, F with E train 2.00 - 2.03, Hover over cricket on mid back floor, land low mid back wall, HS with E train down at cricket, F with E train 2.03 - 2.04, land mid back LH wall, HS with E train, CW with E train, different cricket CW up back LH corner post, 2.07 bat investigate, F with E train 2.14 - 2.17, land low LH back wall, HS with E train, F with E train 2.19 - 2.20, land on first cricket on mid back floor, capture C1</td>
<td>mid back floor, land high back RH wall</td>
<td>6.55 - 6.58</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>2.50 - 3.10</td>
<td>2</td>
<td>eating C1</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>4.10 - 4.30</td>
<td>3</td>
<td>eating C1</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>5.30 - 5.50</td>
<td>4</td>
<td>eating C1, finish 6.30</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>6.50 - 7.10</td>
<td>5</td>
<td>HS with E trian, F with E train, HS with E train</td>
<td>mid back floor, land high back RH wall</td>
<td>6.55 - 6.58</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>8.10 - 8.30</td>
<td>6</td>
<td>HS with E train, CW with E train, HS with E train, CW with E train, HS with E train</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>9.30 - 9.50</td>
<td>7</td>
<td>CW with E train, HS with E train, CW with E train, CW with E train, CW with E train</td>
<td>high RH front wall</td>
<td>181</td>
</tr>
<tr>
<td>Time</td>
<td>Duration</td>
<td>Event Description</td>
<td>Location</td>
<td>Time</td>
<td></td>
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<td></td>
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</tr>
<tr>
<td>10.50 - 11.10</td>
<td>8</td>
<td>CW, HS with E train, F with E train, HS with E train</td>
<td>land, top RH wall</td>
<td>10.50 - 11.06</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>12.10 - 12.30</td>
<td>9</td>
<td>CW with E train, HS with E train, CW with E train, HS with E train</td>
<td>low RH front wall</td>
<td>10.58 - 11.06</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>13.30 - 13.50</td>
<td>10</td>
<td>CW with E train, HS with E train, CW with E train, HS with E train</td>
<td>top mid RH wall</td>
<td>14.52 - 14.56, 14.58 - 15.01</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>17.30 - 17.50</td>
<td>13</td>
<td>HS with E train, CW with E train, F with E train, HS with E train, top RH back wall</td>
<td>land high back LH wall</td>
<td>17.38 - 17.48</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>18.20 - 18.47</td>
<td>14</td>
<td>eating C2, bat high mid back wall, CW with E train to left, then to right towards cricket in top RH corner, HS with E train towards cricket, Cw with E train, capture 18.46, F with E train and C2 18.47 - 18.51, land top RH back wall, consume</td>
<td>hi back wall</td>
<td>17.38 - 17.48</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>18.50 - 19.10</td>
<td>14</td>
<td>eating C2</td>
<td></td>
<td>17.38 - 17.48</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>20.10 - 20.30</td>
<td>15</td>
<td>eating C2</td>
<td></td>
<td>17.38 - 17.48</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>21.30 - 21.50</td>
<td>16</td>
<td>eating C2</td>
<td></td>
<td>17.38 - 17.48</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>22.50 - 23.10</td>
<td>17</td>
<td>eating C2</td>
<td></td>
<td>17.38 - 17.48</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>24.10 - 24.30</td>
<td>18</td>
<td>eating C2, finish 24.34</td>
<td></td>
<td>17.38 - 17.48</td>
<td></td>
<td></td>
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<tr>
<td>Time</td>
<td>Index</td>
<td>Notes</td>
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<tr>
<td>25.30 - 25.50</td>
<td>19</td>
<td>HS with E train</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>26.50 - 27.10</td>
<td>20</td>
<td>HS with E train, HS with E train, top RH back wall</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>28.10 - 28.30</td>
<td>21</td>
<td>HS with E train, HS with E train, HS with E train,</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>29.30 - 29.50</td>
<td>22</td>
<td>HS with E train, HS with E train,</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>30.50 - 31.10</td>
<td>23</td>
<td>HS with E train, HS with E train,</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>32.10 - 32.30</td>
<td>24</td>
<td>nothing</td>
<td></td>
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<td></td>
<td></td>
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</tr>
<tr>
<td>33.30 - 33.50</td>
<td>25</td>
<td>HS with E train,</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>34.50 - 35.10</td>
<td>26</td>
<td>HS with E train,</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>36.10 - 36.30</td>
<td>27</td>
<td>nothing</td>
<td></td>
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<td>37.30 - 37.50</td>
<td>28</td>
<td>nothing</td>
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<td></td>
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<tr>
<td>38.50 - 39.10</td>
<td>29</td>
<td>nothing</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>40.10 - 40.30</td>
<td>30</td>
<td>nothing</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>41.30 - 41.50</td>
<td>31</td>
<td>HS with E train,</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>42.50 - 43.10</td>
<td>32</td>
<td>HS with E train</td>
<td></td>
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<td>44.10 - 44.30</td>
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<td>HS with E train, crickets walking around bat - good example for cricket behaviour</td>
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<td>45.30 - 45.50</td>
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<td>HS with E train, crickets just stop and freeze near bat, no running away, but also, walk around with no cares less than 50cm from bat</td>
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<td>50.50 - 51.10</td>
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<td>54.50 - 55.10</td>
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<td>57.30 - 57.50</td>
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<td>45</td>
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<td>END EXP</td>
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Appendix 6

Chapter 5

Descriptive statistics of scored behaviours exhibited by *Nyctophilus bifax* (n = 2) and *Nyctophilus gouldi* (n = 3) during live interaction trials with live and intact crickets, deaf crickets, dead crickets and moths. Data shown for head scan, crawl wall, crawl floor, flight and echolocation alone are expressed as percentage proportion of all active behaviours; all scored behaviours were exhibit with detectable echolocation. Consumption time pooled for alive crickets but excluded for dead crickets which were never eaten in full and spat out. All data shown as mean ± SEM values.

<table>
<thead>
<tr>
<th></th>
<th>Live Crickets</th>
<th>Deaf Crickets</th>
<th>Dead Crickets</th>
<th>Moths</th>
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<tbody>
<tr>
<td><strong>Head Scan (%)</strong></td>
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<tr>
<td><em>N. bifax</em></td>
<td>52.57 ± 4.57</td>
<td>62.58 ± 15.91</td>
<td>41.72 ± 14.64</td>
<td>59.53 ± 2.15</td>
</tr>
<tr>
<td><em>N. gouldi</em></td>
<td>39.00 ± 13.39</td>
<td>59.74 ± 13.39</td>
<td>60.07 ± 10.62</td>
<td>73.93 ± 13.05</td>
</tr>
<tr>
<td><strong>Crawl Wall (%)</strong></td>
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</tr>
<tr>
<td><em>N. bifax</em></td>
<td>11.15 ± 3.15</td>
<td>13.80 ± 6.21</td>
<td>16.40 ± 1.32</td>
<td>10.71 ± 4.04</td>
</tr>
<tr>
<td><em>N. gouldi</em></td>
<td>21.31 ± 6.29</td>
<td>16.57 ± 4.01</td>
<td>21.91 ± 7.05</td>
<td>15.33 ± 7.77</td>
</tr>
<tr>
<td><strong>Crawl Floor (%)</strong></td>
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<tr>
<td><em>N. bifax</em></td>
<td>12.00 ± 12.00</td>
<td>5.20 ± 0.14</td>
<td>4.59 ± 0.62</td>
<td>0.84 ± 0.84</td>
</tr>
<tr>
<td><em>N. gouldi</em></td>
<td>0.64 ± 0.32</td>
<td>0.47 ± 0.47</td>
<td>0.73 ± 0.73</td>
<td>0.74 ± 0.38</td>
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<tr>
<td><strong>Flight (%)</strong></td>
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<tr>
<td><em>N. bifax</em></td>
<td>15.15 ± 0.86</td>
<td>13.77 ± 4.91</td>
<td>15.78 ± 3.28</td>
<td>24.02 ± 5.99</td>
</tr>
<tr>
<td><em>N. gouldi</em></td>
<td>13.65 ± 3.38</td>
<td>12.84 ± 6.03</td>
<td>12.80 ± 5.01</td>
<td>1.82 ± 0.93</td>
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<tr>
<td><strong>Echolocation alone (%)</strong></td>
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<tr>
<td><em>N. gouldi</em></td>
<td>25.41 ± 4.56</td>
<td>10.38 ± 3.71</td>
<td>4.49 ± 2.75</td>
<td>8.17 ± 4.14</td>
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<tr>
<td><strong>Flight duration (sec)</strong></td>
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<tr>
<td><em>N. bifax</em></td>
<td>2.33 ± 0.80</td>
<td>1.91 ± 0.24</td>
<td>2.11 ± 0.30</td>
<td>2.35 ± 0.27</td>
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<tr>
<td><em>N. gouldi</em></td>
<td>3.85 ± 0.39</td>
<td>2.15 ± 0.32</td>
<td>2.77 ± 0.29</td>
<td>2.75 ± 0.63</td>
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<tr>
<td><strong>Total Captures</strong></td>
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<tr>
<td><em>N. bifax</em></td>
<td>5</td>
<td>3</td>
<td>1</td>
<td>6</td>
</tr>
<tr>
<td><em>N. gouldi</em></td>
<td>6</td>
<td>7</td>
<td>4</td>
<td>5</td>
</tr>
<tr>
<td><strong>Consumption time (sec)</strong></td>
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<td></td>
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<td></td>
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<tr>
<td><em>N. bifax</em></td>
<td>265.5 ± 22.97</td>
<td>incomplete</td>
<td>45.13 ± 11.54</td>
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<tr>
<td><em>N. gouldi</em></td>
<td>269.6 ± 24.67</td>
<td>incomplete</td>
<td>65.00 ± 15.04</td>
<td></td>
</tr>
</tbody>
</table>
Appendix 7

Chapter 5
Extracts from a video sequence illustrating typical attack and capture by *Nyctophilus* bats of *Teleogryllus commodus* (walking on the arena floor in this example). Total event duration = 3 seconds.
Appendix 8

Chapter 5
Extracts from a video sequence illustrating typical attack and capture by *Nyctophilus* bats of moths (perched on arena wall in this example). Total event duration = 2.5 seconds.