Refining technology to examine animal movement in modified landscapes

by

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Preface – List of Publications

This thesis comprises four papers that present my PhD research (Chapters 2 - 5). The General Introduction (Chapter 1) provides a brief review of the relevant literature and outlines the key themes underlying the research, while the Synthesis (Chapter 6) describes links between the papers and places the research in a broader context.

The data chapters have been prepared as stand-alone papers for publication in collaboration with co-authors. Therefore, there is some overlap in chapter content, particularly with regards to descriptions of the study area, and the pronoun ‘we’ is used instead of ‘I’ in recognition of the co-authors’ contributions.

The papers, my contributions, and the contributions of the co-authors are as follows:

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<th>Thesis Section</th>
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<td>Contributions: BMA and EGR conceived the study. JPYA assisted with the technology. BMA conducted the fieldwork and analysed the data. BMA and EGR wrote the manuscript with editorial guidance from JPYA and JKM</td>
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<td>My contribution: 70%</td>
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<tr>
<td></td>
<td>Contributions: BMA, DGN, and EGR conceived the study. BMA conducted the fieldwork. DGN and BMA analysed the data. BMA, EGR and DGN wrote the manuscript with editorial guidance from JPYA and JKM</td>
</tr>
<tr>
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<td>My contribution: 65%</td>
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Contributions: BMA and JPYA conceived the study. BMA conducted the fieldwork with guidance from JPYA (and assistance from Dr Rod Collins). JRS analysed the blood samples for DLW. DGN, BMA, and JPYA analysed the data. BMA, JYPA, and EGR wrote the manuscript with editorial guidance from DGN.

My contribution: 60%


Contributions: BMA, DGN, and EGR conceived the study. BMA conducted the fieldwork. DGN and BMA analysed the data. BMA, EGR and JKM wrote the manuscript with editorial guidance from JPYA and DGN

My contribution: 70%

This work was conducted under Ethics Approval from Deakin University A45-2011, and B33-2012.

I also contributed to the following publications during my PhD:


Finally, I prepared and published a manuscript relating to separate research during my PhD, and have another in preparation:


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Chapter 1: General introduction

The environment is being modified at an unprecedented post-historical rate and geographic extent due to human activities such as agriculture and urbanisation (Fischer & Lindenmayer 2007). Through changing resource distribution and availability, and other altered environmental conditions, ecosystem-, community-, and population-composition is being affected (Brawn et al. 2001). Species’ ranges are shifting, contracting, expanding, or becoming fragmented (Fletcher et al. 2012), and in turn many species are declining, and some have become extinct (Sih et al. 2011, Lowry et al. 2013, Haddad et al. 2015). From a conservation and management perspective therefore, it is important to understand how species respond and might survive in the face of such environmental upheaval. Such information can guide proactive biodiversity conservation measures, such as establishing protected areas and ecosystem and habitat restoration.

Resources for conservation are severely limited, it is essential therefore that investment is guided by appropriate ecological information about species of interest (Bottrill et al. 2008, McDonald-Madden et al. 2008, Ochoa-Ochoa et al. 2011). To do so we must find reliable, and ideally quantitative methods of understanding how species respond to anthropogenic environmental change. Such methods will lead to a more comprehensive understanding of how a species distribution and abundance are affected, including predicting which taxa might be most vulnerable to habitat loss and modification, as well as the possible over-arching consequences for community composition and ecosystem function (Kremen et al. 1993, Rosenblatt et al. 1999, Hughes et al. 2000).
The following sections provide a global overview of the key elements in assessing species habitat use, before focussing on new technological methods to record information regarding animal movement, and finally the application and advantages of combining different technologies to answer related ecological questions.

1.1 Species habitat use

There are three main questions ecologists want to answer regarding how species use their environment: 1) Where do species occur (i.e. their physical location)? 2) How do species use resources where they occur? and 3) How do different environmental features affect species (e.g. behavioural and physiological consequences)? Detailed information relating to these three questions offers the potential to understand spatial population processes as the ultimate consequence of individual behaviour, physiological constraints, and fine-scale environmental influences (Patterson et al. 2008), yet we have insufficient practical information on how to measure all these aspects related to habitat use (Poisot et al. 2012).

Behaviour, including movement, is a key factor governing the ability of species to respond to environmental variation and change (Frair et al. 2005, Fahrig 2007, van Moorter et al. 2013). Behavioural responses to anthropogenic environmental change fall into several main categories; avoiding or coping with novel enemies (e.g. predators, parasites, diseases), adopting and using novel resources or habitats (e.g. artificial structures and cities), avoiding or coping with novel abiotic stressors (e.g. pollutants, noise), and adjusting to changing spatiotemporal conditions (e.g. habitat fragmentation, climate change) (Sih et al. 2011). These behavioural responses can lead to changes in species interactions, population dynamics and evolutionary processes,
which ultimately shape population persistence and speciation (Tuomainen & Candolin 2011). Therefore, the accurate measurement of animal behaviour in different environmental contexts could greatly further our ecological knowledge.

The importance of the links between environmental change, behaviour, population dynamics, and evolutionary processes have repeatedly been stressed, however research in this area has faced obstacles common to movement ecology in general (Harris et al. 1990, Mårell et al. 2002, Ganskopp & Johnson 2007, Dujon et al. 2014). Movement of wildlife can be recorded via direct observation by humans, however difficulty arises in measuring the movement and behaviour of free-living animals in situ, as observer presence potentially interferes with natural behaviours, ethical concerns, and other issues (e.g. observer safety in the presence of dangerous animals). For example, the presence of observers can cause animals to increase their vigilance or frequency of alarm calls, potentially confounding study results and ecological inference (Patterson et al. 2008).

1.2 Technology for measuring animal behaviour

Ecologists often rely on technology to quantify ecological phenomena, and technological advancements have often been the catalyst for enhanced understanding of ecosystems and their parts (Keller et al. 2008). Recent technological developments provide new ways of collecting behavioural data, including movement. Technologies, both current and emerging, have the capacity to generate ‘next generation’ ecological data that, if harnessed effectively, will transform our understanding of the ecological world. In order to understand where animals persist, spatial movement recording technology such as VHF tracking, and more recently GPS, have been used to provide
insights into animal space-use in modified landscapes (Fryxell et al. 2008, Gautestad et al. 2013, Vasudev & Fletcher 2015). GPS technology uses the triangulation of satellites to determine high quality location data (i.e., errors ≤10 m), 24-hours per day and under all weather conditions (Rodgers et al. 1996). GPS data can be used to measure changes in spatial location, and the movement between those points can be extrapolated to create time-activity models and activity estimates (Lachica & Aguilera 2005). This method has shown potential in long-term studies on animals with large home ranges and clearly defined active and resting periods (Hulbert et al. 1998, Johnson et al. 2002, Lachica & Aguilera 2005, Ungar et al. 2005).

Examining how animals use the environment and obtain resources has been undertaken using technology and techniques such as spool and line tracking (Boonstra & Craine 1986), camera traps (Brook et al. 2012), and GPS tracking (Allan et al. 2013), but these approaches have been limited in their capacity to capture certain information. Spool and line techniques provide a very limited timeframe, camera traps can only capture what happens in restricted locations, and GPS technology only records individual spatial locations. However, recently, fine scale spatial and temporal animal movement has been quantified using accelerometers (Fryxell et al. 2004, Halsey et al. 2011, Rothwell et al. 2011, Elliott et al. 2013). Accelerometers are small, reusable, externally mounted electronic devices which record movement as a change in acceleration at a very fine scale (0.001 g) and rate (>100 Hz) across all three dimensions of movement (x, y, z), providing finer temporal resolution than many other methods (Halsey & White 2010, Bidder et al. 2012). By examining the fine-scale movement data recorded by the accelerometer, researchers can infer and quantify specific animal behaviours such as grooming, fighting, and mating in cryptic species.
such as pumas (*Puma concolor*) (Williams *et al.* 2014), and cheetahs (*Acinonyx jubatus*) (Grunewalder *et al.* 2012). This allows researchers to gather substantial data on animal behaviour without the need to directly observe the animal, providing unprecedented insight into the behaviour of free-living animals (Naito *et al.* 2010, Soltis *et al.* 2012, Awkerman *et al.* 2014).

Animals are known to use different behavioural strategies to survive in changing environments, yet there has been little research on how this links to, and affects, overall energy expenditure. The doubly-labelled water (DLW) technique is one of the most widely used methods of calculating energy expenditure, however, it is expensive, invasive, single-use, and provides only a single estimate of energy expenditure over the study period (Bevan *et al.* 1994, Butler *et al.* 2004, Halsey *et al.* 2008, Qasem *et al.* 2012). Due to these limitations, some have used fine scale movement as a proxy for energy expenditure (Green *et al.* 2009, Gleiss *et al.* 2011, Fossette *et al.* 2012). Movement converts metabolic energy into mechanical work and, therefore, accurate quantification of movement has the potential to correlate with the energy expended to produce it (Cavagna & Kaneko 1977, Fancy & White 1985, Speakman 2000, Yoda *et al.* 2001, Gleiss *et al.* 2011). However, there have been few studies examining the accuracy with which movement can predict energy expenditure under field conditions, incorporating a range of ‘active’ and 'resting' natural behaviours or phases (night time vs. daytime) (Halsey & White 2010, Elliott *et al.* 2013, Miwa *et al.* 2015). This is necessary as laboratory studies suggest that, as activity decreases, the predictive ability of movement models also decreases (Wilson *et al.* 2006, Green *et al.* 2009, Halsey *et al.* 2009a, Gleiss *et al.* 2011). Consequently, there is a need for additional studies,
incorporating a range of animal behaviour, in order to fully assess the ability of accelerometry to accurately predict energy expenditure in free-living animals.

1.3 Combining technology to advance ecological understanding

The full potential of technology in ecology can be realised by using different technologies in combination. For instance, GPS technology only measures one broad aspect of animal movement: the change in the location of the individual over time (Nathan et al. 2008). Conversely, accelerometers record fine-scale activity irrespective of any change in spatial location, but without spatial reference. By combining these technologies we not only record elements of a species’ space-use, but also movements that don’t result in spatial displacement, or occur in a fraction of a second, such as a toad flicking its tongue to capture prey (Dean 1980, Duckworth 1998). These types of behaviours are too often overlooked due to the coarse temporal resolution of most spatial recording technologies (Wilson et al. 2006). Furthermore, the incorporation of both technologies may also provide information pertaining to how different behaviours affect energy use at an individual scale.

1.4 Study area and species

In Australia, many landscapes have been cleared or heavily modified for agriculture, forestry, urbanisation and grazing since European settlement (Radford et al. 2005, Selwood et al. 2009). The resulting matrix of forest fragments and linear roadside strips is surrounded by varying types of agriculture, timber production, and buildings. The extent and pattern of landscape disturbance varies spatially. For instance, coastal regions such as south-west Gippsland in Victoria are moderately populated and have been extensively modified through the channelling of swamps and extensive clearing
to create agricultural land. There are now very few remnant patches > 100 years old, limiting the landscape’s use for wildlife, particularly hollow-dependent species (Gibbons & Lindenmayer 2002, Harper et al. 2005). Conversely, Strathbogie Ranges in north-eastern Victoria, less than 200 km away, is much less populated. While much of the area has still been cleared, it has primarily been for silviculture, and there are still remnant patches that have only been selectively logged, resulting in trees in excess of 150 years old. This variation in anthropogenic disturbance makes Australia a model system to analyse and assess the movement of animals in modified landscapes using emerging technology.

Australia has in excess of 400 hollow dependent vertebrate species, most of which are vulnerable to forest modification (Bennett et al. 1991, Lindenmayer et al. 1997, Banks et al. 2011). Two such sympatric and congeneric species are the common brushtail possum (Trichosurus vulpecula) and the mountain brushtail possum, or bobuck, (Trichosurus cunninghami). Both species are medium-sized (2 – 4 kg), nocturnal, semi-arboreal marsupials. Common brushtail possums are mainly folivores, but also consume a wide variety of fruits, and are known to eat birds' eggs, insects, and small mammals such as rats (Shipley et al. 2009). While populations have declined extensively in the wild, common brushtail possums have adapted well to urban landscapes, and are one of Australia’s most widely distributed marsupials. Bobucks, however, are patchily distributed throughout wet sclerophyll forests and sub-tropical forests of eastern Australia, and are not known to have adapted to urban landscapes. They require silver wattle as a food source, and hollow-bearing trees for den sites (Ims 1987, Lindenmayer et al. 1990, Downes et al. 1997, Martin & Martin 2007), and until
recently (Hynes & Cleeland 2005) were believed to be restricted to higher elevation areas and cooler climates.

1.5 Research aims and thesis structure

The aim of my thesis was to investigate how emerging technology could be used to characterise, quantify, and compare animal movement and other behaviour in relation to variation in habitat attributes associated with fragmented and modified ecosystems. Common brushtail and bobucks were the focal species for my research. Both species were examined across two geographically and structurally distinct habitats in Victoria, Australia; the mountainous Strathbogie Ranges, and coastal south-west Gippsland. Individuals from habitats subject to different degrees of anthropogenic influence (heavily modified linear-strip habitat, and remnant forest fragments) were tracked with custom-made collars containing both GPS, and accelerometer data loggers. These data was combined with morphological and demographic data to create behavioural profiles of how these species respond to changing environments.

My chapters and their specific objectives were as follows:

Chapter 2: A cost-effective and informative method of GPS tracking wildlife

Aim: The development and modification of a relatively new and inexpensive off-the-shelf GPS device to provide high spatial and temporal resolution information on the movement patterns of individuals (bobucks). This included examining how movement varied through time, and how individuals interacted with each other.

Specific aims:

1) To modify and adapt consumer GPS devices for use in wildlife research.
2) To collect data equivalent to that captured by commercial wildlife GPS tracking systems, in order to allow for the examination and analysis of individual movement, habitat preference, and intraspecific interactions.

This chapter has been published in Wildlife Research.


A demonstration video was produced and posted to YouTube:

https://www.youtube.com/watch?v=UaSvS0grVjw

Chapter 3: The secret life of possums: data-loggers reveal the movement ecology of an arboreal mammal in a fragmented landscape

Aim: To compare and contrast the different movement patterns of male and female bobucks using information derived from using GPS and accelerometer data loggers, and the information that can be obtained by combining technologies. Both male and female bobucks were tracked in a highly fragmented forest ecosystem consisting of forest fragments and linear roadside habitat.

Key predictions:

1) Males were expected to travel further, have higher levels of overall activity, and have a higher activity level per metre travelled than females due to actions such as territory defence and competition (Schmidt et al. 2003, Zschille et al. 2012, Haan & Halbrook 2015).
2) Based on home range studies (Martin & Handasyde 2007), and the composition of key resources such as silver wattle and tree hollows (Martin 2006, Martin et al. 2007) bobucks in forest fragments were expected to travel further, have higher levels of overall activity, and have a higher activity level per metre travelled than bobucks in linear-strip environments.

This chapter has been written for submission to Ecosphere, and is currently being prepared for submission.

Chapter 4: Validation of accelerometry to measure energy expenditure in a free-living, scansorial mammal

Aim: To investigate the efficacy of accelerometry and GPS spatial movement to measure energy expenditure in a scansorial mammal, the bobuck (Trichosurus cunninghami), in south-eastern Australia. Movement was derived from accelerometers to calculate vectorial dynamic body acceleration (VeDBA) and behavioural states, and GPS to calculate distance travelled. These were compared to estimates of field metabolic rate derived from Doubly Labelled Water (DLW).

Key predictions:

1) GPS data will be a poor predictor of energy expenditure as the recording interval is too coarse.

2) VeDBA will only be a moderate predictor of energy expenditure, for while it is recorded at a high temporal rate, a direct comparison between VeDBA and energy expenditure assumes that they scale evenly.
3) Time-activity analysis based on behavioural states will be the best predictor of energy expenditure, as it allows for the calculation of different rates of energy expenditure for different activities.

4) The inclusion of morphological and demographic traits will improve the fit of the models.

This chapter has been written for submission to *Scientific Reports*, and is currently being prepared for submission.

**Chapter 5: Contrasting congener behaviour in relation to environmental variation**

Aim: To compare and contrast the habitat use, movement, and energy expenditure of two sympatric and congeneric species across two geographically and structurally distinct habitats. Male bobucks and common brushtail possums were tracked in linear strip habitat in two distinct regions; the mountainous Strathbogie Ranges, and coastal south-west Gippsland.

*Key predictions:*

1) Bobucks in south-west Gippsland are believed to be at the limit (edge) of their geographic range, and in habitat less suitable than the Strathbogie Ranges. Therefore, Bobucks in south-west Gippsland were expected to find it more difficult to obtain key resources such as nesting hollows and food such as silver wattle (Lawton 1993). We believe this difficulty to obtain resources will be exhibited in higher nightly distances travelled, higher activity levels, more time in high-activity behavioural states, and energy expenditure.
2) Bobucks are physically larger than common brushtail possums, and have larger home ranges, and were therefore expected to have higher movement and energy expenditure.

3) Common brushtail possums in the Strathbogies were expected to be inferior competitors compared with bobucks. Thus, they are expected to be more resource limited and have higher movement values. This may result in potentially higher energy expenditure, than common brushtail possums in south-west Gippsland.

This chapter has been written for publication, however the journal for submission is still in discussion.

Chapter 6: Synthesis

To synthesise the main findings of my thesis, identify knowledge gaps for future research, and discuss broader implications for ecological theory, conservation and management.
Chapter 2: A cost-effective and informative method of GPS tracking wildlife

Schedule A: Authorship statement (Approved by Academic Board on 13 September 2016)

This schedule is made pursuant to the Authorship Procedure.

1. Details of publication and senior author

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<th>Academic Unit/Division if based at Deakin; Organisation and address if non-Deakin</th>
<th>Email or phone</th>
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<tr>
<td>Blake Allan</td>
<td>School of Life and Environmental Science</td>
<td><a href="mailto:bmallan@deakin.edu.au">bmallan@deakin.edu.au</a></td>
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2. Inclusion of publication in a thesis

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<th>If Yes, please complete Section 3 If No, go straight to Section 4.</th>
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3. HDR thesis author's declaration

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<th>Academic Unit/Division if based at Deakin</th>
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<tr>
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<td>School of Life and Environmental Science</td>
<td>Refining technology to examine animal movement in modified landscapes</td>
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</table>

I was involved in conceiving the study and designing the methodology. I designed and built the collars and collected and analysed the data. I drafted the manuscript, and revised and edited it based on other authors reviews and suggestions.

I declare that the above is an accurate description of my contribution to this paper, and the contributions of other authors are as described below.

Signature and date

4. Description of all author contributions

<table>
<thead>
<tr>
<th>Name and affiliation of author</th>
<th>Contribution(s) (for example, conception of the project, design of methodology or experimental protocol, data collection, analysis, drafting the manuscript, revising it critically for important intellectual content, etc.)</th>
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<tr>
<td>Dr. Evan G. Ritchie, Chief Supervisor, Deakin University</td>
<td>Assistance in conceiving the study, assistance in writing the manuscript and revising it critically</td>
</tr>
<tr>
<td>Dr. John P. Y. Arnould, Co-Supervisor, Deakin University</td>
<td>Assistance with the experimental protocol (technology), and revising the manuscript critically</td>
</tr>
<tr>
<td>Dr. Jennifer K. Martin, Co-Supervisor, The University of Melbourne</td>
<td>Assistance with the experimental protocol (possum handling), and revising the manuscript critically</td>
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</table>
Schedule A: Authorship statement (Approved by Academic Board on 13 September 2016)

This schedule is made pursuant to the Authorship Procedure.

5. Author Declarations
I agree to be named as one of the authors of this work, and confirm:

i. that I have met the authorship criteria set out in the Deakin University Authorship Procedure,

ii. that there are no other authors according to these criteria,

iii. that the description in Section 4 of my contribution(s) to this publication is accurate,

iv. that the data on which these findings are based are stored as set out in Section 7 below.

If this work is to form part of an HDR thesis as described in Sections 2 and 3, I further

v. consent to the incorporation of the publication into the candidate’s HDR thesis submitted to

Deakin University and, if the higher degree is awarded, the subsequent publication of the thesis

by the university (subject to relevant Copyright provisions).

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<td></td>
<td>19/12/2016</td>
</tr>
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<td>Dr. John P. Y. Arnould</td>
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<tr>
<td>Dr. Jennifer K. Martin</td>
<td></td>
<td>19/12/2016</td>
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6. Other contributor declarations

I agree to be named as a non-author contributor to this work.

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<th>Contribution</th>
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* If an author or contributor is unavailable or otherwise unable to sign the statement of authorship, the Head of Academic Unit may sign on their behalf, noting the reason for their unavailability, provided there is no evidence to suggest that the person would object to being named as author.

7. Data storage

The original data for this project are stored in the following locations. (The locations must be within an appropriate institutional setting. If the executive author is a Deakin staff member and data are stored outside Deakin University, permission for this must be given by the Head of Academic Unit within which the executive author is based.)

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This form must be retained by the executive author, within the Academic Unit in which they are based.

If the publication is to be included as part of an HDR thesis, a copy of this form must be included in the thesis with the publication.
2.1 Abstract

In wildlife research, our ability to GPS track sufficient numbers of individuals is always limited by cost, which restricts inference of species-habitat relationships. Here we describe the modification and use of a relatively new and inexpensive off-the-shelf GPS device, to provide detailed and accurate information on the movement patterns of individuals (mountain brushtail possums, or bobucks; *Trichosurus cunninghami*), including how movement varies through time, and how individuals interact with each other. Our results demonstrate that this technology has enormous potential to contribute to an improved understanding of the movement patterns and habitat preferences of wildlife at a fraction of the cost of traditional GPS technology.

2.2 Introduction

There are several commercial suppliers specialising in various types of wildlife GPS tracking devices. However, GPS tracking remains a relatively expensive method of collecting location data compared with traditional methods such as spool-and-line tracking or VHF tracking, with wildlife GPS devices costing thousands to tens of thousands of dollars (Matthews et al. 2013). This high expense typically reduces the number of units that can be purchased by researchers and, as a result, the number of individuals able to be tracked simultaneously. This can create statistical problems (e.g. low power) and limits the inferences which can be made about populations, such as habitat use and interactions between individuals. Furthermore, the purchase of commercially available wildlife GPS tracking devices does not always guarantee successful deployment, as many fail due to construction error or damage sustained

A cheaper alternative is to purchase a GPS data logger or data transmitter built for purposes such as travel, sport, domestic pet tracking, or personal tracking (see Table 2.1). These pre-assembled GPS devices usually comprise a GPS antenna, processor, storage device, power supply, and often, timer chips. Stripping these units of excess packaging, and attaching them to an animal is the easiest means of creating a cheap and effective tracking device. However, challenges arise in the repackaging of devices in ways which reduce size, while creating sufficient protection against both the environmental conditions and the species to which they are attached.

We describe a novel technique for customising and modifying cheap GPS devices to increase aspects such as durability, orientation, and battery life. These cost-effective GPS wildlife tracking devices can be constructed either as data loggers or as data transmitters, and can be constructed for as little as $USD 50.

2.3 GPS Modification

We designed our GPS devices to study the ecology and movement patterns of an arboreal mammal, the bobuck (Trichosurus cunninghami) (Martin & Martin 2007). From our data, we aimed to examine individual possum movements within the habitat, and examine interactions between possums in the same habitat. Collaring all of the possums resident in a habitat patch simultaneously could potentially require a large number of collars, so we required a cost-effective method.
We modified and collar-mounted the Mobile Action i-gotU GT-120 (Table 2.1) as it was the cheapest available including postage, and is small (44.5 x 28.5 x 13 mm) and lightweight (20 g, 15 g without casing, 7 g chipboard only). A GPS antenna is most accurate and most efficient when it is pointed towards the sky with nothing obscuring its view (Belant 2009, Williams et al. 2012), so we moved the position of the battery on the collar to counterweight the GPS antenna. We also increased the size of the battery, as larger batteries will allow the device to record for longer periods of time (data storage permitting), and larger batteries are also heavier, creating a better counterbalance. We re-encased the device using epoxy resin, as this is relatively lightweight, very strong and does not cause skin irritation to animals.

The total cost was $USD 300 per collar including a VHF transmitter ($USD 220). The GPS in the collars is also rechargeable, making subsequent deployments effectively free. The VHF is not re-chargeable, however the battery lasts for 15 months. Therefore, the finished collar can be deployed and re-deployed for 15 months, at which time it can be re-furbished for approximately $USD 230 by removing and re-mounting a new VHF transmitter. A full demonstration video on how collars were constructed is available at (https://www.youtube.com/watch?v=UaSvS0grVjw).
Table 2.1: Examples of commercially available GPS devices.

Prices accurate as of February 2013

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<tr>
<th>Device Name</th>
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2.4 Field Trials

All trappable male bobucks were collared simultaneously along a roadside. We decided to focus solely on males for the field trial because their home ranges are over twice that of females (Martin et al. 2007). Using only males also limited the number of possums required for testing the collars. The collars were set to record from 19:00 - 06:00 h (local time) every day, to coincide with sunset and sunrise, and were set to record in 5 min intervals until the battery died. For accuracy purposes, only data points with an Expected Horizontal Position Error (EHPE) of <10 m were deemed accurate enough for our fine-scale analysis (Frair et al. 2010).
Three individual male bobucks were captured (Identification codes M1, M2, and M3). Individual M1's collar recorded for 110 hours (10 nights) with 1375 attempted fixes. Of these, 1003 fixes were successful, 76% of which had an EHPE <10 m. Individual M2's collar recorded for 44 hours (4 nights) with 465 attempted fixes. Of these, 378 fixes were successful, 70% of which had an EHPE <10 m. Individual M3's collar recorded for 94 hours (9 nights) with 912 attempted fixes. Of these, 610 fixes were successful, 65% of which had an EHPE <10 m. The accuracy and frequency of the GPS fixes is adequate to clearly divide the roadside into three home ranges with very little overlap (Figure 2.1). From this, we can surmise that male bobucks occupy exclusive home ranges along roadsides.

The battery life varied greatly among the 3 collars due to inferior batteries not meeting their listed milliamp hour (mAh) capacity specifications. We have subsequently rectified this variation using a different brand of batteries.

Due to the variation in recording time, we chose the individual with the most fixes (M1) to analyse activity per night (Figure 2.2). The GPS recorded an average of 100.3 successful fixes per night (SD = 23.63), of which an average of 76.4 (SD = 24.83) had an EHPE <10 m. Fixes with an EHPE >10 m tended to be in groups of 3 to 4 consecutive fixes at a time. The average time between fixes was 6 min 35 seconds, however, each night tended to have blocks of unsuccessful fixes at the beginning and the end of the recording time. Possums do not forage for the entire night (J. Martin pers. obs.), and subsequent spotlighting has led us to believe that the blocks of unsuccessful fixes represent the time the possum is in the tree hollow. The average length of time that fixes were recorded was 8.5 hours per night (SD = 1.63 hours). If we remove the blocks of unsuccessful fixes from the beginning and end of each night,
only 18 fixes over the entire 10 nights were unsuccessful. The average time between fixes also drops from 6 min 35 seconds to 4 min 49 seconds, slightly faster than the 5-minute interval the collars were set for.

2.5 GPS Performance

The GPS tracking collars used for this study cost $USD 300 including the VHF transmitter. While this is only a fraction of the cost of a commercial wildlife GPS tracking collar, the GPS devices used were still able to record the majority of their fixes with an Expected Horizontal Position Error (EHPE) of <10 m, which we deemed accurate enough for fine-scaled analysis of the animal's movement (Frair et al. 2010). Furthermore, the collars were all retrieved with no damage sustained, and could be re-deployed after recharging the batteries.

Building your own GPS devices has a considerably higher investment of time to obtain successfully recording re-useable devices, and the modification of the components used obviously voids all warranties. However, there is also greater flexibility to customise the design to specifically suit a particular species. The scope of cost-effective GPS tracking of wildlife is vast. Furthermore, once built, these devices can be re-charged and re-deployed as often as required, until the battery in the VHF transmitter runs out. The construction of a re-chargeable VHF transmitter could greatly increase the life-span of these collars.

The increased commercial availability of relatively inexpensive GPS devices for purposes such as sport or domestic pet tracking, has made it possible to obtain high-quality GPS data cheaply. Such advancements allow for many more individuals to be
tracked at once, providing a better picture of population dynamics and individual interactions.

Figure 2.1: GPS locations of three male bobucks (M1 = yellow, M2 = blue, M3 = red) in the vegetation (green) along a roadside (in the Strathbogie Ranges, northeastern Victoria, Australia).

Each point encompasses the estimated location of the animal for each fix. The larger the point, the less accurate the location fix.
Figure 2.2: GPS location of one male bobuck (M1) in vegetation (green) along a roadside in the Strathbogie Ranges, north-eastern Victoria, Australia, for 11 consecutive nights.

Different colours represent different nights. Each point encompasses the estimated location of the animal for each fix. The larger the point, the less accurate the location fix.
Chapter 3: The secret life of possums: data-loggers reveal the movement ecology of an arboreal mammal in a fragmented landscape

3.1 Abstract

Understanding animal movement patterns is fundamental to ecology, as it allows inference about species’ habitat preferences and their niches. Such knowledge therefore also underpins our ability to predict how animals may respond to environmental change, including habitat loss and modification. Data logging devices such as GPSs and accelerometers are rapidly becoming cheaper and smaller, allowing them to be applied more often and on a broader range of animal species. By combining animal movement technologies and the different information they can record, it may be possible to expand our understanding of animal behavior in response to habitat variation and modification. We examined the different insights derived from using GPS and accelerometer data loggers in isolation, and together, to examine arboreal mammal (bobuck, *Trichosurus cunninghami*) movement patterns, in a highly fragmented forest ecosystem (consisting of forest fragments and linear roadside habitat). GPS data were used to examine the distance travelled by bobucks, while accelerometry was used to create behavioral states and measure activity. Used in isolation, the accelerometer and GPS data found different movement patterns in relation to sex and habitat type: the GPS data showed males in linear strips travelled a greater distance than females in linear strips, but no difference in the distance travelled by males and females in forest fragments. The Accelerometer data showed higher
activity in males and females in linear strip environments compared to forest fragments. By coupling GPS and accelerometer data we uncovered three important ecological insights: 1) bobucks in linear strips had higher activity when moving the same distance compared with bobucks in forest fragments; 2) male bobucks had higher activity levels than female bobucks for a given distance travelled; and 3) that differences in movement patterns between sexes and habitat types were most apparent when the distance travelled was greater. Our findings suggest habitat fragmentation changes the amount and type of activity bobucks perform while moving. Combining information from different movement logging devices has great potential to improve our understanding of habitat use by individuals and species in ‘energetically-challenging’ scenarios such as linear forest strips, by managing the spatial patterning of key resources.

3.2 Introduction

Anthropogenic landscape modification is the greatest threat to biodiversity globally (Fahrig 2001, Laurance et al. 2008, Selwood et al. 2009). The modification and loss of habitat affects the spatial configuration and the amount of resources available to species (Fahrig 2001, Rothermel & Semlitsch 2002, Foley et al. 2011), which in turn impacts their growth, reproduction and survival. Understanding how biodiversity responds to and in some cases persists in modified landscapes is therefore critical for species conservation (Rhodes et al. 2005, Tscharntke et al. 2005, Cattarino et al. 2015).

Examining patterns of animal movement allows examination of how individuals respond to habitat variation and change. Movement of an organism can be defined in
two ways: a change in the spatial location of the whole individual in time (Nathan et al. 2008), or changes in behavioural states irrespective of physical location (Nams 2014). These two aspects of animal movement are interwoven, with behavioural states often leading to changes in spatial location, and are key to assessing the ability of species to persist in modified environments (Frair et al. 2005, Fahrig 2007, van Moorter et al. 2013). However, research in this area has faced obstacles common to movement ecology in general (Ganskopp & Johnson 2007, Dujon et al. 2014).

Spatial recording technology such as VHF tracking, and more recently GPS, has been used to provide insights into animal space-use in modified landscapes (Fryxell et al. 2008, Gautestad et al. 2013, Vasudev & Fletcher 2015). However, these technologies measure only one coarse aspect of animal movement: the change in the location of the entire individual over time (Nathan et al. 2008). While these data are often of ecological interest as they detail elements of an individual’s space-use (Frair et al. 2005, Patterson et al. 2008, Cagnacci et al. 2010), other important aspects of animal movement are overlooked (Belant 2009, Bidder et al. 2012, Williams et al. 2012).

Some movements pivotal to the fitness of individuals and the growth of populations do not result in spatial displacement: for instance, intense localized foraging or mating (Duckworth 1998). Similarly, important movements may occur in a fraction of a second, such as a toad flicking its tongue to capture prey (Dean 1980). These too are often overlooked due to the coarse temporal resolution of most spatial recording technologies (Wilson et al. 2006).

Recently, accelerometer loggers have been used to quantify animal movement at fine spatial and temporal scales (Fryxell et al. 2004, Halsey et al. 2011, Rothwell et al. 2011, Elliott et al. 2013). Accelerometers are small, reusable, externally-mounted, and
relatively inexpensive electronic devices which record movement as a change in acceleration at a very fine scale (0.001 g) and rate (>100 Hz) across all three dimensions of movement. Furthermore, the data recorded can provide finer temporal resolution than many other methods (Halsey & White 2010, Bidder et al. 2012). By examining the fine-scale movement data recorded by accelerometers, researchers can discern movement irrespective of any change in spatial location, and can even infer specific animal behaviours (Halsey & White 2010, Grunewalder et al. 2012, Krop-Benesch et al. 2013). This allows researchers to gather substantial information about animal behaviour without the need to directly observe the animal, providing unprecedented insight into the ‘private lives’ of wild animals (Naito et al. 2010, Soltis et al. 2012, Awkerman et al. 2014). Accelerometers have already been used to examine movement and prey capture in cryptic species such as pumas (Puma concolor), revealing new information in energy expenditure and individual variations (Williams et al. 2014). However, accelerometers by themselves also have shortcomings, namely that they do not provide spatial data. Thus, when combined, GPS loggers and accelerometers have the potential to provide complementary insights into the movement ecology of individuals, yet to date the collection of this type of data has been rare (but see Nams (2014)).

Here, we use GPS and accelerometer data loggers to examine the movement ecology of an arboreal mammal in forest fragments embedded within an agricultural landscape in south-eastern Australia. The study species is the bobuck (Trichosurus cunninghami), a medium-sized (2.6–4.2 kg), arboreal, nocturnal, hollow-nesting marsupial (How 1981, Lindenmayer et al. 2002). Habitat availability for the bobuck has reduced since European settlement, primarily by changing the abundance of the
two key resources required: large hollow-bearing trees for den sites and the leaves of the silver wattle (*Acacia dealbata*) for food (Ims 1987, Lindenmayer *et al.* 1990, Downes *et al.* 1997, Martin & Martin 2007). Once a continuous forest, the study landscape is now a matrix of agricultural land, and two types of remnant forest: forest fragments and linear roadside strips. The bobuck persists within both types of remnants, and the effect remnant type has on bobuck population structure, social and mating system has been examined (Martin & Handasyde 2007, Martin *et al.* 2007), yet little is known of how the modified landscape affects individual movement at finer temporal and spatial resolutions.

Our aim was to use GPS and accelerometer data to examine how habitat modification and fragmentation affect the movement behaviour of bobucks in the two types of forest remnants. First, we used GPS data to quantify the nightly distances travelled by bobucks, and accelerometer data to quantify nightly activity and identify key behavioural states. Next, we examined whether the nightly distance travelled, nightly activity or the time spent in particular behavioural states differed between individuals from forest fragments and linear strips and between sexes. Finally, we highlight the complementarity of GPS and accelerometer data by examining how the relationship between distance travelled and activity differs between individuals in forest fragments and linear strips and between sexes.
3.3 Methods

3.3.1 Study area and experimental design

Our study area was in the Strathbogie Ranges, north-eastern Victoria. The study area ranged from 550 to 750 m above sea level, and has an annual rainfall of ~ 900 mm. The vegetation consists of open sclerophyll forest dominated by manna gum (Eucalyptus viminalis), Victorian blue gum (Eucalyptus globulus bicostata), narrow-leaf peppermint (Eucalyptus radiata) and broad-leafed peppermint (Eucalyptus dives). Key middle and understory species include silver wattle (Acacia dealbata), dogwood (Cassinia aculeata), cherry ballart (Exocarpos cupressiformis), blackwood (Acacia melanoxylon), and austral bracken (Pteridium esculentum). Approximately 70% of the native vegetation has been cleared for agriculture and softwood (Pinus radiata) plantation (Downes et al. 1997).

We trapped bobucks in three contiguous forest fragments (> 160 ha and an average vegetation width > 750 m, termed 'forest fragments' throughout) and three linear roadside strips (> 1 km length and an average vegetation width < 40 m, termed 'linear strips' throughout) (Figure 3.1). Sites (fragments and linear strips) were confined to areas of habitat that consisted primarily of native vegetation and containing trees large enough to provide suitable hollows (DBH > 50 cm) (Smith & Lindenmayer 1988, Pausas et al. 1995). Each site was separated by at least 500 m in order to reduce the chances of the same individual being caught at two locations, based on home range data from Martin & Handasyde (2007).
Figure 3.1: Study sites in the Strathbogie Ranges, Victoria, Australia.

Blue shaded ovals indicate forest fragments and yellow shaded ovals indicate linear strips.

We conducted three nights of trapping in each of the six study sites. Each site was comprised of two rows of eight large (30 x 30 x 90 cm) wire cage traps, placed on the ground and baited with peanut butter and apple. We transferred trapped individuals from the traps to hessian bags. Traps were approximately 50 m apart. On linear strips, the two rows were placed within the roadside vegetation, and were separated by a minimum of 200 m. In forest fragments, one row was placed along the edge of the fragment, and the other placed within the fragment, starting a minimum of 100 m from the edge, in order to sample both the core and edges of the fragment. We set the traps
before dusk and checked them before sunrise. Traps were partially covered with plastic to protect animals from weather.

3.3.2 Data collection

Trapping sessions of three nights at each trap site were undertaken over eight consecutive seasons from spring 2011 to winter 2013 inclusive. For processing, we anaesthetized individuals with an intramuscular injection of tiletamine/zolazepam (6 mg kg⁻¹; Zoletil®; Virbac Australia, Peakhurst, NSW, Australia) to facilitate handling and minimize distress for the animals. We injected individuals with Passive Integrated Transponder (PIT) tags (Trovan, Ltd.) for subsequent identification. We then fitted individuals with self-made data-logging collars (80 g) comprised of a VHF transmitter, GPS data logger and 3-axis accelerometer modified from the design in Allan et al. (2013). We set the collars to start recording data as soon as they were attached to the animal with GPS data set to record at 10-minute intervals, and accelerometers at 25 Hz. We only used adult individuals for this study (classed as tooth-wear ≥ 3 (Winter 1980)). In order to allow individuals to recover completely from handling and sedation and to avoid releasing bobucks (which are strictly nocturnal) in daylight, we held the animals after processing until dusk on that day. We released the bobucks within 10 m of the site where they were captured. We recaptured individuals 3-7 days later and removed the data-logging collars.

3.3.3 Data processing

Home range analysis of bobucks has shown they use resources, and the environment, differently based on both sex and habitat type (McDonald-Madden et al. 2004, Martin 2006, Martin & Handasyde 2007, Martin et al. 2007), however, it is not
known how this habitat use is reflected daily. Therefore, we split the data into groups based on sex (male vs. female) and habitat type (forest fragment or linear strip) for analysis, creating four groups (male forest fragment, female forest fragment, male linear strip, and female linear strip) in order to reduce confounding variation in the results.

**GPS** - GPS devices acquire positional fixes from orbiting satellites to triangulate location. However, if the GPS device is obscured by factors such as dense canopy cover or due to its orientation on the animal, it can take longer to acquire a fix, or fail to do so (Williams et al. 2012). As such, although the GPS devices were set to record at 10 minute intervals, the interval between fixes was almost never exactly 10 minutes: some fixes failed to be recorded, and no fixes were recorded while bobucks were denning inside tree hollows. Furthermore, the error of each location fix varies depending on the accuracy with which the location can be triangulated. In order to standardize the data, we used a continuous-time correlated random walk model to convert the GPS location data into nightly interpolated movement tracks through the environment using the **CRAWL** package in R statistical environment (Johnson 2012). Correlated movements imply the animal's location at a given time is dependent on all previous locations, not just the last one. Continuous-time formulation allows data that have been non-uniformly collected over time to be modelled without sub-sampling, interpolation, or aggregation to obtain a set of locations uniformly spaced in time (Johnson et al. 2008).

**Accelerometer** - The total acceleration recorded by the accelerometers is made up of two components: static acceleration and dynamic acceleration (Shepard et al. 2008). Static acceleration refers to the gravitational field of the earth. An accelerometer not
moving is expected to record a cumulative total of 1 g across its three axes due to the gravitational force of the earth. Dynamic acceleration represents the change in velocity as a result of body motion, and has shown great potential as a predictor of energy expenditure (Wilson et al. 2006, Gleiss et al. 2011). To obtain a measure of dynamic acceleration, we first smoothed each accelerometer channel to derive the static acceleration using a running mean over three seconds, and then subtracted this static acceleration from the raw data, leaving only dynamic acceleration (Gleiss et al. 2011). We then converted the values for dynamic acceleration to positive values, and calculated the vector of the dynamic body acceleration to provide a single value for partial vectorial dynamic body acceleration (VeDBA) at 25 Hz (Qasem et al. 2012, Elliott et al. 2013). These values were then summed in 1-second intervals to create partial VeDBA. The accelerometers we used were capable of measuring ± 8 g, therefore any value outside of these range was deemed an outlier and removed (<0.001%).

We undertook behavioural state analysis on the partial VeDBA values, measured at 25 Hz, in Igor Pro version 6.36 (Wavemetrics, Portland, OR, USA) using the program Ethographer (Version 2.02). Ethographer is an automated program for visualizing, and analysing catalogues of discrete behaviours typically employed by a species, known as ethograms, from acceleration data (Sakamoto et al. 2009). We converted the time series accelerometer data into a spectrum via continuous wavelet transformation, then categorized each second of the spectrum into one of 10 specified behaviour groups by unsupervised cluster analysis, using k-means methods. Due to the possibility for the axes to shift in relation to the orientation of the body, fine-scale behavioural states could not be calculated, instead we used the 10 identified groups to create four broad
behavioural states measured at 1-second intervals, characterized by the periodicities of body acceleration and the time of acceleration:

1. Denning – Measurements taken during the day (mean VeDBA = 0.028 ± 0.001 m/s²)
2. Resting at Night - very low VeDBA values, but while the bobucks were out of the den (mean VeDBA = 0.108 ± 0.001 m/s²)
3. Moving - moderate VeDBA values and during the night, including normal foraging behaviour (mean VeDBA = 0.180 ± 0.001 m/s²)
4. High Activity - Activity values much higher than all the others, accounting for behavioural states such as mating, fighting, intense foraging, predator avoidance, etc. (mean VeDBA = 0.260 ± 0.002 m/s²)

We examined the behavioural states over a 24-hour period (midnight to midnight GMT), including when the bobucks were denning and removed any recordings which did not span the full 24-hour time period. Given animals could potentially display different movement patterns after release, we removed the nights of release and capture from both movement measures.

Response variables – We tracked thirty-two individual bobucks for 2-7 nights at a time, totalling 149 nights of data across the eight consecutive seasons (males in forest fragments = 10 individuals and 36 nights; females in forest fragments = 16 individuals and 48 nights; males in linear strips = 6 individuals and 21 nights; and females in linear strips = 12 individuals and 44 nights). Animals classed as inhabiting linear strip environments spent > 80 % of their nightly movement in linear strips, and 9 of the individuals strictly inhabited linear strip environments. Animals classed as inhabiting
forest fragments ranged more widely, but had > 60 % of GPS points recorded within the forest fragments, and made use of the forest fragments on a nightly basis. The average time between GPS fixes across the study was 14 minutes 59 seconds (range 2 minutes 04 seconds to 63 minutes 29 seconds). We considered data points with an error > 40 m (6.65% of data) too inaccurate and removed them, resulting in an average Estimated Horizontal Position Error (EHPE) of 10 m (range 2.72 to 39.84 m).

**GPS data** - We created two variables from the GPS data; the total distance travelled in a 24-hour period (midnight to midnight GMT), termed ‘nightly distance travelled’ measured in metres, and distance travelled in 10-minute intervals, termed ‘interval distance travelled’, also measured in metres. Using midnight in GMT meant that the break between one day and the next fell during daylight hours in Australia, which is when the bobucks are denning, meaning no GPS fixes, and a clear break as to when one GPS track finished, and the next began. For nightly distance travelled, we measured the distance of the interpolated movement tracks for each full night of movement. For interval distance travelled, we determined locations at 10-minute intervals along the interpolated movement tracks, and measured the distance between these locations.

**Accelerometer data** - The accelerometer data created two continuous datasets: VeDBA values, and the time spent in the four behavioural states. As stated previously, VeDBA is the velocity of the body motion, or activity, of the animal, and this activity has shown great potential as a predictor of energy expenditure (Wilson et al. 2006, Gleiss et al. 2011). We created three variables from the Accelerometer data: 1) ’24-hour activity’ which is the sum of the partial VeDBA values measured at 25 Hz over 24 hours, commensurate to ‘nightly distance travelled’; 2) ‘interval activity’ which is the sum of
the partial VeDBA values measured at 25 Hz in 10 minute intervals matching ‘interval
distance travelled’; and 3) ‘behavioural state’ which is the amount of time animals
spent in each of four behavioural states, measured in 1-second intervals, over the same
24-hour period as ‘nightly distance travelled’ ‘24 hour activity’. A list of the measures
of animal movement is provided in Table 3.1.

Table 3.1: Outline of the measures of animal (Trichosurus cunninghami)
movement

<table>
<thead>
<tr>
<th>Device</th>
<th>Measurement</th>
<th>Unit of Measurement</th>
<th>Timeframe of measurement</th>
<th>Method of measurement</th>
</tr>
</thead>
<tbody>
<tr>
<td>GPS</td>
<td>Nightly Distance Travelled</td>
<td>Metres (m)</td>
<td>24 hours</td>
<td>Summed distance based on interpolated movement track from GPS points over 24 hours</td>
</tr>
<tr>
<td></td>
<td>Interval Distance Travelled</td>
<td>Metres (m)</td>
<td>10 minute intervals</td>
<td>Nightly interpolated movement track broken into 10 minute intervals</td>
</tr>
<tr>
<td>Accelerometer</td>
<td>24 Hour Activity</td>
<td>Gravitational Force (g)</td>
<td>24 hours</td>
<td>Summed activity based on accelerometer values measured at 25 Hz over 24 hours</td>
</tr>
<tr>
<td></td>
<td>Interval Activity</td>
<td>Gravitational Force (g)</td>
<td>10 minute intervals</td>
<td>Summed VeDBA values, measured at 25 Hz, into 10 minute intervals</td>
</tr>
<tr>
<td></td>
<td>Behavioural State</td>
<td>Categorical</td>
<td>1 second intervals over 24 hours</td>
<td>VeDBA values, measured at 25 Hz, used in Ethographer to create four behavioural states measured in 1-second intervals</td>
</tr>
</tbody>
</table>

**Predictor variables** - All response variables were related to two predictor variables
and their interaction. First, to examine the impact of patch type on bobuck movement,
we included a two-level categorical variable indicating the patch type within which the
animal was captured: either forest fragment or linear strip. Second, as the sex of
animals can affect movement behaviours (Beck et al. 2003), a second two-level
categorical variable was included indicating the sex of the animal: male or female.

3.3.4 Statistical analysis
We used Generalized Linear Mixed Models (GLMMs) to analyse the effects of the predictor variables on measures of animal movement derived from GPS and accelerometer data. Mixed models were required as they can consider both fixed and random effects, the latter of which can account for correlated data (Zuur et al. 2009) including repeated sampling of the same individuals over time (Zuur et al. 2009). Thus, the identity of individual animals was specified as a random effect in all models to account for repeated sampling of individuals over several days. We included the site and season within which data was collected as additional random effects to account for season-to-season variance.

We generated GLMMs of the relationship between the movement variables measured over 24 hours (nightly distance travelled, nightly activity and the time spent in each of the four behavioural states) and the two predictor variables. We fitted a global model between each response variable and the two categorical variables (patch type and sex) and their interaction. We ran four separate models to examine the time bobucks spent in different behavioural states over a 24-hour period, corresponding to each of the four behavioural states: denning, resting at night, moving, high activity. We ran the models with each group (males in linear strips, males in forest fragments, females in linear strips, and females in forest fragments) as the reference category in order to determine the differences between all four groups. We applied a Bonferroni correction to the \( p \) values to infer significant differences between groups after accounting for multiple comparisons. To evaluate the ‘significance’ of differences we observed, we report effect sizes, confidence intervals, and \( p \) values, with alpha set at \( p < 0.1 \). We chose this value for alpha because we didn’t have many observations (nights) for some levels of tests, and hence a more conservative \( p \) value (0.05) might have made it harder to detect
‘significant differences’, as per results and guidance from (Nakagawa & Cuthill 2007) and (Jennions & Møller 2003). While $p < 0.1$ creates a higher risk of false positives in the analysis, we have included information regarding effect sizes and confidence intervals to assist in indicating the biological importance of the results (Nakagawa & Cuthill 2007). We assessed model fit using r-squared calculated using the r.squaredGLMM function in the MuMIn package.

We examined activity in relation to distance travelled as a proxy for the energetic cost of bobuck spatial movement in each of the patch types and for both sexes. We analysed these data at a finer temporal scale as variation in activity often occurs over short time periods (Wilson et al. 2006): we used a 10-minute time interval, the shortest period we could with the current GPS technology. To understand the additional insights from coupling these technologies, we modelled partial VeDBA (response variable) as a function of distance travelled and a four-level categorical variable that concatenated the patch type and sex predictor variables (i.e. male linear strip, male forest fragment, female linear strip, and female forest fragment). We specified an interaction between these two predictor variables to allow a separate curve for the relationship between VeDBA and distance travelled for each patch type and sex combinations. Differences in the slopes of VeDBA with distance travelled would be indicative of animals investing different amounts of activity per unit of distance travelled, depending on their patch type and sex. We used the lstrends function in the lsmeans package (Lenth 2016) to test for differences in the slopes between the patch type and sex combinations. We again used a Bonferroni correction to account for multiple comparisons, but set alpha to 0.05 given the larger number of samples at the finer temporal resolution. As movements at the scale of 10-minute intervals are likely to be temporally auto-
correlated, we fit an autoregressive models of order one (AR1) to account for residual temporal correlation in the data. The AR1 model residuals at a given time $t$ as a function of the residuals at previous times $t-1$ allowing residuals to be correlated in time, with residuals further away in time less correlated than those closer in time (Zuur et al. 2009). GLMMs were generated using the nlme package in the R statistical environment (R Core Development Team 2014).

### 3.4 Results

The nightly distance travelled by bobucks was significantly higher for males in linear strips than all other groups, and was higher for males in forest fragments than females in linear strips, but there was no significant difference between males and females in forest fragments (Figure 3.2 and Table 3.2 in Chapter 3 appendix). The activity of bobucks over 24 hours, as measured by VeDBA, was also significantly higher for males in linear strips than all other groups (Figure 3.3 and Table 3.3 in Chapter 3 appendix). An example of a bobuck’s movement patterns relative to activity for a single night has been depicted in Figure 3.4.
Figure 3.2: The average distance travelled (m) over 24 hours by bobucks (*Trichosurus cunninghami*) in south-eastern Australia, by sex and habitat type.

The coloured points indicate the raw data. The error bars indicate Standard Error. Categories sharing a letter did not show significantly different relationships between the coefficients.
Figure 3.3: The average VeDBA (g) measured over 24 hours for bobucks (Trichosurus cunninghami) in south-eastern Australia, by sex and habitat type.

The coloured points indicate the raw data. The error bars indicate Standard Error. Categories sharing a letter did not show significantly different relationships between the coefficients.
Figure 3.4: A visual representation of the movement and activity of a bobuck (*Trichosurus cunninghami*) in 10-minute intervals for a single night in southeastern Australia.

Each section of line represents a 10-minute interval. The length of the line represents the distance travelled, while the colour ramp (red-to-blue corresponding to high-to-low activity respectively) represents the level of activity. The white crosses indicate the GPS points.

All groups spent a similar amount of time denning, resting at night, and moving (Figure 3.5 and Tables 3.4a, 3.4b, and 3.4c in Chapter 3 appendix). However, differences were observed for time spent in the high activity behavioural states. Males in linear strips spent significantly more time in high activity than all other groups, while males in
fragments spent similar time in high activity as the females in linear strips, and significantly more than females in fragments. Females in fragments and females in linear strips spent similar time in high activity (Figure 3.5 and Table 3.4d in Chapter 3 appendix).

Figure 3.5: The average time spent by bobucks (*Trichosurus cunninghami*) in each behavioural state over a 24-hour period (midnight to midnight GMT) in south-eastern Australia, by sex and habitat type.

The coloured points indicate the raw data. The error bars indicate Standard Error. Categories sharing a letter did not show significantly different relationships between the coefficients.
There was a significant interaction between the ‘group’ an individual belonged to (i.e. male in linear strip, female in linear strip, male in forest fragment, female in forest fragment) and distance moved over-ten minute intervals when explaining activity levels (measured as 10 minutes summed VeDBA). Model predictions show (1) that bobucks in linear strips have higher summed VeDBA values when moving the same distance compared to bobucks in forest fragments; (2) that males had higher summed VeDBA values than females for a given distance travelled; and (3) that differences between the four groups (i.e. males in fragments, female in fragments, males in linear strips, females in linear strips) were most apparent when the distance travelled was greater (Figure 3.6 and Table 3.5 in Chapter 3 appendix).
Figure 3.6: The relationship between activity and the distance travelled per ten-minute interval for bobucks (*Trichosurus cunninghami*) in south-eastern Australia.

Lines and shaded area represent the fitted relationship and 95% confidence intervals from generalized linear mixed models, respectively. Solid line, yellow shading = female bobuck in forest fragments; dotted line, blue shading = male bobucks forest fragments; dashed broken line, green shading = female bobucks in linear strip; dotted and dashed broken line, grey shading = male bobucks in linear strips. Categories sharing a letter did not show significantly different relationships between the coefficients.
3.5 Discussion

Understanding variation in patterns of animal movement is critical to both theoretical and applied ecology (Ponchon et al. 2013). Despite this, finding techniques that can simply and reliably quantify an individual’s movement is challenging. Here, we show the unique insights that can be gained by combining the use of accelerometers and GPS for terrestrial species. While GPS data showed male bobucks in linear strips were moving furthest as compared to other groupings over a 24-hour period, accelerometer data showed that these animals also more frequently engaged in bouts of very high activity. These bursts of high activity help explain why male bobucks in linear strips display higher levels of activity overall (and probably exert more energy) per unit of distance travelled.

We found male bobucks in linear strips travelled significantly further than all other groups. Males travelling further than females of the same species is consistent with studies of the movement of a host of mammal species, including rodents (Maroli et al. 2015), minks (*Neovison vison*) (Haan & Halbrook 2015), wolves (*Canis lupus*) (Jedrzejewski et al. 2001), Irriomote cats (*Prionailurus bengalensis iriomotensis*) (Schmidt et al. 2003), and arctic foxes (*Alopex lagopus*) (Anthony 1997), as well as reptiles such as lizards (Rose 1981, Thompson et al. 1999) and turtles (Aresco 2005). In these instances, males travelled greater distances due to larger body sizes and higher energy demands, to maximize home range overlap with females for breeding, and for mate guarding (Schmidt et al. 2003, Zschille et al. 2012, Haan & Halbrook 2015). On the other hand, the daily movement of females is presumed to be only as far as
necessary for efficient foraging (Schmidt et al. 2003), and restricted due to caring for young (Jedrzejewski et al. 2001). Males in forest fragments did not travel greater distances than females in forest fragments, and females in linear strips travelled the least distance, so we do not believe the increased movement by male bobucks is best explained by foraging requirements as related to food availability. Rather, one possibility, as suggested in Schmidt et al. (2003), is that males in linear strips are travelling greater distances to guard both mates and territory. Martin & Martin (2007) reported much greater population densities of both male and female bobucks in linear strips within the Strathbogies than fragments. The higher population density may result in greater vigilance being required to guard mates.

Female bobucks in linear strips travelled similar distances to females in forest fragments, and had similar activity patterns over 24 hours, yet they had a higher cost of movement per unit distance travelled. This disparity may be due to how arboreal species traverse their environment. An arboreal mammal can move considerable distances climbing up and down trees vertically, without resulting in a change to its two-dimensional position measured by the GPS. Accelerometers are able to capture this three-dimensional activity because they are recording on all three axes of animal movement, providing a much more comprehensive picture of the animal’s true movement. Ryan et al. (2013) showed a similar pattern when studying koalas, finding males moved farther and defended territory more, but had the same amount of activity as females. In our case, we propose that females in linear strip environments may undertake more intense foraging, ascending and descending trees, and predator vigilance, all of which can occur within a few metres of horizontal spatial movement, which is within the error of the GPS devices we used.
Male bobucks in linear strips also had the highest activity over 24 hours, showing a similar pattern to distance travelled. The behavioural state analysis again showed bobucks in linear strips spend more time in high activity behavioural states, commensurate to more activity than the other groups. Males in fragments also spent more time in the high activity behavioural state compared with females in fragments. This may be due to the additional activities males undertake while moving, such as defending their territories from other males (Martin et al. 2007). These types of activities are important sources of energy expenditure for a range of species (Shamoun-Baranes et al. 2012, Christiansen et al. 2013), but are obscured when using GPS technology alone. However, females in linear strips travelled the least distance, so other factors must also be influencing the more active behaviour in linear strips. Female bobucks in fragments were the least active group. We also found no difference in any of the behavioural states for male bobucks in fragments and females in linear strips.

The sex of an individual clearly affected their movement, such that males have higher activity for a given distance travelled as compared with females. We also found that the differences between sexes were amplified in particular habitats—the difference between males and females was far greater in linear strips than forest fragments, as males in linear strips moved greater distances than females in linear strips. We expected females in linear strips to travel the least distance, as a previous study showed linear strips have greater access to their key food source (silver wattle), and greater access to their key shelter (tree hollows) (Martin & Martin 2007). Male movement is more influenced by defending their territories, and the greater number of bobucks in linear strips may result in more movement for defence (Martin et al. 2007).
Linear strip environments have significantly altered the behaviour of bobucks. Male bobucks are travelling further distances each night, with many more bursts of high activity, while females have maintained similar distances travelled, however, their activity levels in so doing have increased. Linear strip environments often differ greatly in vegetation composition and density when compared with forest fragments, and thus the distribution and availability of resources can vary widely (Sabino-Marques & Mira 2011), yet in the environment in question, linear strip environments have higher abundance of both silver wattle and tree hollows, the key resources for bobucks, than the surrounding remnant vegetation (Martin & Martin 2007). Based on resource variables alone, bobucks would be expected to preferentially select for linear strips over other environments to reduce movement (van der Ree 2002, Pereira & Rodriguez 2010). Martin et al. (2007) did hypothesize that males would exert more energy to maintain a home range of equivalent size in the linear strips owing to the much greater distances between the ranges' extremities. However, the same hypothesis does not explain the activity of females in linear strips, who travelled similar distances to females in forest fragments, yet exhibited higher activity. A comparative analysis showed that both males and females on linear strips are investing more energy per metre they move than bobucks in forest fragments. Based on this information, there is an additional cost associated with living in linear strip environments compared with their counterparts in forest fragments which is not identified by distance travelled alone.

Linear strip environments have been shown to affect species by changing movement patterns (Bonnot et al. 2013), increasing predation (Estrada et al. 2002) and disease risk (Brearley et al. 2013), creating barriers to movement (Asari et al. 2010), and
changing the shape of home ranges (van der Ree & Bennett 2003). The altered forest structure in linear strip environments can create an environment less permeable to movement due to reduced connectivity, especially in the composition and abundance of groundcover and mid-story vegetation (McLean et al. 2016). Conversely, individuals in remnant forest fragments may have greater flexibility to choose movements via “least-cost” pathways by either reducing vertical distance travelled, or travelling more direct routes (Hopkins 2011). Mapping the bobuck’s activity-to-movement ratio in relation to forest structure could aid in understanding the connectivity implications of different patterns of forest structure.

Linear strips have also been shown to increase animal stress levels (Van Meter et al. 2009, Arroyo-Rodriguez & Dias 2010, Brearley et al. 2012, Johnstone et al. 2012). Detrimental effects such as more active behavioural states for bobucks in linear strip environments were directly identified, but the drivers are most likely linked to pressures not able to be examined as part of this study. For instance, predators of bobucks such as powerful owls (Ninox strenua) have been found to prey more heavily on the closely related common brushtail possum (T. vulpecula) in highly disturbed landscapes (Cooke et al. 2006), while introduced predators such as foxes (Vulpes vulpes) and cats (Felis catus) also take advantage of the more disturbed environments for hunting (Claridge 1998). The added predation pressure would be expected to increase both stress and vigilance for bobucks in linear strip environments. Linear strips also have denser populations of both bobucks (Martin et al. 2007) and other arboreal species as they use these corridors to traverse the environment (Beier & Noss 1998), so encounters resulting in either fighting or fleeing would also be expected to be higher, potentially explaining the greater bursts of high activity seen in both males
and females in linear strips. The impact of these detrimental effects on growth and survival rates requires further investigation.

Both types of loggers can be used to measure animal movement and predict behaviour, but they measure different aspects of animal movement. By coupling data from the movement loggers, we were able to create a more comprehensive picture of animal behaviour. We identified that both environmental context (habitat fragment type and shape) and individual traits (sex) strongly affect the amount of activity individuals undertake in order to move a given distance. Notably, there is important variation within this pattern: both male and female bobucks in linear strips had disproportionately higher activity levels per unit distance compared with bobucks in forest fragments. It is only through this combined data that we can show the increase in activity is not accounted for by greater distances travelled, and must therefore be caused by higher activity at small spatial scales. This supports the theory that linear strip environments detrimentally affect animal behaviour irrespective of smaller home ranges, as higher activity levels will, in turn, result in higher energetic demands, potentially impacting growth and survivorship (Wilson et al. 2006, Elliott et al. 2013, Schell et al. 2013, Almasi et al. 2015).

The relationship between activity and distance travelled can help infer behaviours that would be missed if either technology was used in isolation. For example, a large activity value from an accelerometer over a given time interval could be due to an animal moving between areas or defending their territory. As accelerometers do not contain spatial data, it is only possible to say that an animal undertook a given amount of dynamic acceleration. Similarly, GPS data would overlook any movement that does not involve an animal travelling from one point to another. For instance, when
examining the distance travelled by bobucks, we can identify components of each night's movement where animals stayed in the same place for an extended period of time, and assume the animal is resting (Heurich et al. 2012). However, if we include the summed VeDBA information, we identify that only some of these periods have the low activity levels expected while resting, while others have very high activity levels. This can be the difference between resting and behaviours such as intense foraging, fighting, or mating. By using both data loggers together, we can more accurately characterise animal movement and potential explanations.

We argue that GPS data loggers are able to provide broader scale spatial and temporal information within the environment, while accelerometer data loggers are able to record finer scale activity and behavioural states. By combining these movement loggers, we were able to build a detailed picture of an individual’s spatio-temporal activity budgets as a whole, and specific behavioural states at a very fine scale. Our approach allows animal movement to be examined and quantified at a scale rarely achieved for free-ranging animals, and will be simple to replicate for many other species in different systems. In addition to the fine temporal resolution of data from accelerometers, the data also had fewer missed recordings. This is due to the accelerometer using its own inertial measurement sensor to record information, which is not affected by forest cover like the GPS. As such, the accelerometers can provide information to estimate animal activity during poor GPS reception. This is particularly important for arboreal species, which spend long periods in dense forest cover.

Our study highlights the difference between the spatial and temporal movement information collected by GPS and accelerometer data loggers, and the significant advantage of coupling these two movement recording technologies to better describe
and quantify the spatio-temporal activity budgets of animals as influenced by habitat variation. By combining the information from these loggers, we achieved a greater understanding of how individuals interact with their environment. Such information could be used in practical conservation applications, such as the design of vegetation corridors or placement of nest boxes relative to food resources within the environment. Individual activity and behaviour across different habitat compositions could also be used to predict responses to environmental change (habitat loss and modification).
Chapter 4: Measuring energy expenditure using animal-borne movement data loggers in a free-ranging scansorial mammal

4.1 Abstract

While the ability to measure the energy expenditure of free-living animals in their natural habitat is integral to understanding their physiology and ecology, obtaining accurate data is logistically and ethically difficult using conventional laboratory techniques. Consequently, various alternative methods have been developed to derive estimates of energy expenditure in free-living animals using data logging technology, with accelerometry recently being proposed as an ideal method. We examined the efficacy of accelerometry and GPS spatial movement to measure energy expenditure in a scansorial mammal, the bobuck (*Trichosurus cunninghami*), in south-eastern Australia. Using accelerometers to derive vectorial dynamic body acceleration (VeDBA) and behavioural states, and GPS to derive distance travelled, we compared these indices of energy expenditure with doubly labelled water (DLW) derived estimates of field metabolic rate. The GPS distance travelled only explained 0.8 % of the variation in energy expenditure values derived from DLW, while VeDBA measurements explained 41.8 %. However, a multivariate model incorporating accelerometry-derived behavioural states was able to explain 70.8 % of the variation in total energy expenditure of the bobucks, confirming that accelerometry has high potential for estimating energy expenditure in scansorial animals.
4.2 Introduction

Measurement of energy expenditure can be used in ecology to attribute a physiological ‘cost’ to different animal activities which, in turn, can be used to assess how animals behave and optimise their energy use (Ricklefs & Wikelski 2002, Shepard et al. 2009, Wright et al. 2014). The ability of species to occupy environments is determined by their energetic requirements, and the availability and distribution of resources (Humphries et al. 2002). Therefore, knowledge of the energy expenditure of free-living animals in relation to their habitat is integral to understanding animal physiology and ecology which, in turn, can provide insights into how species might respond to environmental variability and change (Nagy 1987, Withers et al. 2006, Laich et al. 2011).

An animal’s metabolic rate can be determined most accurately in the laboratory by open-circuit respirometry (± 3-5 % (Withers 2001)). However, this method requires the subject to be enclosed in a chamber which constrains natural behavioural movement, and the results obtained may not be representative of the full range of normal activity related to energy expenditure in free-ranging animals (Halsey & White 2010, Gleiss et al. 2011). Consequently, ecologists have explored methods to accurately measure the energy expenditure of free living animals in the wild (Speakman 2000, Butler et al. 2004, Wilson et al. 2006).

The doubly-labelled water (DLW) technique was one of the first methods used to measure energy expenditure in free-living animals (Bennett & Nagy 1977, Bryant et al. 1985). It has been previously validated by comparison with direct calorimetry in a range of small mammals, and provides an accurate measure of energy expenditure over
several days, with an estimated accuracy of ± 8 - 10% (Nagy 1989, Speakman et al. 1994, Speakman 1997). While this method has been used widely for many taxa (Corp et al. 1999, Halsey & White 2010, Wright et al. 2014), it is expensive, and provides only a single estimate of energy expenditure averaged over the study period (Butler et al. 2004, Halsey et al. 2008, Qasem et al. 2012). Consequently, it is not possible to assign energy expenditures to specific behaviours, limiting the ability to identify the variation between individuals relative to their actions and habitat features.

Movement has been examined as a proxy for measuring energy expenditure (Green et al. 2009, Gleiss et al. 2011, Fossette et al. 2012). Movement converts metabolic energy into mechanical work and, therefore, accurate quantification of movement has the potential to correlate with the energy expended to produce it (Speakman 2000, Yoda et al. 2001, Gleiss et al. 2011). Measurement of movements can be recorded from direct observation (D'Amico & Hemery 2007). However, the effectiveness of direct observation is limited in free-living animals as often insufficient replicates can be acquired, direct human observation may modify animal behaviour, and/or some animals and terrains are non-conducive to direct observations. As such, technology is employed to detect and quantify the movement of animals (Rutz & Hays 2009).

Location information derived from GPS data loggers has been used extensively to track the spatial movements of a wide variety of animals (Weimerskirch et al. 2002, Hebblewhite & Haydon 2010, Matthews et al. 2013) and extrapolated to create time-activity models and activity estimates (Lachica & Aguilera 2005). This method has shown potential in long-term studies on animals with large home ranges and clearly defined active and resting periods (Hulbert et al. 1998, Johnson et al. 2002, Lachica & Aguilera 2005). However, GPS derived movement models require a spatial change,
meaning behaviours with little or no change in location such as grooming, fighting, and mating, cannot be determined accurately. While there have been some investigations of GPS derived distance and behaviour relative to energy expenditure, the resulting relationships have been poor (Ganskopp & Johnson 2007, Munn et al. 2013, Marteinson et al. 2015).

Accelerometer data loggers have been proposed as a new method to record animal activity. Accelerometers are reusable, and can record acceleration data at a very high resolution (0.001 g) and rate (>100 Hz) across all three dimensions of movement. This equates to a device which can record the vibrations created from the hum of a computer hard-drive, and measure that vibration 100 times a second, giving a finer temporal resolution than many other methods (Halsey & White 2010, Bidder et al. 2012). Accelerometry has shown great potential as a predictor of energy expenditure in laboratory conditions (R^2 of 0.81 to 0.94) (Wilson et al. 2006, Fahlman et al. 2008, Halsey et al. 2009b, Gleiss et al. 2011) and it has been used to predict behavioural states in free-living animals (e.g. (Papailiou et al. 2008, Shepard et al. 2008, Elliott et al. 2013)). However, there have been relatively few studies examining the accuracy with which accelerometers can predict energy expenditure under field conditions, covering few taxa, transport modes, and habitats (Elliott et al. 2013, Jeanniard-du-Dot et al. 2016, Stothart et al. 2016). In addition, even fewer studies have incorporated the whole range of 'active' and 'resting' natural behaviours. This is necessary as laboratory studies suggest that, as activity decreases, the predictive ability of accelerometry models also decreases (Wilson et al. 2006, Green et al. 2009, Gleiss et al. 2011). Consequently, it is integral to determining how the relationships between behavioural states and energy expenditure vary in relation to different environmental conditions.
The bobuck (*Trichosurus cunninghami*) is a medium-sized (2.6–4.2 kg), hollow-nesting, scansorial marsupial (How 1981, Lindenmayer *et al.* 2002). It occupies a three-dimensional environment within wooded areas, incorporating both vertical and horizontal movement within the canopy and across the ground, and is strictly nocturnal with clearly defined active periods at night and resting periods during the day (Smith *et al.* 1984). Understanding the energetic requirements of bobucks in relation to behaviour and habitat is necessary in determining how these animals use, and persist within, the current landscape as well as how they may respond to environmental change. However, there is currently no information on the behavioural energetics of the species. Unlike in birds (flight or walking (Elliott *et al.* 2013)) and fur seals (diving, surface travel or walking on land (Jeanniard-du-Dot *et al.* 2016)), where various behaviours involving movement are easily detectable/quantifiable with accelerometry and incur very different transport costs, little is known of the three-dimensional movement patterns of mammals like the bobuck and their energetic costs (Franz *et al.* 2005, Nams 2014).

The aims of this study, therefore, were to examine in bobucks: 1) the relationships from GPS and accelerometry derived movement information and energy expenditure; and 2) assess the factors which may influence their accuracy.

### 4.3 Methods

#### 4.3.1 Study area, animal handling, and instrumentation

This study was conducted in March 2013 in the Strathbogie Ranges, north-eastern Victoria. Bobucks were captured in large wire cage traps (30 x 30 x 90 cm) placed on the ground and baited with peanut butter and apple. Trapping was undertaken in three
contiguous forest fragments and three linear roadside strips (Figure 4.1). Trapping sessions comprised one trap night in each location to avoid recaptures. The traps, partially covered with plastic to protect animals from adverse weather conditions, were set before dusk and checked before sunrise. Captured individuals were transferred from the traps to hessian bags. Only adult individuals were used for this study (classed as tooth-wear ≥ 3 (Winter 1980)).

Figure 4.1: Study sites in the Strathbogie Ranges, Victoria, Australia.

Blue shaded ovals indicate forest fragments and yellow shaded ovals indicate linear strips.
In order to reduce handling stress, animals were anaesthetised during processing using isoflurane delivered via a facemask attached to a portable gas vaporizer (Stinger™, Advanced Anaesthesia Specialists, Gladesville, NSW, Australia (Gales & Mattlin 1998)). Individuals were weighed (± 0.05 kg) in the Hessian bag using a suspension scale (Pesola Macro-Line 80005). All individuals were fitted with data-logging collars (80 g, < 3 % of body mass) comprised of a VHF transmitter, GPS data logger and 3-axis accelerometer modified from the design in Allan et al. (2013). The collars were set to start recording data as soon as they were attached to the animal with GPS data set to record at 10 minute intervals, and accelerometers at 25 Hz.

The energy expenditure of individuals was calculated using the doubly labelled water (DLW) technique (Lifson & McClintock 1966). This method has been previously validated by comparison with indirect calorimetry in a range of marsupials, and provides an accurate measure of energy expenditure over periods of several days (Berteaux et al. 1996, Speakman & Krol 2005). Individuals were injected with DLW at the same time collars were fitted.

Following instrumentation, a pre-dose blood sample (2 mL) was obtained by venipuncture of a forearm vein for determination of the background isotope enrichments of $^2$H and $^{18}$O (method C of (Speakman & Racey 1987)). A known mass (± 0.001 g) of DLW (approximately 1 ml/kg; 30% atom $^{18}$O and 15% atom $^2$H) was then administered intravenously through a catheter. The individuals were placed back in their Hessian bags and left undisturbed for a 90 - 120 min period to allow the isotopes to equilibrate in the body water pool (Krol & Speakman 1999) before a second blood sample (2 mL) was obtained to determine initial isotopic enrichment. Blood samples were kept cool (4 °C) for several hours before being centrifuged and the
plasma fraction separated. Eight plasma aliquots for each individual were then stored in flame sealed 75-μl glass micro-capillary tubes at room temperature until analysis in the laboratory.

In order to allow individuals to recover completely from handling and sedation, and to avoid release of a strictly nocturnal animal in daylight, they were kept in hessian bags until being released <10 m from the capture site at sunset (approximately 6-8 h following post-dose blood sampling). Individuals were recaptured 5-7 days after their release to remove the data-logging collars and take a final blood sample (2 mL) to determine isotope elimination rates.

In the laboratory, the plasma samples were vacuum distilled (Nagy 1983) and water from the resulting distillate was used to produce CO₂ and H₂. The isotope ratios ¹⁸O : ¹⁶O and ²H : ¹H were analysed using gas-source isotope ratio mass spectrometry (Isoprime IRMS and Isochrom μG; Micromass, Manchester, United Kingdom). Background isotope levels were determined from the pre-dose blood sample. The water obtained was used for isotope ratio mass spectrometric analysis of ²H and ¹⁸O. Isotope enrichments were converted to values of daily energy expenditure using a single pool model (Speakman 1993). Equation 7.17 of Speakman (1997) was used as it has been established to minimize error in a range of conditions (Visser & Schekkerman 1999). Daily energy expenditure was converted into overall energy expenditure for the time the animal was injected with DLW.
4.3.2 Sample analysis and data processing

The GPS spatial data points with an error > 40 m (5.63% of data) were deemed too inaccurate and removed, resulting in an average Estimated Horizontal Position Error (EHPE) of 9.41 ± 0.13 m. The spatial data was then converted into continuous-time correlated random walk models, using the CRAWL package in R (Johnson 2012), to re-create the animal's track through the environment. Correlated movements imply the animal's location at a given time is dependent on all previous locations, not just the last one, and continuous-time formulation allows data that have been non-uniformly collected over time to be modelled without sub-sampling, interpolation, or aggregation to obtain a set of locations uniformly spaced in time (Johnson et al. 2008). Nightly movement tracks were derived for the movements of each animal based on the spatial information, and from these tracks calculated the distance travelled by each individual for the duration of the study.

The accelerometer was mounted to a collar around the animal's neck and, while it was weighted in order to assist in orientation, there was the possibility for the collar to rotate around the animal’s neck and shift the accelerometer’s axes in relation to the orientation of the body. Any shift in the accelerometer has the potential to either misidentify a behaviour, causing more behavioural states than actually exist to be categorised, or identifying different behavioural states as the same. As such, Vectorial Dynamic Body Acceleration (VeDBA) was used across all three axes as it is less sensitive to changes in device orientation (Gleiss et al. 2011, Halsey et al. 2011, Qasem et al. 2012). VeDBA was calculated at 25 Hz using the equation:

\[
\text{VeDBA} = \sqrt{(A_x - S_x)^2 + (A_y - S_y)^2 + (A_z - S_z)^2}
\]
The static acceleration (S), measured in gravitational force (g), was separated from the total acceleration (A) for each of the three axes using a running mean of three seconds (Gleiss et al. 2011). The resulting VeDBA values were summed to create a total acceleration (VeDBA_total) for the duration of the DLW study period.

Behavioural state analysis was undertaken in Igor Pro version 6.36 (Wavemetrics, Portland, OR, USA) using the Ethographer (Version 2.02) module (Sakamoto et al. 2009). The time series VeDBA data was converted into a spectrum by continuous wavelet transformation. Then, each second of the spectrum was categorized into one of 10 behavioural states by unsupervised cluster analysis, using k-means methods, and measured at 1-second intervals.

The time spent in each behavioural state was summed for each animal. Energy expenditure per behavioural state was calculated by fitting the following model:

\[ EE = (C_1 \times T_1) + (C_2 \times T_2) + \ldots (C_i \times T_i) \]

where EE is the total energy expenditure (in KJ), \( C_i \) are the estimates (which correspond to the rate of energy expenditure, in KJ per second) for the parameters \( T_i \), the time (seconds) spent per behavioural state listed above \( (i) \), following the methodology of Elliot et al. (2013). The intercept was forced through 0 because no energy is spent if no time passes (Jeanniard-du-Dot et al. 2016). As \( R^2 \) values get overinflated in models without intercepts, \( R^2 \) was computed as 1 - (RSS / ESS), where RSS is the regression sum of squares and ESS the error sum of squares of the models, as an additional means of comparison of the variance between models.
4.3.3 Statistical analyses

Generalised Linear Mixed Models (package MuMIn in R statistical environment (R Core Development Team 2014)) were used to investigate the relationships between DLW-derived estimates of energy expenditure for each individual and predictor variables: VeDBA and distance travelled. Energy expenditure is often standardised by mass ($E_{\text{Eemass}}$) or mass$^{0.75}$ ($E_{\text{Eemass 0.75}}$) (Nagy et al. 1999, Nagy 2005) and, therefore, both were also explored relative to VeDBA. Similarly, other studies have also compared an average VeDBA ($\text{VeDBA}_{\text{Average}}$) to Daily Energy Expenditure (DEE) (Elliott et al. 2013) so these were also explored. Multivariate models were used to include other variables as random effects, such as sex, mass, and age. Unless otherwise stated, data are presented as Means ± SE.

4.4 Results

Matched GPS, accelerometry, and energy expenditure data were obtained from 17 individuals (7 M, 10 F). Age (approximately 4 years, estimated from average tooth wear 4.35 ± 0.29), and body mass (3.20 ± 0.08 kg) did not differ significantly between the sexes. The duration of the DLW measurement period across all animals was 5.58 ± 0.13 days, with a total energy expenditure of 3651.44 ± 172.19 KJ and daily energy expenditure (DEE) of 651.37 ± 20.65 KJ/d. The total distance travelled by bobucks during the study was 4976.92 ± 404.28 m. The total VeDBA (recorded at 25 Hz) was 973594.96 ± 30282.44 g with an average of 0.081 ± 0.002 g (Table 4.1).
Table 4.1: Summary statistics for the 17 (7 M, 10 F) bobucks (*Trichosurus cunninghami*) examined in this study in south-eastern Australia.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Mean</th>
<th>Standard Error</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tooth Wear</td>
<td>4.35</td>
<td>0.29</td>
</tr>
<tr>
<td>Mass (kg)</td>
<td>3.2</td>
<td>0.08</td>
</tr>
<tr>
<td>Measurement Period (days)</td>
<td>5.58</td>
<td>0.13</td>
</tr>
<tr>
<td>Total Energy Expenditure (kJ)</td>
<td>3651.44</td>
<td>172.19</td>
</tr>
<tr>
<td>Daily Energy Expenditure (kJ/d)</td>
<td>651.37</td>
<td>20.65</td>
</tr>
<tr>
<td>Distance Travelled (m)</td>
<td>4976.92</td>
<td>404.28</td>
</tr>
<tr>
<td>Total VeDBA (g)</td>
<td>973594.96</td>
<td>30282.44</td>
</tr>
<tr>
<td>Average VeDBA (g)</td>
<td>0.081</td>
<td>0.002</td>
</tr>
</tbody>
</table>

The distance travelled by bobucks was a poor predictor for energy expenditure, whether comparing total distance travelled (Distance$_{Total}$) or daily distance travelled (Distance$_{Daily}$), explaining < 1% of the variation in both cases (Table 4.2 in Chapter 4 Appendix).

VeDBA$_{Total}$ was a moderate predictor of total energy expenditure (EE), explaining 41.8% of the variation in total energy expenditure. This was improved marginally to 46.6% with the inclusion of distance travelled. Neither energy expenditure standardised by mass (EE$_{mass}$), and mass$^{0.75}$ (EE$_{mass}^{0.75}$) proved to be a better predictor of total energy expenditure, with total acceleration (VeDBA$_{Total}$) only explaining 24.6% and 33.1% of the variation in the standardised energy expenditures respectively (Figure 4.2, Table 4.3 in Chapter 4 Appendix).
**Figure 4.2:** The relationship between total energy expenditure (kJ) and total VeDBA (g) for bobucks (*Trichosurus cunninghami*) in south-eastern Australia.

Lines and shaded area represent the fitted relationship and 95% confidence intervals from generalised linear mixed models, respectively. Solid line, yellow shading = overall energy expenditure (EE); dotted line, blue shading = mass standardised overall energy expenditure (EEmass); dashed broken line, green shading = mass$^{0.75}$ standardised total energy expenditure (EEmass$^{0.75}$).

Average acceleration (VeDBA$_{Average}$) was compared to daily energy expenditure (DEE), but was found to be a poor predictor, only explaining 11.8% of the variation in DEE. While DEE standardised by mass (EEmass), and mass$^{0.75}$ (EEmass$^{0.75}$) marginally improved the relationship with VeDBA$_{Average}$, explaining 28.5% and 27.5% respectively, neither proved to be a good predictor of daily energy expenditure (Figure 4.3, Table 4.4 in Chapter 4 Appendix).
Figure 4.3: The relationship between daily energy expenditure (kJ) and average VeDBA (g) for bobucks (*Trichosurus cunninghami*) in south-eastern Australia.

Lines and shaded area represent the fitted relationship and 95% confidence intervals from generalised linear mixed models, respectively. Solid line, yellow shading = daily energy expenditure (DEE); dotted line, blue shading = mass standardised daily energy expenditure (DEEmass); dashed broken line, green shading = mass$^{0.75}$ standardised daily energy expenditure (DEEmass$^{0.75}$).

As specific behavioural states could not be validated visually, the 10 identified behaviours categorised by unsupervised cluster analysis using k-means methods were analysed in a frequency distribution taking into account time of day, and the behavioural states both preceding and following each value (Figure 4.4). From this, four broad behavioural categories were identified.
1. Denning – Measurements taken during the day, and validated via GPS data (mean VeDBA = 0.028 ± < 0.001 m/s²)

2. Resting at Night - very low VeDBA values, but while the bobucks were out of the den (mean VeDBA = 0.108 ± < 0.001 m/s²)

3. Moving - moderate VeDBA values and during the night, including normal foraging behaviour (mean VeDBA = 0.180 ± < 0.001 m/s²)

4. High Activity - Activity values much higher than all the others, accounting for behavioural states such as mating, fighting, intense foraging, predator avoidance, etc. (mean VeDBA = 0.260 ± 0.002 m/s²)
Figure 4.4: A depiction of the summed VeDBA (25 Hz) per second, the behavioural states (1 = denning, 2 = resting at night, 3 = moving, and 4 = high activity), and the distance travelled (m) for a single bobuck (*Trichosurus cunninghami*) over 24 hours.

The two inserts are exploded views of the data over 10 minutes.
The average proportion of time animals time spent ‘denning’ was 52.7 ± 1.2%, ‘resting at night’ was 26.4 ± 0.8 %, ‘moving’ was 20.5 ± 0.9 %, and ‘high activity’ was 0.4 ± <0.1 %. Using the time spent in each behavioural state, multiplied by the rate of energy expenditure for that state explained 60.6 % (R² = 0.606) of the variation in total energy expenditure (EE) of the bobucks (Table 4.5).

**Table 4.5: Model selection results for the generalised mixed models comparing energy expenditure to behavioural states for bobucks (Trichosurus cunninghami) in south-eastern Australia.**

Overall energy expenditure (kJ) was compared to the time spent (seconds) in each of four behavioural states (Denning, Resting at Night, Moving and Foraging, and High Activity), with all models including morphological variables. AICc values, differences in AICc values (Δi) and Akaike weight (wi) are shown for models with Δi < 10.

<table>
<thead>
<tr>
<th>Denning</th>
<th>Resting at Night</th>
<th>Moving</th>
<th>High Activity</th>
<th>Distance Travelled</th>
<th>Sex</th>
<th>Tooth Wear</th>
<th>Mass</th>
<th>R²</th>
<th>df</th>
<th>AICc</th>
<th>Δi</th>
<th>wi</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.010309</td>
<td>0.006495</td>
<td>0.022378</td>
<td>0.134078</td>
<td></td>
<td></td>
<td></td>
<td>-0.463</td>
<td>0.708</td>
<td>6</td>
<td>124.746</td>
<td>269.89</td>
<td>0</td>
</tr>
<tr>
<td>0.008275</td>
<td>-0.00236</td>
<td>0.017135</td>
<td>0.096801</td>
<td></td>
<td></td>
<td></td>
<td>0.606</td>
<td>5</td>
<td>127.289</td>
<td>270.03</td>
<td>0.13</td>
<td></td>
</tr>
<tr>
<td>0.008264</td>
<td>-0.00116</td>
<td>0.016624</td>
<td>0.133869</td>
<td>-0.034</td>
<td></td>
<td></td>
<td>0.610</td>
<td>6</td>
<td>127.202</td>
<td>274.80</td>
<td>4.91</td>
<td></td>
</tr>
<tr>
<td>0.013765</td>
<td>0.001251</td>
<td>0.024565</td>
<td>0.092517</td>
<td></td>
<td>+</td>
<td></td>
<td>0.715</td>
<td>7</td>
<td>124.534</td>
<td>275.51</td>
<td>5.62</td>
<td></td>
</tr>
<tr>
<td>0.010298</td>
<td>0.001685</td>
<td>0.021867</td>
<td>0.171096</td>
<td>-0.033</td>
<td></td>
<td></td>
<td>-0.463</td>
<td>0.712</td>
<td>7</td>
<td>124.62</td>
<td>275.70</td>
<td>5.81</td>
</tr>
</tbody>
</table>

The best predictors of total bobuck energy expenditure were the behavioural states as well as mass, and explained 70.8 % (R² = 0.708) of the variation in total energy expenditure (EE) of the bobucks (Figure 4.5, Table 4.5). The rate of energy expenditure for each behaviour was; denning: 0.0103 ± 0.003 kJ/s, resting at night: 0.0005 ± 0.006 kJ/s, moving: 0.0224 ± 0.008 kJ/s, and high activity: 0.1341 ± 0.212
kJ/s. The two significant variables for predicting energy expenditure in bobucks were the behavioural states ‘denning’ and ‘moving’ (Table 4.6).

Figure 4.5: The relationship between total energy expenditure (kJ) as measured by DLW, and the best predictor of bobuck energy expenditure, including the four behavioural states and mass, explaining 70.8 % ($R^2 = 0.708$) of the variation in total energy expenditure (EE) of the bobucks (*Trichosurus cunninghami*) in south-eastern Australia.

Lines and shaded area represent the fitted relationship and 95% confidence intervals from generalised linear mixed models.
Table 4.6: Parameter estimates from the best Time-Activity model comparing the overall energy expenditure (kJ) of bobucks (*Trichosurus cunninghami*) to the time spent (seconds) in each of four behavioural states (Denning, Resting at Night, Moving and Foraging, and High Activity) and mass.

The model was forced through the intercept as no energy is spent if no time passes.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Coefficient</th>
<th>Standard Error</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Denning</td>
<td>0.0103 kJ/s</td>
<td>0.003</td>
<td>0.002</td>
</tr>
<tr>
<td>Resting at Night</td>
<td>0.0005 kJ/s</td>
<td>0.006</td>
<td>0.930</td>
</tr>
<tr>
<td>Moving</td>
<td>0.0224 kJ/s</td>
<td>0.008</td>
<td>0.019</td>
</tr>
<tr>
<td>High Activity</td>
<td>0.1341 kJ/s</td>
<td>0.212</td>
<td>0.539</td>
</tr>
<tr>
<td>Mass (g)</td>
<td>-0.4626</td>
<td>0.226</td>
<td>0.063</td>
</tr>
</tbody>
</table>

4.5 Discussion

The ability to quantify the behavioural and energetic information for free-living animals across a broad range of animal movement allows researchers to determine the physiological costs associated with particular behaviours of animals in the field (Wilson *et al.* 2006, Halsey & White 2010, Elliott *et al.* 2013). This knowledge is crucial in understanding an animal’s physiology and ecology and, in turn, species’ limitations (distribution and abundance) with respect to the influence of resource availability and distribution, and predicting the effects of environmental change (Halsey & White 2010). This study found that estimates of energy expenditure both from GPS data and raw accelerometer data were poor. However, accelerometer-derived behavioural states have the potential to accurately estimate energy expenditure in a free-living, scansorial mammal, across both active and resting behavioural states. The behavioural state estimates of free-living bobucks in this study had a predictive
accuracy similar to studies conducted on other species under laboratory conditions (Wilson et al. 2006, Halsey et al. 2009b).

4.5.1 DLW and energy expenditure

Bobucks were tracked for 5-7 days in order to provide adequate isotope elimination rates for the DLW (Speakman 1997). The average energy expenditure recorded for this time was comparatively low compared to other studies on similarly sized mammals (1810 kJ/d for a 3.20 kg mammal) (Nagy 2005). However, marsupials such as the bobuck are known to have a metabolic rate approximately 30% lower than that of eutherian mammals (Dawson & Hulbert 1970, Nagy et al. 1999), and arboreal frugivorous and folivorous species also tend to have lower basal metabolic rates than other mammals (McNab 1995). There was also high variability in the daily activity both between and within individuals, meaning that there was potentially high variation in the daily energy expenditure as well. Unfortunately, DLW provides only a single value for the study period, so this cannot be explored further.

Measures of energy expenditure for free-living bobucks have not been undertaken before, so direct comparisons with other studies and study areas are not possible. However, Nagy & Bradshaw (2000) found the general DEE of marsupials to be $10.1 \times M^{0.59}$ kJ/day, where $M$ is body mass in grams. Using this equation, the average daily energy expenditure of a 3.20 kg bobuck would be 1181 kJ/d, which is almost double the $651 \pm 22$ kJ/d recorded in our study. Other studies on free-living marsupials also found higher energy expenditures (e.g. spectacled hare wallaby (*Lagorchestes conspicillatus*), body mass 2529g, DEE 680 kJ/day (Nagy & Bradshaw 2000), and the female tammar wallaby (*Macropus eugenii*), body mass 3328 g, DEE 964 kJ/day
(Nagy et al. 1990). A laboratory-based study on the closely related common brushtail possum also found higher energy expenditure (T. vulpecula, body mass 2478 g, DEE 833 kJ/day (Williams & Turnbull 1983)).

4.5.2 Distance and energy expenditure

Distance travelled, derived from GPS data, was a poor predictor of energy expenditure in bobucks. This is most likely due to the manner in which a GPS records data. A GPS requires the change in spatial location to be greater than the error associated in the location recording. In this study, the average GPS error was 9.41 m, meaning activities which occur within a small spatial area, such as intense foraging or fighting, may not have been recorded. The relatively coarse recording rate (10 minutes) may also affect the distance recorded, as travel is calculated as a straight line between points, whereas animals may often travel a more circuitous route (Munn et al. 2013). Furthermore, when the bobuck was stationary, the error between location fixes can create false recordings of movement. In a study on cattle, this false movement was found to increase the daily distance an animal travelled by as much as 15 % (Ganskopp & Johnson 2007). On average, bobucks spent over half their time at night in low-movement behaviour, which could lead to a much greater measure of false movement.

A GPS records changes in spatial location, however, it only records changes in horizontal location, and not changes in vertical location. Measures of horizontal movement may be appropriate for non-climbing terrestrial species, but spool-and-line tracking of several scansorial species has shown they can move considerable distances vertically, climbing up and down trees (Cunha & Vieira 2002, Wells et al. 2006). The inability of the GPS to record these movements can lead to underestimating the
distance travelled by scansorial species. Conversely, accelerometers are able to capture this three-dimensional activity, record movement irrespective of a change in spatial location, and derive different energy expenditure for different activities. As such, estimates of energy expenditure derived from accelerometry provide a much more comprehensive picture of animal movement.

4.5.3 Accelerometry as a surrogate for recording movement

Accelerometry provides a method to record long-term movement data over days, or even months, for species which are otherwise difficult to observe directly, such as nocturnal and cryptic species, and/or species which live in challenging environments such as underwater, underground, or within tree canopies. The total acceleration ($VeDBA_{Total}$) only proved to be a moderate predictor of energy expenditure. However, accelerometry is capable of providing more than just a direct measure to compare to energy expenditure, it was also able expand on the knowledge of bobuck ecology. During this study, the accelerometry identified a clear circadian rhythm of nocturnal activity and diurnal inactivity. This is well documented for possum species, which are considered a strictly nocturnal species (Smith et al. 1984), and is also shown in the GPS data. However, unlike spatially recording devices such as GPS, the accelerometer is recording multiple times a second, and irrespective of external data connection. For example, while bobucks only spent about 50% of their time denning, the accelerometry data was able to identify cycles of resting during the night, bringing the total time spent in low activity states to approximately 80% of their day. Given the large amount of time spent in behavioural states with low accelerometry values, accurate field measurements of energy expenditure necessitate the prediction of all behaviours contributing to energy expenditure (Gleiss et al. 2011).
The high temporal resolution recording provides information which can, in turn, be used to provide information relating to behavioural states. By calculating energy budget ethograms to derive behavioural states we were able to create time-activity budgeting for each individual. This allowed for the calculation of different rates of energy expenditure for different activities. As shown in studies by Elliott et al. (2013) and Jeanniard-du-Dot et al. (2016), the rate of energy expenditure for behavioural states is different from the rate of acceleration. For instance, the behavioural state ‘moving’ had an average VeDBA almost 6.5 times higher than ‘denning’, but a rate of energy expenditure only approximately twice as high. The ability to assign different rates of energy expenditure to different behavioural states ultimately led to behavioural states explaining the most variation in DLW derived energy expenditure.

Accelerometry has the potential to identify a greater number of specific behavioural states. However, the ability to estimate energy expenditure from behavioural states relies on the precision of determining the different activities and behavioural states from the accelerometer data, and the consistency of energy expenditure for that behaviour (Corp et al. 1999). For example, the denning behaviour category consists of occasional short temporal-scale spikes of higher activity, as seen in Figure 4.2. These specific activities, which could not be identified in the present study, presumably include actions such as grooming, mating, and other social interactions. These other activities are believed to drive the higher rate of energy expenditure during denning compared to resting at night. The use of broad behavioural states means that the energy coefficient for some states will have a greater margin of error than others, and ultimately some identified behavioural states will estimate energy expenditure better than others. A validation study on the identification of fine-scale behavioural signals
in acceleration data could potentially provide a wider range of identified behavioural states, greater accuracy in prediction of energy expenditure, and a greater understanding of how individuals use the environment.

Accelerometry also has the potential to be paired with other movement recording technology to better identify and refine measures of both behavioural states and energy expenditure relative to spatial environmental data. GPS devices were used in combination with accelerometry in Chapter 3 to compare between spatial movement and activity. Similarly, GPS devices have been used in combination with accelerometry to identify behavioural states (Nams 2014). In respect to arboreal and aerial species, barometers could also be incorporated to measure both the elevation, and relative changes in altitude in animal movement, better identifying vertical movement (Hunter et al. 2007).

4.5.4 Other influences on energy expenditure

Mass is well established as being one of the dominant factors influencing the variation in basal metabolic rate (BMR) and field metabolic rate (FMR) between different species (Dawson & Hulbert 1970, Harris et al. 1985, Speakman 2000). Mass influences energy expenditure via thermal regulation, food requirement, and the cost of moving, as mechanical power output for an action is relative to the mass required to move (Nagy 2005, Speakman 2005). Directly scaling energy expenditure by mass did not improve the relationships with accelerometry or GPS data, but including mass as a variable did improve the relationship in analyses such as the behavioural states. This may be due to the study focussing on multiple individuals of the same species. While general equations for energy expenditure based on mass between different
species are common (Nagy & Bradshaw 2000), the influence of mass on energy expenditure between individuals of the same species is less well known.

Sex and age are also known to have the potential to influence metabolic rate (Nagy 1987, Gillooly et al. 2001, White & Seymour 2003). Sex can influence the rate of energy expenditure due to the fundamental physiological differences related to size, hormones, body composition, and breeding, which can cause variation in the rate of EE independent of movement (Beck et al. 2003, Cryan & Wolf 2003, Careau et al. 2013). Similarly, age can influence energetic requirements based on caloric intake and activity (Kirkwood & Holliday 1979, Ramsey et al. 2000). Therefore, sex and age (measured by tooth wear) were also included as potential influences to energy expenditure. However, neither influenced the relationship between distance travelled, VeDBA, or accelerometer derived behavioural states and energy expenditure. There was no significant difference between the mass of male and female bobucks, and the study was conducted during the non-breeding season, which may account for why sex did not influence the relationship. Similarly, juveniles were not included in the study, reducing the influence of age.

In summary, the results of the present study indicate that accelerometry can be used to accurately predict total energy expenditure in free-living, scansorial, medium-sized mammals, such as bobucks, and is most informative when the accelerometry data are also used to derive behavioural information. The incorporation of behavioural information allows for the allocation of different rates of energy expenditure relative to the activity level of the animal. This information will greatly improve energetics studies conducted under field conditions, which include both active and resting behavioural states. Unfortunately, the information collected via GPS was a poor
predictor of energy expenditure, meaning that retrospectively examining energy expenditure for GPS tracked animals is not possible. However, given the ability of accelerometry to predict energy expenditure in free-living animals, future research into how behaviour is shaped by habitat variation and environmental change could help advance ecological theory (e.g. species’ niches) and guide conservation actions (e.g. reserve design and habitat restoration).
Chapter 5: Contrasting congener behaviour in relation to environmental variation

5.1 Abstract

Habitat loss and modification are the greatest threats to biodiversity globally. To predict how species might respond to future environmental change, we must first understand how the environment limits species’ current distribution. Advances in GPS and accelerometer technology provide new methods to accurately collect species’ movement and behavioural data, providing insight into how habitat variation and modification affect animals. Using GPS and accelerometry data, we examined movement and other behaviours of two congeners, the common brushtail possum (*Trichosurus vulpecula*) and bobuck (*T. cunninghami*), in two spatially and structurally distinct sites, the Strathbogie Ranges (foothill forest > 500 m a.s.l.) and Grantville in Gippsland (heavily cleared coastal and lowland forest with an average elevation < 100 m a.s.l.) in Victoria, Australia. Bobucks in Grantville spent more time resting at night, and had reduced abundance, body mass, and a restricted distribution in Grantville. Despite this, individual bobucks at both locations had similar daily energy expenditure. These behavioural patterns and differences in morphology may relate to constraints in resource availability. Our low bobuck capture success in Grantville suggests there is limited suitable habitat in the region, reducing bobuck movement and activity, and constraining them to a limited set of resources. Grantville bobucks may be close to the limits of their niche space. Common brushtail possums had much greater body mass in the Grantville region compared with the Strathbogies, counter. Common brushtail possums in the Strathbogies may be experiencing
ecological character displacement; only persisting in more modified environments, denning for longer, spending less time in high activity behavioural states, and having lower body mass and daily energy expenditure compared to bobucks, in order to occupy similar habitat. These findings suggest that species’ responses to different environments can change greatly both intra- and inter-specifically. As such, effective conservation and management requires ecological understanding of species across their distributions in order to understand the possible range of responses to environmental change.

5.2 Introduction

A fundamental goal of ecology is to describe and understand which factors affect patterns of species distribution and abundance. Resource availability, which affects an individual’s growth, survival, and reproduction (Johnson 1980, Hoffmann et al. 2012, Fordyce et al. 2015), is important in this context. Under ideal conditions, individuals select habitats promoting their vital rates, freely and without cost (Fretwell & Lucas 1969), however there are typically constraints that limit an animal’s habitat use, such as dispersal ability, habitat connectivity, predation risk, and competition (Potter et al. 2012). The environment in which a species can survive given resource availability and other constraints is often referred to as its niche. Niche statistics are also used to predict a species’ future distribution in response to environmental change (Hirzel & Le Lay 2008), and hence, can be used to establish conservation priority areas and select reserve designs (Kearney & Porter 2009).

Habitat loss and modification are the largest threats to biodiversity globally, greatly impacting species’ niches (Fahrig 2001, Laurance et al. 2008, Selwood et al. 2009).
Anthropogenic modification such as urbanisation, roads, agriculture, and timber production, reduces the amount of unmodified habitat available to species (Tuomainen & Candolin 2011). While habitat loss is the immediate effect, the long-term effects can include disruptions to ecosystem, community, and population structure by creating a landscape mosaic of natural fragments surrounded by less hospitable, modified environments, which in turn leads to changes in species distribution and abundance (McCall et al. 2010, Pike et al. 2011, Lowry et al. 2013).

To understand how species might respond to habitat change and loss, we must first understand how the environment limits their current distribution. Anthropogenic environmental changes currently occurring in ecosystems are often detrimental for the survival of species (Lawton 1993, Pounds et al. 1999, Harvell et al. 2002). For instance, climate warming is drastically reducing sea ice in the arctic, which is the primary habitat for polar bears (*Ursus maritimus*), which in turn is causing their population decline and has resulted in them becoming vulnerable to extinction (Stirling & Derocher 2012, IUCN 2016). However, for other species, such as the black rat (*Rattus rattus*), environmental change and urbanisation has increased both available habitat, and rat population numbers, often at the expense of other species (Feng & Himsworth 2014). Species such as black rats are capable of adjusting to a range of environmental conditions and novel ecosystems (Morris 1996, Devictor et al. 2008), and can become invasive (Tuomainen & Candolin 2011). Studying fragmented ecosystems enables us to examine the consequences of habitat loss and modification, how this might impact habitat processes, and allow predictions regarding the likelihood of species persistence and survival in the face of future environmental change.
In the midst of extensive habitat loss and modification, it is essential to accurately classify species’ habitat requirements and what factors influence these (Barnosky et al. 2011, Ceballos et al. 2015). Presence-absence models have traditionally been used to identify habitat suitability (Dorazio 2012, Haby et al. 2012, Matthews & Whittaker 2015). While data on species presence can describe habitat associations, it does not provide any information on how the resources are exploited (Shipley et al. 2009, Eycott et al. 2012, Vasudev & Fletcher 2015). Given the relative plasticity some species exhibit in response to varying resource availability, models not taking resource exploitation into account, and its effects on animal movement and other behaviour, have limited scope for predicting a species reaction to a changing environment (Jeffree & Jeffree 1994, Tilman 1994, Ritchie et al. 2008, Loxdale et al. 2011). Therefore, we require new methods focussing on animal movement and behaviour to quantify how animals use their environment.

Animal movement governs the ability of species to persist in, and respond to, changing environments, as resource selection is strongly influenced by movement decisions (Frair et al. 2005, Fahrig 2007, Fordyce et al. 2015). Animals move to acquire resources (Bell 2012), avoid predators and competition (Creel & Christianson 2008, Ritchie & Johnson 2009), and to be near conspecifics for mating and other social interactions (Fahrig 2007). Furthermore, the initial response of animals to habitat disturbance is often behavioural (Tuomainen & Candolin 2011). These behavioural responses can result in changes to species interactions, population dynamics and evolutionary processes, which ultimately determine population persistence and speciation (Tuomainen & Candolin 2011). Therefore, the accurate measurement of
movement and behaviour could greatly further our understanding of how animals use the environment.

Recent advances in technology provide new methods to accurately collect movement and behavioural data, particularly the combination of GPS and accelerometry. GPS has been used to provide insights into animal space-use in modified landscapes (Fryxell et al. 2008, Gautestad et al. 2013, Vasudev & Fletcher 2015). However, these technologies measure only one coarse aspect of animal movement: the change in the location of the individual over time (Nathan et al. 2008). Conversely, accelerometers record movement as a change in acceleration at a very fine scale (0.001 g) and rate (>100 Hz) across all three dimensions of movement. Using accelerometry, several studies have shown that an animal’s free-ranging movement at a fine temporal scale is correlated to energy expenditure (Wilson et al. 2006, Elliott et al. 2013) Chapter 4). Therefore, by combining these two technologies we are able to measure the movement and behaviour of animals. Such methods lead to a more comprehensive understanding of ecological interactions, species’ niches, and allow us to predict not only which taxa might be vulnerable to habitat loss, but also some of the consequences for community composition and ecosystem function (Kremen et al. 1993, Rosenblatt et al. 1999, Hughes et al. 2000).

Arboreal and scansorial animals are especially vulnerable to habitat modification, as they require habitat connectivity among the canopy to traverse the environment, or else must come to ground and face potential increased predation risk (Louys et al. 2011, Mendonca et al. 2015, Vasudev & Fletcher 2015). Closely-related congeneric species provide good opportunities to compare and contrast how different behavioural responses might affect species and individuals in changing environments. Two
sympatric arboreal and scansorial species capable of living in heterogeneous landscapes are the common brushtail possum (*Trichosurus vulpecula*) and the mountain brushtail possum, or bobuck, (*T. cunninghami*). Both species are medium-sized (2 – 4 kg), nocturnal, semi-arboreal marsupials. While populations of the common brushtail possum have declined extensively in the wild, they have adapted well to urban landscapes, and are one of Australia’s most widely distributed marsupials. Bobucks, however, have a patchy distribution throughout wet sclerophyll forests and sub-tropical forests of eastern Australia, and are not found in urban environments. Unlike common brushtails, bobucks are considered more specialised and dependent on a few key resources (Martin & Martin 2007), particularly a food tree (silver wattle, *Acacia dealbata*). This may mean bobucks are more limited in their ability to respond to changes such as urbanisation, habitat loss and modification. Therefore, while these species are sometimes sympatric, and exploit some of the same resources, they are not always found together.

Our aim was to examine the movement and behavioural strategies employed by common brushtails and bobucks in two spatially and structurally distinct sites, the Strathbogie Ranges (foothill forest > 500 m a.s.l.) and Grantville in Gippsland (heavily cleared coastal and lowland forest with an average elevation < 100 m a.s.l.). Examining distance travelled and activity levels on a nightly basis, we expected little difference in bobucks across the two regions as we expected them to be less able to adapt behaviourally to change, and to therefore be more limited in their habitat choices in the Grantville region (Bonier *et al.* 2007, Jiguet *et al.* 2007). Conversely, we expected to observe greater variation in the behaviour and habitat use of common brushtail possums between the two regions, as they adapted their behaviour to exploit different
resources available between the two locations. Finally, we examined how the movement and behavioural strategies of each species affected energy expenditure. By examining these different aspects of behaviour, we aimed to better understand how these two species use different environments, and their ability to respond to and survive future environmental change.

5.3 Methods

5.3.1 Study area and design

The study areas were the Strathbogie Ranges in north-eastern Victoria, and Grantville in southern Victoria (Figure 5.1). The straight-line distance between the two study areas is approximately 165 km. The vegetation in the Strathbogie Ranges mainly consists of herb-rich foothill forest and grassy dry forest dominated by manna gum (Eucalyptus viminalis), Victorian blue gum (Eucalyptus globulus bicostata), narrow-leaf peppermint (Eucalyptus radiata) and broad-leafed peppermint (Eucalyptus dives). Key middle and understorey species include silver wattle (Acacia dealbata), dogwood (Cassinia aculeata), cherry ballart (Exocarpos cupressiformis), blackwood (Acacia melanoxylon) and austral bracken (Pteridium esculentum) (Martin & Handasyde 2007). The Grantville vegetation is more variable with a mix of lowland forest, heathy woodland, swampy woodland, riparian scrub, and even mangrove shrubland. The vegetation is predominantly eucalypts such as messmate (Eucalyptus obliqua) and narrow-leaf peppermint. Key understorey species include blackwood, prickly tea-tree (Leptospermum continentale), she-oak (Casuarina spp.), sweet pittosporum (Pittosporum undulatum), mangroves (Avicennia marina), and various sedges, bracken, and grasses (Hynes & Cleeland 2005).
Figure 5.1: The study areas: the Strathbogie Ranges (foothill forest > 500 m a.s.l.) in north-eastern Victoria, and Grantville (heavily cleared coastal and lowland forest with an average elevation < 100 m a.s.l.) in southern Victoria, Australia.

The habitat configuration in Grantville greatly differs from the Strathbogie ranges. First and foremost is the history of anthropogenic influence. Grantville has been more extensively cleared since European Settlement, leaving little remnant old-growth vegetation > 100 years old. Furthermore, extensive fires in 1898 reduced much of the old-growth forest, the result of which is stands of trees which are a uniform age of approximately 120 years, not considered old enough to have hollows for large arboreal species (> 150 years) (Lindenmayer et al. 1991). The region is also coastal, with a
dense understory of prickly tea-tree, a species not used by bobucks (Gloury & Handasyde 2016), and stunted tree growth due to strong coastal winds.

We undertook trapping sessions over eight consecutive seasons from spring 2011 to winter 2013 inclusive. Within each study site, we trapped for male bobucks and common brushtail possums. We targeted male possums because they do not have factors that complicate the measurement of mass and movement (i.e. pouch young, back young, and milk production during different times of the year). We trapped possums in linear strip environments (> 1 km length and an average vegetation width of ~ 40 m, termed 'linear strips' throughout). Our sites were confined to areas of habitat consisting primarily of native vegetation and containing trees large enough to provide suitable hollows (DBH > 50 cm) (Smith & Lindenmayer 1988, Pausas et al. 1995). Each site was separated by at least 500 m to reduce the chances of the same individual being caught at two locations, based on home range data from Martin & Handasyde (2007). After four consecutive trapping sessions in Grantville we had few possum captures. Based on local knowledge we moved three trap lines which had zero captures from their placement on linear strips to target gully lines in the forest fragments.

Each site had two rows of eight traps (50m apart), with each row a minimum of 200 m apart. Trapping sessions comprised three trap nights in each of the trap locations. We captured individuals in large (30 x 30 x 90 cm) wire cage traps placed on the ground and baited with peanut butter and apple. We set the traps before dusk and checked them before sunrise. Traps were partially covered with plastic to protect animals from weather.

5.3.2 Data collection
For processing, we sedated individuals with an intramuscular injection of tiletamine/zolazepam (6 mg kg⁻¹; Zoletil®; Virbac Australia, Peakhurst, NSW, Australia) to facilitate handling and minimise distress for the animals. We weighed individuals (± 0.05 kg) in hessian bags using a suspension scale (Pesola Macro-Line 80005). We injected individuals with Passive Integrated Transponder (PIT) tags (Trovan, Ltd.) for subsequent identification. We then fitted individuals with self-made data-logging collars (80 g) comprised of a VHF transmitter, GPS data logger and 3-axis accelerometer modified from the design in Allan et al. (2013). We set the collars to start recording data as soon as they were attached to the animal with GPS data set to record at 10-minute intervals, and accelerometers at 25 Hz. We only used adult males for this study (classed as tooth-wear ≥ 3 (Winter 1980)). In order to allow individuals to recover completely from handling and sedation, and to avoid releasing possums (which are strictly nocturnal) in daylight, we held the animals after processing until dusk on that day. We released the possums within 10 m of the site where they were captured. We recaptured individuals 3-7 days later and removed the data-logging collars.

5.3.3 Data processing

We expected the two possum species to use resources and the environment differently based on both species and study site location. Therefore, we split the data into species (bobucks (*T. cunninghami*) and common brushtails (*T. vulpecula*)) and location (Strathbogies and Grantville) for analysis, creating four groups (bobucks Strathbogies, bobucks Grantville, common brushtails Strathbogies, and common brushtails Grantville) in order to reduce confounding variation in the results.
GPS data – We converted the raw GPS data into two variables; the total distance travelled each night, termed ‘nightly distance travelled’ measured in metres, and distance travelled in 10 minute intervals, termed ‘interval distance travelled’ also measured in metres, following the methods described in Chapters 3 and 4. The nights of release and capture were removed from both, as we cannot be sure a complete night of data was collected. We examined the nightly distance travelled because both species den in tree hollows during daylight hours. It also created a clear break as to when one GPS track finished, and the next began. For interval distance travelled, we determined locations at 10-minute intervals along the interpolated movement tracks, and measured the distance between these locations.

Accelerometer data – We converted the raw accelerometer data into 1-second intervals of partial VeDBA following the methods described in Chapters 3 and 4. We then used partial VeDBA to create 3 different variables: 1) ’24-hour activity’ which is the sum of the partial VeDBA values measured at 25 Hz over 24 hours, commensurate to ‘nightly distance travelled’; 2) ‘interval activity’ which is the sum of the partial VeDBA values measured at 25 Hz in 10 minute intervals matching ‘interval distance travelled’; and 3) ‘behavioural state’ which is the amount of time animals spent in each of four behavioural states, measured in 1-second intervals, over the same 24-hour period as ‘nightly distance travelled’ ‘24 hour activity’, again following the methods described in Chapters 3 and 4.

We derived the energy expenditure of each individual using the most accurate method found in Chapter 4, which included the accelerometer-derived behavioural states and mass, using the equation:
This equation explained 70.8 % (R^2 = 0.708) of the variation in total energy expenditure (EE) of the bobucks in the Strathbogies (See Chapter 4). The energy demands of individuals may vary moving through different forest structures. However, the classification of movement into four broad behavioural states instead of energy allocation for specific movements should help account for the variation of forest structure. We calculated the total energy expenditure (kJ) for each individual, and then converted to daily energy expenditure (DEE kJ/day) for comparison, as the number of days each individual was active varied. A list of the measures of animal movement is provided in Table 5.1.

Table 5.1: Outline of the measures of animal (bobuck, *Trichosurus cunninghami*, and common brushtail possum, *T. vulpecula*) movement.

<table>
<thead>
<tr>
<th>Device</th>
<th>Measurement</th>
<th>Unit of Measurement</th>
<th>Timeframe of measurement</th>
<th>Method of measurement</th>
</tr>
</thead>
<tbody>
<tr>
<td>GPS</td>
<td>Nightly Distance Traveled</td>
<td>Metres (m)</td>
<td>24 hours</td>
<td>Summed distance based on interpolated movement track from GPS points over 24 hours</td>
</tr>
<tr>
<td></td>
<td>Interval Distance Traveled</td>
<td>Metres (m)</td>
<td>10 minutes intervals</td>
<td>Nightly interpolated movement track broken into 10 minute intervals</td>
</tr>
<tr>
<td>Accelerometer</td>
<td>24 Hour Activity</td>
<td>Gravitational Force (g)</td>
<td>24 hours</td>
<td>Summed activity based on accelerometer values measured at 25 Hz over 24 hours</td>
</tr>
<tr>
<td></td>
<td>Interval Activity</td>
<td>Gravitational Force (g)</td>
<td>10 minutes intervals</td>
<td>Summed VeDBA values, measured at 25 Hz, into 10 minute intervals</td>
</tr>
<tr>
<td></td>
<td>Behavioural State</td>
<td>Categorical</td>
<td>1 second intervals over 24 hours</td>
<td>VeDBA values, measured at 25 Hz, used in Ethographer to create four behavioural states measured in 1-second intervals</td>
</tr>
<tr>
<td></td>
<td>Daily Energy Expenditure</td>
<td>Kilojoules (kJ)</td>
<td>24 hours</td>
<td>Daily energy expenditure (kJ/d) calculated from the behavioural state information, using the equation from Chapter 4</td>
</tr>
</tbody>
</table>

*Predictor variables* - All response variables were related to two predictor variables and their interaction. First, to examine the impact of species on movement and energy expenditure, we included a two-level categorical variable indicating the species...
examined: either bobuck (*T. cunninghami*) or common brushtail (*T. vulpecula*). A second two-level categorical variable was included indicating the individual possums’ locations, either Strathbogies or Grantville.

5.3.4 Statistical analysis

We used Generalized Linear Mixed Models (GLMMs) to analyse the effects of the predictor variables on measures of animal movement derived from GPS and accelerometer data, following the analysis conducted in Chapter 3. We examined the movement variables measured over 24 hours (nightly distance travelled, nightly activity and the time spent in each of the four behavioural states), and activity in relation to distance travelled and two predictor variables (individuals, species and site). GLMMs were generated using the *nlme* package in *R* (R Core Development Team 2014). We derived total energy expenditure for each individual by following the equation from Chapter 4, and divided it by the time each individual was collared to calculate DEE. While this model was developed for bobucks, common brushtail possums are ecologically, morphologically and physiologically similar, and evolutionarily closely-related (Smith *et al.* 1984, Kerle & Saunders 2001). We generated GLMMs of the relationship between the DEE and the predictor variables and determined the r-squared value for the resulting model using the *r.squaredGLMM* function in the *MuMIn* package. Second, we ran models with each discrete group as a predictor variable in order to determine the mean DEE and the significant differences between the three groups.

We applied a Bonferroni correction to the *p*-values to infer significant differences between groups after accounting for multiple comparisons. To evaluate the
‘significance’ of differences we observed, we report effect sizes, confidence intervals, and $p$-values, with alpha set at $p < 0.1$ for all multiple comparisons except the interval comparison. We chose $p < 0.1$ for alpha because we didn’t have many observations (nights) for some levels of tests, and hence a more conservative $p$-value (0.05) might have made it harder to detect ‘significant differences’, as per results and guidance from (Nakagawa & Cuthill 2007) and (Jennions & Møller 2003). The interval comparison had a larger number of samples at a finer temporal resolution, so we set alpha to 0.05 for this comparison.

5.4 Results

We trapped bobucks and common brushtail possums in both the Strathbogie Ranges and Grantville. Male bobucks were found in both forest fragments and linear strips in the Strathbogie Ranges, but were only in found in linear-strip environments in Grantville, with all but two individuals trapped in gullies. We collared a total of 8 male bobucks in the Strathbogie Ranges (SB) (average mass: 3.29 kg, range: 2.50 – 3.55 kg), and 5 male bobucks in Grantville (GB) (average mass: 2.86 kg, range: 2.65 – 3.10 kg). In the Strathbogie Ranges, we only trapped common brushtail possums in linear strip environments, while common brushtail possums in Grantville were trapped in forest fragments, gullies, and linear roadside strips. We collared a total of 6 male common brushtail possums in the Strathbogie Ranges (SC) (average mass: 2.72 kg, range: 2.60 – 2.85 kg). While we did trap 6 male common brushtail possums in Grantville (average mass: 3.58 kg, range: 3.45 – 3.65 kg), only 3 were successfully collared, therefore their movement data was not formally analysed. In total, nineteen individuals were successfully collared and analysed across the eight consecutive seasons, totalling 99 nights of behavioural data. Due to collar malfunctions, not all the
individuals could be used to address each of the aims. The average time between GPS fixes for individuals across the study was 14 minutes 17 seconds (range 4 minutes 09 seconds to 119 minutes 31 seconds). Data points with an error > 40 m were removed (11.11% of data) resulting in an average Estimated Horizontal Position Error (EHPE) of 10.71 m (range 2.88 to 39.68 m).

5.4.1 Nightly Distance Travelled

Eighteen individuals (GB = 5, SB = 7, SC = 6) were used to compare the nightly distance travelled by each species. The nightly distance travelled by bobucks in the Strathbogie Ranges was 45% further than common brushtail possums in the Strathbogie Ranges. There was no significant difference in distance travelled between bobucks in Grantville and bobucks in the Strathbogie Ranges, and bobucks in Grantville and common brushtail possums in the Strathbogie Ranges (Figure 5.2 and Table 5.2 in Chapter 5 appendix).
Figure 5.2: The average distance travelled (m) over 24 hours by bobucks (*Trichosurus cunninghami*) and common brushtail possums (*T. vulpecula*) in their respective locations: the Strathbogie Ranges (foothill forest) and Grantville (heavily cleared coastal and lowland forest).

The coloured points indicate the raw data. The error bars indicate Standard Error. Categories sharing a letter did not show significantly different relationships between the coefficients.
5.4.2 24-hour Activity

Sixteen individuals (GB = 4, SB = 7, SC = 5) were used to compare the activity of individuals over a 24-hour period. The 24-hour activity of common brushtail possums was approximately 25% less than bobucks in Grantville and bobucks in the Strathbogie Ranges. There was no significant difference between the 24-hour activity of bobucks in the Strathbogie Ranges and bobucks in Grantville (Figure 5.3 and Table 5.3 in Chapter 5 appendix).
Figure 5.3: The average VeDBA (g) measured over 24 hours for bobucks (*Trichosurus cunninghami*) and common brushtail possums (*T. vulpecula*) in their respective locations: the Strathbogie Ranges (foothill forest) and Grantville (heavily cleared coastal and lowland forest).

The coloured points indicate the raw data. The error bars indicate Standard Error. Categories sharing a letter did not show significantly different relationships between the coefficients.
5.4.3 Behavioural State Analysis

Sixteen individuals (GB = 4, SB = 7, SC = 5) were included in behavioural state analysis. Four separate models were run to examine the time spent in different behavioural states over a 24-hour period, corresponding to each of the four behavioural states; Denning, Resting at Night, Moving & Foraging, and High Activity. Common brushtail possums in the Strathbogie Ranges spent over 13% more time, or 1 hour and 45 minutes, denning than bobucks, while bobucks in Grantville spent 11% more time, or approximately 35 minutes, ‘Resting at Night’ compared to both species in the Strathbogie Ranges. Common brushtail possums in the Strathbogie Ranges spent 30% less time, or 1 hour and 10 minutes, ‘Moving and Foraging’ than bobucks in the Strathbogie Ranges, but no significant difference compared to bobucks in Grantville. There was no difference between sites for bobucks ‘Moving and Foraging’ and in ‘High Activity’. Common brushtail possums in the Strathbogie Ranges spent 300% less time, or 16 minutes, in ‘High Activity’ than bobucks in both locations (Figure 5.4 and Table 5.4 in Chapter 5 appendix).
Figure 5.4: The average time spent by bobucks (*Trichosurus cunninghami*) and common brushtail possums (*T. vulpecula*) in each behavioural state over a 24-hour period (midnight to midnight GMT) in their respective locations: the Strathbogie Ranges (foothill forest) and Grantville (heavily cleared coastal and lowland forest).

The coloured points indicate the raw data. The error bars indicate Standard Error. Categories sharing a letter did not show significantly different relationships between the coefficients.
5.4.4 Interval Comparison

Fourteen individuals (GB = 4, SB = 5, SC = 5) were included in interval comparison. Model predictions were created by plotting the model fit for the three discrete predictor variables; bobucks in Grantville, bobucks in the Strathbogie Ranges, and common brushtail possums in the Strathbogie Ranges (Figure 5.5 and Table 5.5 in Chapter 5 appendix). These results showed: (1) that common brushtail possums in the Strathbogie Ranges have a much lower level of activity compared with their distance travelled; (2) that bobucks in Grantville have high activity levels for short distances travelled; and (3) that bobucks in the Strathbogies had high activity levels when travelling greater than 200 m in 10 minutes.
Figure 5.5: The relationship between activity and the distance travelled per ten-minute interval for bobucks (*Trichosurus cunninghami*) and common brushtail possums (*T. vulpecula*) in their respective locations: the Strathbogie Ranges (foothill forest) and Grantville (heavily cleared coastal and lowland forest).

Lines and shaded area represent the fitted relationship and 95% confidence intervals from generalised linear mixed models. Dashed broken line, pink shading = bobucks in Grantville; dotted line, green shading = Bobucks in the Strathbogie Ranges; solid line, blue shading = common brushtail possums in the Strathbogie Ranges. Categories sharing a letter did not show significantly different relationships between the coefficients.
5.4.5 Energy Expenditure

Sixteen individuals (GB = 4, SB = 7, SC = 5) were included in Daily Energy Expenditure analysis. The DEE of common brushtail possums in the Strathbogie Ranges was 10% (74.9 kJ) less than DEE of bobucks in Grantville and approximately 15% less (119.66 kJ) than bobucks in the Strathbogie Ranges. There was no significant difference in DEE between bobucks in Grantville and the Strathbogie Ranges (Figure 5.6 and Table 5.6 in Chapter 5 appendix).
Figure 5.6: The average Daily Energy Expenditure (DEE) by bobucks (Trichosurus cunninghami) and common brushtail possums (T. vulpecula) in their respective locations: the Strathbogie Ranges (foothill forest) and Grantville (heavily cleared coastal and lowland forest).

The coloured points indicate the raw data. The error bars indicate Standard Error. Categories sharing a letter did not show significantly different relationships between the coefficients.
5.5 Discussion

Animals can alter their behaviour in response to changing environmental conditions (Gilliam & Fraser 1987, Fortin et al. 2005, Schuttler et al. 2015), and by so doing, adapt to shifting resource availability and habitat modification (Badyaev 2005, Tornroos et al. 2015). However, for most species we have insufficient information about the impacts such changes have, including behavioural and physiological consequences, and ultimately, species persistence. Here, we have described and quantified the ways arboreal mammals respond to variation in resource composition and distribution. Bobucks showed changes in their movement patterns between the Strathbogies and Grantville, resting more and moving less distance in Grantville, but this did not significantly alter their energy expenditure, despite the difference in habitat composition and body mass of the individuals. Common brushtail possums employed a different behavioural strategy from bobucks within the same environment, moving less and resting more, ultimately resulting in lower energy expenditure.

5.5.1 Comparison of bobuck behaviour between habitat types

Bobucks exhibited different behavioural patterns across two spatially and structurally distinct habitat types: foothill forest > 500 m a.s.l. (Strathbogies) and heavily cleared coastal and lowland forest with an average elevation < 100 m a.s.l. (Grantville). When habitat structure is considered (Martin & Martin 2007, Martin & Handasyde 2007, Banks et al. 2008), it was not surprising bobucks in Grantville were found almost exclusively in riparian zone gullies, where large, hollow-bearing trees remain, and the cooler microclimate associated with permanent water provides more reliable access to food resources (e.g. fungi and silver wattle) year round. The restricted distribution of
this habitat raises questions regarding bobuck population genetics and their ongoing survival in the region. Continued land clearing may reduce connectedness between these already naturally patchily-distributed habitats, with the potential to isolate bobuck populations and reduce genetic flow, ultimately leading to population collapse, as seen for other species in similar situations (Bender et al. 1998). Genetic analysis of the remaining bobuck populations would assist in understanding their likelihood of survival, and what conservation actions might be required (e.g. habitat corridors and stepping stones (Soanes et al. 2013)).

Bobucks in the Strathbogies exist in the core of their range (Martin 2006, Martin & Handasyde 2007), and were found in both habitat types surveyed (habitat fragments and linear strip environments). The behaviour of bobucks in the forest fragments is believed to be more representative of behaviour in undisturbed habitat, with lower abundance, pair bonding, and lower activity patterns ((Martin & Handasyde 2007), see Chapter 3). Common brushtails were not found in forest fragments, so this study focussed on bobucks in the more modified linear strip environments to allow for comparison. Linear strips have been shown to alter bobuck behaviour; support higher abundance and a polygynous mating system (Martin et al. 2007), and males have increased movement and activity, ultimately resulting in an environment more energetically costly to the individuals (see Chapter 3). A comparison of the movements of bobucks in forest fragments with common brushtails in linear strips may identify greater similarity between the two species, and more difference between bobucks in the Strathbogies and bobucks in Grantville.

Bobucks in Grantville spent more time resting at night and travelled significantly shorter distances on a nightly basis, than bobucks in the Strathbogies. Bobucks in
Grantville also had a much lower body mass than bobucks in the Strathbogies, and were in fact more similar in mass to the common brushtail possums in Strathbogies. These behavioural patterns and differences in morphology may relate to the ways in which animals obtain the resources required for their survival, encompassing both habitat resources and energetic requirements (Shamoun-Baranes et al. 2012, Nams 2014). Bobucks in the Strathbogies must cope with much colder temperatures in winter, so a larger body size and higher energy expenditure may be required for homeostasis and thermoregulation (Speakman 2005). However, while mass and behavioural patterns varied, bobucks in Grantville had similar daily energy expenditure to bobucks in the Strathbogies. This suggests the overall energy requirements of individual bobucks did not differ between these regions even though bobucks in Grantville were almost 15% lighter, or, conversely, that their energy expenditure relative to mass is higher in Grantville than the Strathbogies. Smaller animals are known to work harder than larger animals to meet their energetic requirements (Taylor et al. 1982), however, bobucks in Grantville would still be expected to have a lower daily energy expenditure. High stress environments can cause higher energy expenditure through behaviours such as increased vigilance or reduced sleep (Careau et al. 2008, Tuomainen & Candolin 2011), which is worth further examination in the more modified Grantville site.

Previous studies have described how species’ home ranges and resource requirements shift between habitat types and locations (Angert et al. 2011, Clapp & Beck 2015, Merkle et al. 2015). Measuring movement at a fine spatial (< 10 m) and temporal (< 1 s) scale allows for the quantification of changes in behaviour and energy use based on habitat use, informing us about species-specific costs associated with habitat
change. Our limited capture success of bobucks across the Grantville region suggests there is limited suitable habitat for bobucks in the Grantville region, reducing their movement and activity, and constraining them to a limited set of resources. This may mean that bobucks living in Grantville are close to the limits of their niche space. Understanding the limits of a species niche provides information regarding their ability to respond to change, and persist in the face of future habitat modification. Bobucks in Grantville would not be expected to persist if the vegetation in gullies was cleared.

5.5.2 Comparison of common brushtail possums across sites

The average mass of common brushtail possums in the Strathbogie s was only approximately 75% of those in Grantville. Common brushtail possums have an extensive distribution, and their mass is known to vary greatly within it (1200 g to 4500 g (Kerle & Saunders 2001)). According to Bergmann’s Rule, temperature is often thought to be a main driver of morphological plasticity in species’ mass, with larger individuals in cooler climates (Ashton et al. 2000, Briscoe et al. 2015). This phenomenon has been observed for common brushtail possums across large latitudinal clines (Yom-Tov et al. 1986). However, the Strathbogie Ranges is on average cooler (average maximum temperature of 18.6°C, and an average minimum of 6.2°C) than Grantville (average maximum temperature of 18.7°C and an average minimum of 11.7°C) (Bureau of Meteorology 2016), therefore, this contradicts the prediction of Bergmann’s Rule. The number of individual common brushtail possums caught at each site was similar in this study, but Grantville had far fewer bobucks. Common brushtail possums may be out-competed by bobucks for resources in the Strathbogies, leading to smaller body size (McNab 2010), but this may not be the case in Grantville where bobuck abundance is lower and more spatially restricted. A comparison of the
morphology and behaviour of common brushtail possums throughout their distribution, relative to the abundance of other species, could examine competition and its potential effect on body size in relation to environmental and climatic gradients.

5.5.3 Comparison of congener behaviour

Common brushtail possums in the Strathbogies were found in the same habitat as bobucks, but displayed different behavioural patterns. Common brushtail possums were physically smaller, only travelled approximately 70% of the distance of bobucks each night, denned longer, spent less time foraging, and ultimately had less daily energy expenditure than bobucks. Common brushtail possums were also only found in linear strip environments within the Strathbogies, while bobucks are known to exist in both remnant vegetation and linear strip environments (Chapter 3). Linear strip environments are modified and disturbed, altering the availability and distribution of resources (Andren 1994, Ewers & Didham 2006). In the case of the Strathbogie Ranges, linear strip environments actually have a higher abundance of suitable tree hollows (large, old remnant trees), and a greater density of food trees (e.g. silver wattle), than forest fragments (Martin et al. 2007). Therefore, the small size of common brushtails in Grantville may also be a reaction to the resources available (Berumen et al. 2005, Pinaud et al. 2005), and only linear strip environments have enough resources to support both common brushtail and bobuck possums.

The difference in movement, other behaviours, and energy expenditure between common brushtail possums and bobucks may also potentially be an adaptation by common brushtail possums to use a different environmental niche than the more abundant bobucks, also known as ecological character displacement (Schoener 1965).
Closely-related sympatric species often must develop different behavioural strategies or change body size to minimise competition and co-exist in a habitat of limited resources (Dayan & Simberloff 2005, Tobias et al. 2014). For example, competition within a population of three-spine sticklebacks (*Gasterosteus aculeatus*) has been shown to cause niche variation in diet (Svanback & Bolnick 2007), while different mustelids in Great Britain have shown changes in skull size and tooth diameter in order to specialise on different prey species (Dayan & Simberloff 1994). Both bobucks and common brushtail possums use tree hollows as nest sites, so being physically smaller may allow common brushtail possums to use smaller hollows not available to bobucks (Saunders et al. 1982, Lindenmayer et al. 1991). This could be examined by installing nest boxes with different entrance sizes and assessing their relative use by bobucks and common brushtail possums in different habitats.

**5.6 Conclusion**

Environmental change, including habitat loss, modification, and climate change, are affecting the behaviour, distribution and survival of species. To understand how such processes will affect species both now and in the future, we need individual- and population-level behavioural data within species’ core distributions and range limits. This would allow an assessment of species’ responses and adaptability to change, as well as determine which species are most at risk. Using a combination of accelerometry and GPS, we can gauge the movement and energy requirements of animals, compare their movements across different regions, and assess their ability to adapt to change. This information could aid in the design and selection of reserves to protect at-risk species, and identify key restoration projects.
The ability to remotely measure movement data at a temporal scale capable of capturing animal behaviour is still relatively new (Wilson et al. 2006, Green et al. 2009, Halsey & White 2010), and its uses have not been fully explored. Accelerometry is providing the ability to record animal movement at a fraction of a second, in three-dimensions, and irrespective of external influence. When coupled with GPS, we can place the fine-scale movement of individuals within environmental contexts to better understand the behaviour of animals in respect to habitat variation and modification. This technology has the potential to identify the vertical use of environments, which is lacking from most terrestrial analyses and hence our ecological understanding (but see (Tracey et al. 2014)). For arboreal and scansorial animals, the vertical structure and composition of the environment is just as important as resources in the horizontal plane. Habitat modification can cause changes in the vertical structure of the habitat (e.g. forestry can remove shelter such as hollows and decrease the availability of food items (Root et al. 2003, Attum et al. 2006, Nepstad et al. 2008)). Furthermore, many species rarely or reluctantly come to ground, and will only cover short distances when they do so. By examining three-dimensional habitat use, we can improve our understanding of how arboreal and scansorial animals use the environment, leading to better-informed conservation of suitable habitat and management of reserves, and greater chances of protecting the habitat elements important to these species in the face of environmental change.
Chapter 6: Synthesis

Anthropogenic habitat modification and climate change are major threats to environments and biodiversity globally, contributing to population decline and species extinctions (Thomas et al. 2004, Cahill et al. 2013). In order to tackle this conservation challenge, and protect at-risk species into the future, we need reliable methods for describing and quantifying resource use by animals. Animal behaviour governs how species use and react to their environment, and therefore offers great potential for understanding how species respond to environmental change. Examining animal behaviour will allow predictions regarding how species might survive in the face of novel and rapidly changing environments, and what management actions (e.g. habitat protection or restoration) might assist them.

Emerging technology provides a means of recording and quantifying animal movement, and thus a method of describing and understanding how animals use environments. The movement recording technology I used was GPS and accelerometer data loggers. GPS data loggers have been used to measure the position and movement of numerous species (Obbard et al. 1998, Gautestad et al. 2013, Matthews et al. 2013), while accelerometers are showing potential in measuring the behaviour and activity of animals (Elliott et al. 2013, Wright et al. 2014, Jeanniard-du-Dot et al. 2016). Both types of technology have different advantages and shortfalls (Chapter 3). GPS data provides spatial information, but recording intervals and errors in fixes mean it cannot reliably record fine-scale (< 3 m change in position) movement. Conversely, accelerometers record fine-scale movement, but without location information. By
using these technologies in combination, we can gather more comprehensive datasets regarding animal movement and behaviour (Chapter 5).

While technology provides a means of recording animal movement, new methods of data analysis are also required in order to understand and interpret the raw data. My thesis investigated how emerging technology can be used in ecology, including the means and methods of integrating different technologies to compare and quantify how animals (common brushtail possums and bobucks) use and respond to changing habitats across two geographically separate environments. In this chapter, I outline the key ecological insights from my thesis, provide recommendations for further research, and summarise applications of animal movement recording technology for examining the effects of environmental change on species and their management.

6.1 Key insights

6.1.1 Technological development

The GPS and accelerometer devices used in my thesis were consumer-grade devices which already existed in their most basic form; separate data logging devices. However, these devices weren’t previously integrated, and were not designed for field-based ecology. I was able to find versions of both devices small enough to fit to animals weighing less than 2 kg, logged raw time-stamped data for over seven days, and could be integrated to run simultaneously from a single battery. These devices were designed to be re-charged and re-deployed as often as required, and all collars were used numerous times throughout my study. Finally, by assembling the technology myself, I had much greater flexibility in design features, and could better fit the devices to my study species (possums).
I found that GPS data loggers were able to provide broad scale spatial information within the environment, while accelerometer data loggers recorded fine scale activity and behavioural states. By combining the data, I was able to examine and quantify animal behaviour at a finer spatial- and temporal-scale than achieved for most free-ranging animals, and attain a greater understanding of how individuals interact with their environment. I also identified a strong relationship between behavioural information, and energy expenditure as measured by doubly labelled water. Behavioural states were calculated every second, and allowed for different rates of energy expenditure to be estimated for different movement types, unlike Doubly Labelled Water, which only provides a single value for the study period (Qasem et al. 2012). Using accelerometry to estimate energy expenditure has great potential for understanding the energetic cost different environments impose on animals through effects on their behaviour, and how this varies between individuals and between genders.

6.1.2 Effects of habitat modification on animal movement

Habitat modification in the Strathbogie Ranges appeared to influence the movement of possum congeners, and the two species responded differently. Common brushtail possums were exclusively found in the more modified linear strip environment. Linear strips represented corridors linking the remnant vegetation, and would therefore be expected to have high throughput of other arboreal species moving between patches, leading to potentially higher rates of competition and confrontation (Beier & Noss 1998). The linear strip environment is also more exposed to predators and weather, ultimately leading to habitat which is believed to be less favourable for many native species (Forman & Alexander 1998, McKinney 2002). The occupation of linear strips
by common brushtails may indicate their ability to adapt to changing environments, similar to their success in living in urban environments (Statham & Statham 1997). Notably, where sympatric, common brushtails were significantly lighter than bobucks (Chapter 5), so the move to modified environments may also potentially be competition related, pushing common brushtails into less desirable environments. A study whereby bobucks could be excluded from certain areas which common brushtails could potentially occupy could test this hypothesis. This could assess whether common brushtails occupy forest fragments in the absence of competition with bobucks, and whether brushtail body size differs in these different situations.

Bobucks were found in both the forest fragments and linear roadside vegetation, but their movement patterns differed between habitat types. In the linear strip environments, both males and females had increased activity levels for the distances they travelled, and males were also travelling further distances each night, with many more bursts of high activity (Chapter 3). This is despite the home ranges of bobucks in linear strip environments being smaller, as more silver wattle and tree hollows, the key resources for bobucks (Martin & Martin 2007, Martin & Handasyde 2007), are available. Based on the link between activity and energy expenditure identified in Chapter 4, the increased activity in linear strips suggests there is an additional energetic cost to bobucks associated with living in this anthropogenically-modified habitat. This could be due to influences such as competition, modified distribution of resources, or stressors such as increased predator vigilance and noise (Careau et al. 2008, Tuomainen & Candolin 2011). Field-based experiments examining energy expenditure relative to potential stressors, competition, and resources could explore this further.
6.1.3 The influence of geographic location on morphology and behaviour

Bobucks and common brushtail possums were trapped in both the Strathbogie Ranges and Grantville, but their abundance and capture locations varied within and between environments. Bobucks were found throughout the Strathbogie Ranges, but were only found in linear-strip environments in Grantville, and in much lower population numbers (13 individuals in Grantville versus 101 in the Strathbogies). Meanwhile, common brushtails in Grantville were caught in both forest fragments and linear strip environments, and in similar numbers to the Strathbogies (20 versus 19 respectively). There was also a difference in the average mass of individuals between the Strathbogie Ranges and Grantville, with bobucks in Grantville approximately 15% lighter than bobucks in the Strathbogies, while common brushtails in the Strathbogies were approximately 25% lighter than common brushtails in Grantville. When examined together, this data suggests a potential interaction between the two species that may change in relation to body-size differences between the two sites. In the Strathbogies, bobucks were over 20% heavier than common brushtails, and the more abundant and widely distributed species, while in Grantville common brushtails were approximately 10% heavier and the more abundant and widely distributed species. An examination of trends in possum body size and abundance relationships across a greater number of sites could potentially shed more light on this observation, and the possible underlying mechanisms.

The movement and behaviour of individuals between the sites also differed. Bobucks in Grantville spent more time resting at night and travelled significantly shorter distances on a nightly basis than bobucks in the Strathbogies. However, while the behavioural patterns varied, bobucks in Grantville had similar daily energy
expenditure to bobucks in the Strathbogies. This suggests that the overall energy requirements of individual bobucks does not differ with region even though bobucks in Grantville are almost 15% lighter, or, conversely, that their energy expenditure relative to mass is higher in Grantville than the Strathbogies. Given the limited capture success of bobucks across the Grantville region, and the higher levels of movement recorded, it suggests that bobucks living in Grantville might be approaching their physiological and environmental limits, reducing their movement and activity, and constraining their resource use.

6.2 Knowledge gaps and further research

My research identified how combining emerging technology can be used to more accurately identify and quantify animal behaviour than any one technology alone. However, improvements to the technology used in this thesis, and its application, remain. Initially, I had issues with battery life in the collars, with some devices only recording for half the desired time. This was rectified early in my research by using higher quality components, which increased the recording time and life-span of the collars. Similarly, the construction of re-chargeable VHF transmitters could greatly improve the collar design, increase their life-span, and hence ability to collect data and information on animal behaviour.

Improvements could also be made regarding accelerometer mounting. For this research, the accelerometer was mounted around the possum’s neck on a collar. This meant there was potential for the orientation of the accelerometer to shift during its deployment. While I was still able to use the accelerometry as a measure of activity, I was not able to identify nuanced differences in behavioural state, such as moving
vertically versus moving horizontally. A backpack harness would potentially improve the accuracy of the accelerometry collected by restricting any shift in orientation in the accelerometer. It would also be beneficial to compare the accelerometry data to visual recordings of animal movement, in order to match data patterns to specific behaviours. Mounting a small camera to animals could assist with this and would be superior to direct observation by researchers, which might affect animal behaviour.

My research focussed on GPS and accelerometry technology in order to understand animal behaviour. However, since the commencement of this research, there has been a surge in cost-effective low-powered consumer technology, specifically around Inertial Measurement Units, or IMUs. IMUs are small devices integrating accelerometers, magnetometers, gyroscopes, and barometers to measure force, angular rates, magnetic fields, etc. When coupled with a GPS device, IMUs have the ability to record 3D movement, and in conjunction with 3D habitat maps, reconstruct real-time models of animal habitat use in the field. These reconstructed movement models are already being undertaken as a diagnostic and maintenance tool in technology such as Unmanned Aerial Vehicles (UAVs), so the methodology to process the raw data already exists (da Silva & da Cruz 2016, Wang et al. 2016).

6.3 Implications for management

Insights into animal movement can help improve species conservation and management. Using emerging technology, we can quantify changes in the movement and behaviour of individuals.
In terms of bobucks, I identified that individuals in modified habitats have higher activity than those in forest fragments, even though their home ranges are smaller than individuals living in forest fragments. The higher levels of activity mean there is ultimately a higher energetic cost to bobucks living in modified habitats. This information provides a means of quantifying the impact different environments pose on individuals and populations. This information could be used to understand the possible implications of land clearing on other species, including those of conservation concern.

By comparing between congeneres, I was able to show how each species responded to altered habitats, employed varied behavioural strategies, and exhibited morphological plasticity. My findings suggest that responses to change can differ greatly both intra- and inter-specifically in relation to environmental context. Therefore, it is fraught to broadly generalise about species’ responses to environmental and habitat change, let alone generalise about responses of closely-related species, and different populations of the same species. Effective, well-informed species conservation and management will therefore require ecological understanding of species across their distributions, in order to predict the possible range of responses to environmental change.
References


McKinney, M. L. 2002. Urbanization, biodiversity, and conservation the impacts of urbanization on native species are poorly studied, but educating a highly urbanized human population about these impacts can greatly improve species conservation in all ecosystems. Bioscience 52:883-890.


Appendix

Chapter 3 Appendix

Appendix Table 3.2: Comparison of the average nightly distance travelled by bobucks (*Trichosurus cunninghami*) in south-eastern Australia categorized by sex and habitat type.

A positive estimate indicates a relatively higher average distance travelled during the night, while a negative estimate indicates a relatively lower distance travelled. The *p*-values displayed are corrected for multiple comparisons using Bonferroni correction.

<table>
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<th>Response</th>
<th>Estimate</th>
<th>SE</th>
<th><em>t</em>-value</th>
<th><em>p</em>-value</th>
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<td><em>p</em>&lt;0.001</td>
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Appendix Table 3.3: Comparison of the average VeDBA (g) measured over 24 hours travelled by bobucks (*Trichosurus cunninghami*) in south-eastern Australia categorized by sex and habitat type.

A positive estimate indicates a relatively higher average distance travelled during the night, while a negative estimate indicates a relatively lower distance travelled. The *p*-values displayed are corrected for multiple comparisons using Bonferroni correction.

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<td><strong>3.54</strong></td>
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</tr>
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</table>
Appendix Table 3.4a: Comparison of the average time spent denning within a 24-hour period, measured in seconds, by bobucks (*Trichosurus cunninghami*) in south-eastern Australia categorized by sex and habitat type.

A positive estimate indicates a relatively higher average time spent denning, while a negative estimate indicates a relatively lower time spent denning. The *p*-values displayed are corrected for multiple comparisons using Bonferroni correction.

<table>
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<th>p-value</th>
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<td>0.822</td>
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<td>Male forest fragment</td>
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<td>1637.30</td>
<td>1.52</td>
<td>0.822</td>
</tr>
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<td>Female forest fragment</td>
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<td>Male linear strip</td>
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<td>2389.88</td>
<td>0.91</td>
<td>0.999</td>
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Appendix Table 3.4b: Comparison of the average time spent resting at night within a 24-hour period, measured in seconds, by bobucks (*Trichosurus cunninghami*) in south-eastern Australia categorized by sex and habitat type.

A positive estimate indicates a relatively higher average time spent resting at night, while a negative estimate indicates a relatively lower time spent resting at night. The *p*-values displayed are corrected for multiple comparisons using Bonferroni correction.

<table>
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<th>SE</th>
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<th><em>p</em>-value</th>
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<td>0.999</td>
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<tr>
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<td>Female linear strip</td>
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<td>0.774</td>
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<td>1118.13</td>
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<td>0.999</td>
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<tr>
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<td>Female forest fragment</td>
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<td>1150.83</td>
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<td>1650.76</td>
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<td>0.999</td>
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Appendix Table 3.4c: Comparison of the average time spent moving within a 24-hour period, measured in seconds, by bobucks (*Trichosurus cunninghami*) in south-eastern Australia categorized by sex and habitat type.

A positive estimate indicates a relatively higher average time spent moving, while a negative estimate indicates a relatively lower time spent moving. The *p*-values displayed are corrected for multiple comparisons using Bonferroni correction.

<table>
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<th>SE</th>
<th><em>t</em>-value</th>
<th><em>p</em>-value</th>
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<td>0.999</td>
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<td>923.40</td>
<td>0.68</td>
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<td>1336.60</td>
<td>2.31</td>
<td>0.156</td>
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<td>1343.15</td>
<td>1.84</td>
<td>0.450</td>
</tr>
<tr>
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<td>Female linear strip</td>
<td>Female forest fragment</td>
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<td>941.81</td>
<td>0.80</td>
<td>0.999</td>
</tr>
<tr>
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<td>Male forest fragment</td>
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<td>957.53</td>
<td>0.14</td>
<td>0.999</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Male linear strip</td>
<td>2333.06</td>
<td>1343.02</td>
<td>1.74</td>
<td>0.546</td>
</tr>
</tbody>
</table>
Appendix Table 3.4d: Comparison of the average time spent in high activity within a 24-hour period, measured in seconds, by bobucks (*Trichosurus cunninghami*) in south-eastern Australia categorized by sex and habitat type.

A positive estimate indicates a relatively higher average time spent in high activity, while a negative estimate indicates a relatively lower time spent in high activity. The *p*-values displayed are corrected for multiple comparisons using Bonferroni correction.

<table>
<thead>
<tr>
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<th>Response</th>
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<th>SE</th>
<th><em>t</em>-value</th>
<th><em>p</em>-value</th>
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<td>96.75</td>
<td>3.86</td>
<td>0.006</td>
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<td>-158.89</td>
<td>100.75</td>
<td>1.58</td>
<td>0.750</td>
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<td>5.39</td>
<td><em>p</em>&lt;0.001</td>
</tr>
<tr>
<td></td>
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<td>Female linear strip</td>
<td>214.62</td>
<td>98.13</td>
<td>2.19</td>
<td>0.216</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Male forest fragment</td>
<td>373.50</td>
<td>96.75</td>
<td>3.86</td>
<td>0.006</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Male linear strip</td>
<td>1132.22</td>
<td>138.85</td>
<td>8.15</td>
<td><em>p</em>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Male linear strip</td>
<td>Female forest fragment</td>
<td>-1132.22</td>
<td>138.85</td>
<td>8.15</td>
<td><em>p</em>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Female linear strip</td>
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<td>141.67</td>
<td>6.48</td>
<td><em>p</em>&lt;0.001</td>
</tr>
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<td></td>
<td>Male forest fragment</td>
<td>-758.72</td>
<td>140.72</td>
<td>5.39</td>
<td><em>p</em>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Female linear strip</td>
<td>Female forest fragment</td>
<td>-214.62</td>
<td>98.13</td>
<td>2.19</td>
<td>0.216</td>
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<td></td>
<td>Male forest fragment</td>
<td>158.89</td>
<td>100.75</td>
<td>1.58</td>
<td>0.750</td>
</tr>
<tr>
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<td></td>
<td>Male linear strip</td>
<td>917.61</td>
<td>141.67</td>
<td>6.48</td>
<td><em>p</em>&lt;0.001</td>
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Appendix Table 3.5: Interval comparison of the average distance travelled (m) versus the average VeDBA (g), measured in 10 minute intervals for bobucks (*Trichosurus cunninghami*) in south-eastern Australia categorized by sex and habitat type.

A positive estimate indicates a relatively higher average values, while a negative estimate indicates a relatively lower average values. The *p*-values displayed are corrected for multiple comparisons using Bonferroni correction.

<table>
<thead>
<tr>
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<th><em>p</em>-value</th>
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<td>1.29</td>
<td>8.17</td>
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<td>Female forest fragment</td>
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<td>1.29</td>
<td>8.17</td>
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<td>7.29</td>
<td><strong>&lt;0.001</strong></td>
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<tr>
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<td><strong>Female forest fragment</strong></td>
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<td>1.29</td>
<td>3.48</td>
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<td>1.17</td>
<td>2.12</td>
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</table>
Chapter 4 Appendix

Appendix Table 4.2: Model selection results for the generalised mixed models comparing energy expenditure to distance travelled for bobucks (*Trichosurus cunninghami*) in south-eastern Australia.

Overall energy expenditure (EE, kJ) was compared to Total Distance (DistanceTotal, m), and Daily Energy Expenditure (DEE, kJ/day) was compared to Daily Distance (DistanceDaily, m/day), with both models including variables. AICc values, differences in AICc values (Δi) and Akaike weight (wi) are shown for models with Δi < 10.

<table>
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<th>Tooth Wear</th>
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<th>df</th>
<th>AICc</th>
<th>Δi</th>
<th>wi</th>
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<th>Δi</th>
<th>wi</th>
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Appendix Table 4.3: Model selection results for the generalised mixed models comparing energy expenditure to VeDBA for bobucks (*Trichosurus cunninghami*) in south-eastern Australia.

Overall energy expenditure (EE, kJ), mass standardised overall energy expenditure (EE\(_{\text{mass}}\), kJ), and mass\(^{0.75}\) standardised overall energy expenditure (EE\(_{\text{mass}^{0.75}}\), kJ) were compared to total VeDBA, with all models including variables and the total distance travelled (m). AICc values, differences in AICc values (\(\Delta_i\)) and Akaike weight (\(w_i\)) are shown for models with \(\Delta_i < 10\).

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<th>VeDBA(_{\text{Total}})</th>
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<th>Sex</th>
<th>Tooth Wear</th>
<th>Mass</th>
<th>(R^2)</th>
<th>df</th>
<th>AICc</th>
<th>(\Delta_i)</th>
<th>(w_i)</th>
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Appendix Table 4.4: Model selection results for the generalised mixed models comparing daily energy expenditure to average VeDBA for bobucks (*Trichosurus cunninghami*) in south-eastern Australia.

Daily energy expenditure (DEE, kJ/day), mass standardised daily energy expenditure (DEE<sub>mass</sub>, kJ/day), and mass<sup>0.75</sup> standardised daily energy expenditure (DEE<sub>mass0.75</sub>, kJ/day) were compared to the average VeDBA (VeDBA<sub>Average</sub>), with all models including variables and daily distance travelled (m/day). AICc values, differences in AICc values (Δi) and Akaike weight (w<sub>i</sub>) are shown for models with Δi < 10.

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<th>Tooth Wear</th>
<th>Mass</th>
<th>R&lt;sup&gt;2&lt;/sup&gt;</th>
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| DEE<sub>mass</sub>      |                   |     |            |      |           |    |       |    |         |
| 2515.294                |                   |     |            |      | 0.000    | 3  | 179.28| 0.00| 0.50    |
| +                       |                   |     |            |      | -0.289   | 2  | 180.61| 1.34| 0.25    |
| 407.437                 |                   |     |            |      | 0.010    | 4  | 182.60| 3.32| 0.09    |
| 0.000                   |                   |     |            |      | 0.000    | 4  | 182.76| 3.49| 0.09    |
| 2591.796                | -0.001            |     |            |      | -0.287   | 3  | 183.57| 4.29| 0.06    |
| 459.629                 | -0.001            |     |            |      | 0.011    | 5  | 186.69| 7.42| 0.01    |

| DEE<sub>mass0.75</sub> |                   |     |            |      |           |    |       |    |         |
| 3353.777                |                   |     |            |      | 0.000    | 3  | 185.87| 0.00| 0.48    |
| 812.920                 |                   |     |            |      | -0.279   | 2  | 187.08| 1.20| 0.26    |
| 0.000                   |                   |     |            |      | 0.026    | 4  | 188.92| 3.04| 0.10    |
| 3467.666                | -0.002            |     |            |      | -0.276   | 3  | 190.01| 4.14| 0.06    |
| 885.428                 | -0.001            |     |            |      | 0.028    | 5  | 193.00| 7.13| 0.01    |
Appendix Table 5.2: Comparison of the average nightly distance travelled by bobucks (*Trichosurus cunninghami*) and common brushtail possums (*T. vulpecula*) in their respective locations: the Strathbogie Ranges (foothill forest) and Grantville (heavily cleared coastal and lowland forest).

A positive estimate indicates a relatively higher average distance travelled during the night, while a negative estimate indicates a relatively lower distance travelled. The *p*-values displayed are corrected for multiple comparisons using Bonferroni correction.

<table>
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<tr>
<th>Predictor</th>
<th>Response</th>
<th>Estimate</th>
<th>SE</th>
<th><em>t</em>-value</th>
<th><em>p</em>-value</th>
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Appendix Table 5.3: Comparison of the average VeDBA (g) measured over 24 hours travelled by bobucks (*Trichosurus cunninghami*) and common brushtail possums (*T. vulpecula*) in their respective locations; the Strathbogie Ranges (foothill forest) and Grantville (heavily cleared coastal and lowland forest).

A positive estimate indicates a relatively higher average activity, while a negative estimate indicates a relatively lower average activity. The *p*-values displayed are corrected for multiple comparisons using Bonferroni correction.

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<th><em>t</em>-value</th>
<th><em>p</em>-value</th>
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Appendix Table 5.4: Comparison of the average time spent in the four behavioural states (denning, resting at night, moving, and high activity) within a 24-hour period, measured in seconds, by bobucks (*Trichosurus cunninghami*) and common brushtail possums (*T. vulpecula*) in their respective locations; the Strathbogie Ranges (foothill forest) and Grantville (heavily cleared coastal and lowland forest).

A positive estimate indicates a relatively higher average time spent in a behavioural state, while a negative estimate indicates a relatively lower time spent in a behavioural state. The *p*-values displayed are corrected for multiple comparisons using Bonferroni correction.

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<td><em>T. cunninghami</em></td>
<td>2948</td>
<td>1582</td>
<td>1.863</td>
<td>0.260</td>
<td></td>
</tr>
<tr>
<td>Strathbogies</td>
<td><em>T. cunninghami</em></td>
<td>4244</td>
<td>1486</td>
<td>2.855</td>
<td>0.037</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>T. vulpecula</em></td>
<td>-157</td>
<td>237</td>
<td>0.661</td>
<td>0.999</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>T. vulpecula</em></td>
<td>-965</td>
<td>270</td>
<td>3.573</td>
<td>0.012</td>
<td></td>
</tr>
<tr>
<td>Gippsland</td>
<td><em>T. cunninghami</em></td>
<td>-1122</td>
<td>247</td>
<td>4.541</td>
<td>0.002</td>
<td></td>
</tr>
<tr>
<td>Strathbogies</td>
<td><em>T. cunninghami</em></td>
<td>965</td>
<td>270</td>
<td>3.573</td>
<td>0.012</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>T. vulpecula</em></td>
<td>1122</td>
<td>247</td>
<td>4.541</td>
<td>0.002</td>
<td></td>
</tr>
</tbody>
</table>
Appendix Table 5.5: Interval comparison of the average distance travelled (m) versus the average VeDBA (g), measured in 10-minute intervals for bobucks (*Trichosurus cunninghami*) and common brushtail possums (*T. vulpecula*) in their respective locations: the Strathbogie Ranges (foothill forest) and Grantville (heavily cleared coastal and lowland forest).

A positive estimate indicates a relatively higher VeDBA value, while a negative estimate indicates a relatively lower VeDBA value. The *p*-values displayed are corrected for multiple comparisons using Bonferroni correction.

<table>
<thead>
<tr>
<th>Predictor</th>
<th>Response</th>
<th>Estimate</th>
<th>SE</th>
<th><em>t</em>-value</th>
<th><em>p</em>-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grantville <em>T. cunninghami</em></td>
<td>Strathbogies <em>T. cunninghami</em></td>
<td>-4.85</td>
<td>1.34</td>
<td>3.615</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td>Strathbogies <em>T. vulpecula</em></td>
<td>8.91</td>
<td>1.66</td>
<td>5.381</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Strathbogies <em>T. cunninghami</em></td>
<td>Grantville <em>T. cunninghami</em></td>
<td>4.85</td>
<td>1.34</td>
<td>3.615</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td>Strathbogies <em>T. vulpecula</em></td>
<td>13.76</td>
<td>1.48</td>
<td>9.327</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Strathbogies <em>T. vulpecula</em></td>
<td>Grantville <em>T. cunninghami</em></td>
<td>-8.91</td>
<td>1.66</td>
<td>5.381</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Strathbogies <em>T. cunninghami</em></td>
<td>-13.76</td>
<td>1.48</td>
<td>9.327</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>
Appendix Table 5.6: Comparison of the estimated daily energy expenditure (kJ/d) calculated from the behavioural states using the equation in Chapter 4, for bobucks (*Trichosurus cunninghami*) and common brushtail possums (*T. vulpecula*) in their respective locations: the Strathbogie Ranges (foothill forest) and Grantville (heavily cleared coastal and lowland forest).

A positive estimate indicates a relatively higher daily energy expenditure, while a negative estimate indicates a relatively lower daily energy expenditure. The *p*-values displayed are corrected for multiple comparisons using Bonferroni correction.

<table>
<thead>
<tr>
<th>Predictor</th>
<th>Response</th>
<th>Estimate</th>
<th>SE</th>
<th><em>t</em>-value</th>
<th><em>p</em>-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grantville <em>T. cunninghami</em></td>
<td>Strathbogies <em>T. cunninghami</em></td>
<td>44.76</td>
<td>26.64</td>
<td>1.680</td>
<td>0.350</td>
</tr>
<tr>
<td></td>
<td>Strathbogies <em>T. vulpecula</em></td>
<td>-74.90</td>
<td>29.18</td>
<td>2.567</td>
<td>0.073</td>
</tr>
<tr>
<td>Strathbogies <em>T. cunninghami</em></td>
<td>Grantville <em>T. cunninghami</em></td>
<td>-44.76</td>
<td>26.64</td>
<td>1.680</td>
<td>0.350</td>
</tr>
<tr>
<td></td>
<td>Strathbogies <em>T. vulpecula</em></td>
<td>-119.66</td>
<td>27.77</td>
<td>4.309</td>
<td>0.002</td>
</tr>
<tr>
<td>Strathbogies <em>T. vulpecula</em></td>
<td>Grantville <em>T. cunninghami</em></td>
<td>74.90</td>
<td>29.18</td>
<td>2.567</td>
<td>0.073</td>
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<tr>
<td></td>
<td>Strathbogies <em>T. cunninghami</em></td>
<td>119.66</td>
<td>27.77</td>
<td>4.309</td>
<td>0.002</td>
</tr>
</tbody>
</table>
global biodiversity—especially in such a populous country as China. As with IWT, there is an urgent need to reform existing legislation.

How could this operate? Ivory provides the best model, where in the US, UK, European Union, and Australia, only pre-CITES certified antiques and/or artifacts can be legally owned (but not sold). This is currently not the case in China; thus, we advocate a ban on the manufacture, ownership, and subsequent resale of all post-CITES ivory and all other protected species and related products. Permits might be used to approve family heirloom antique collections on a limited basis but would neither exempt large collections nor authorize new collections. Importantly, all collectors must be subject to the law, irrespective of their wealth and influence. Precious historical artifacts should be taken into State ownership for museum exhibition, available for everyone to appreciate. An alternate solution, farming or ranching of key species to replace products of wild provenance, is unlikely to satisfy consumer demand (Biggs et al. 2013; Challender and MacMillan 2014) and often still involves substantial animal suffering. Furthermore, consumers may continue to seek what is perceived as the “genuine” product (Dutton et al. 2011; Zhou et al. 2014).

But there are signs of progress in May 2015, Zhao Shuang, head of China’s State Forestry Administration, said: “We will strictly control ivory processing and trade until the commercial processing and sale of ivory and its products are eventually halted” – committing China to phasing out its legal, domestic ivory industry. China has also recently imposed a one-year embargo on imports of African ivory carvings acquired after CITES took effect (Zhao 2015). However, so long as private ownership remains a legal loophole, consumer demand will continue to drive IWT, limiting the effectiveness of protective measures within Chinese society.
most UAV operations relevant to conducting science. As a result of the changes in policy, UAV laws in the US now more closely resemble the unambiguous and less restrictive UAV laws in Australia (WebTable 1), where Google and Amazon chose to site their drone delivery testing facilities. Regardless of legislative change, there are ways to incorporate UAVs into research that can avoid some of the issues outlined by Vincent et al. If universities do not want to become registered operators, they can collaborate with industry partners who are registered. We are currently using such an approach in our ecological research. We believe this provides the best starting point for academic institutions to use UAVs for research purposes, without the need for in-house logistical support or expertise to meet legislative requirements. While few universities have UAV Operators Certificate (UOC) approval in Australia (http://bit.ly/2c9Kyc2), 25 academic institutions in the US – as of July 2015 – hold a COA (http://1.usa.gov/1CDyS3W). Thus, if Vincent et al. worked with a registered industry partner who already had a COA, they could work as close as two nautical miles from the airstrip they describe without the requirement to hold their own COA.

To conduct research within two nautical miles of a registered airstrip still requires a COA, and with good reason. A registered airstrip is marked on official aviation maps for all aircraft, and can be used for emergency landings. The last thing that a pilot in distress needs is to mislead a small UAV in close proximity for a large airplane in the distance. After all, UAV operators typically do not monitor aviation radio frequencies to inform pilots otherwise. It is important for the broader research community to recognize that UAVs are not toys; they are certified aircraft used for commercial purposes, and can pose a serious threat to both people and property when used irresponsibly.

Finally, proposed changes to UAV laws in Australia could relax the requirement of a UOC for remotely piloted aircraft under 2 kg (CASA 2014). As ecologists already undertaking research with UAVs under 2 kg, we are excited about the possibilities that such changes could foster. Continued positive changes in UAV-relevant legislation globally – together with industry partnerships – should promote the rapid uptake of UAVs as important tools in conducting ecological field-based studies. Blaise M. Allen, Daniel Ierodiaconou, Dale G. Nimmo, Mathew Herbert, and Evan G. Ritchie

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2Centre for Integrative Ecology, School of Life and Environmental Sciences, Deakin University, Warrnambool, Australia; Victoria UAS Training Pty Ltd, Smythesdale, Australia;
3Charles Sturt University, Albury-Wodonga, Australia


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