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Population trends, habitat requirements and conservation recommendations for an endangered marsupial, the northern bettong (*Bettongia tropica*)

Thesis submitted by
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Statement of contribution of others

For all chapters, I was the primary investigator and was responsible for designing the research project, collecting the data and conducting analyses. I wrote and edited all drafts and incorporated feedback into the final chapters presented in this thesis. However, there were others that substantially contributed to my research and their input is listed below.

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Abstract

This thesis examines the population trends and habitat requirements of the endangered northern bettong (*Bettongia tropica*) (Wakefield 1967) within wet to moist *Eucalyptus* woodland in their core population on the Lamb Range in north-eastern Queensland, Australia. This research has implications for managing habitat used by *B. tropica* and increasing their long-term population viability. Management recommendations to improve the conservation of *B. tropica* are presented.

Effective management strategies depend upon identifying and mitigating against the key threats to population stability. However, the ability to devise suitable management strategies is often impeded by a lack of data. This is frequently the case for endangered species, including *B. tropica*. In Chapter two I overcome this problem by using simulation models to make projections of the future impacts on *B. tropica* under various scenarios. The population viability and survival probability of *B. tropica* populations on the Lamb Range was modelled in response to 1) increased predation; 2) changes in drought and fire frequency predicted with anthropogenic climate change; and 3) synergistic effects of predation, fire, and drought. Population viability analysis (PVA) models suggest that populations were resilient to substantial declines (up to 75%) and recovered to carrying capacity within 10 years when no threats impacted upon the population.

However, modelling showed that a ≥40% increase in predation by cats, *Felis catus*, resulted in the population declining to extinction within 20 years. In contrast, populations were resilient to increases in droughts and fires. However, the impacts of predation could be more severe if predation and fire were to interact to increase the mortality of *B. tropica*. Interestingly, juvenile mortality was the main age class driving population viability, although mortality would need to double from the current rate before extinction was assured. To assist in maximising the long-term viability of *B. tropica* populations, it is recommended that the density of predators (especially cats and foxes) and *B. tropica* populations be regularly and consistently monitored. Predator control measures should be undertaken if high densities of predators are detected.

Bettongia tropica is a keystone species within *Eucalyptus* woodlands on the Lamb Range. The long-term viability of *B. tropica* is important for maintaining ecosystem function within these woodlands. The population density of *B. tropica* was previously assessed between 1994 and 1996 within the three main sub-populations (Davies Creek, Emu Creek and Tinaroo Creek) of the core population on the Lamb Range. During that previous study, the majority of sampling occurred at one sub-population, Davies Creek. No consistent monitoring of *B. tropica*'s core population had been undertaken since 1996, although inconsistent monitoring between 2000 and 2009 at Davies Creek suggested a possible decline. In Chapter three, I re-assessed the population density, fitness (survival rates, body condition

and females with young) and trap success of *B. tropica* in the three main sub-populations using a far more intensive trapping regime than used in previous assessments. Population parameters were quantified during both the wet and dry seasons from nine surveys over two years at each sub-population. Substantially more sampling within each sub-population means that my estimates are more reliable than previous. Population density estimates appeared stable compared to the assessment 20 years prior. Population density was highest at the site with highest rainfall (Tinaroo Creek), with rainfall thought to indicate food abundance. *Bettongia tropica* sub-populations had similar density estimates and fitness during both seasons. Interestingly, trap success was higher during the dry season. Since long-term monitoring studies often use trap success to assess population trends, an accurate assessment of the population trend of *B. tropica* requires regular monitoring during both the wet and dry seasons. The population density varied with spatial distribution, with higher population densities occurring within preferred habitats. Population monitoring should therefore be conducted not only within preferred habitat, but also within more marginal habitats.

Knowledge of the spatial distribution of species can provide an insight into the habitat requirements and behaviours of species. This information can assist in devising management strategies to increase long-term habitat stability and thus population viability. In Chapter, four movement patterns, home range distribution and social interactions of *B. tropica* were investigated using data obtained approximately every 10 minutes from 41 Global Positioning System (GPS) collars. *Bettongia tropica* had home ranges of 20.90 ± 1.55 ha (mean ± SE), with core foraging and nesting areas of 5.53 ± 0.42 ha and 0.67 ± 0.10 ha respectively. An average of six nesting areas were used over an average of 25.43 ± 1.65 days. *Bettongia tropica* maintained separate core foraging and nesting areas, despite having largely overlapping home ranges. This suggests they defend areas with high resource density and are somewhat territorial, a trait not previously recorded for this species.

Across all sites, males had larger home ranges than females, with home ranges of both genders increasing during the dry season. Interestingly, home ranges were similar between sites for males and females. The distribution of males appeared influenced by the distribution of females (seeking mating opportunities) and food resources, whilst females were influenced only by the distribution of food resources. *Bettongia tropica* undertook rapid and direct movements between resource patches and then moved slowly at irregular angles whilst foraging. Fast, linear movements are effective for travelling quickly across areas with minimal resources or few mating opportunities, whilst slower movements maximised the time *B. tropica* spent within areas with high density of resources. From the movement patterns of *B. tropica*, the location of bettong nesting and foraging areas were determined.

In Chapter five, the microhabitat requirements of *B. tropica* were surveyed at nesting and foraging areas. Collared *B. tropica* were also radio-tracked to their nest location to determine the design and material used to construct nests. *Bettongia tropica* mainly constructed nests from grass (*Poaceae* spp.) or nested under the ‘skirts’ (leaves) of grass trees (*Xanthorrhoea johnsonii*). Different habitat parameters were important for nesting and foraging. Nests were situated in steep areas with high grass cover and an abundance of grass trees. Whilst foraging, *B. tropica* selected habitats with a higher density of cockatoo grass (*Alloteropsis semialata*) and a lower density of tree basal area. Predator pressure appeared to influence habitat selection by *B. tropica*. Nesting areas were chosen for camouflage while resting, whilst foraging areas were more open to allow rapid escape from predators. Camera trapping conducted for six sessions recorded capture rates of approximately one predator capture to 60 *B. tropica* and one potential competitor to around 16 *B. tropica*. The presence of invasive predators of *B. tropica* on the Lamb Range means it is vital to regularly and consistently monitor both *B. tropica* and predator populations to assess for changes in density that could impact on the future population viability of *B. tropica*.

The results of this study provide greater detail on the ecology of *B. tropica* and will assist in conserving the species. Food density appeared to have the greatest influence on *B. tropica* population density, which was reflected in how bettongs, especially females, moved throughout their habitat. Tinaroo Creek, which is the wettest site, had the highest population density. At Tinaroo Creek *B. tropica* had smaller home ranges (although not significantly) and females spent more time foraging (indicated by slow, angular movements) and less time travelling between resource patches (indicated by them undertaking rapid, linear movements). Higher rainfall would lead to higher resource density, enabling bettongs to travel shorter distances to access resources. This would allow more bettongs to occur within a given habitat area, with the habitat thus supporting a higher population density.

Camera trapping data shows that the current predation pressure was slightly higher at Emu Creek, with more camera captures of predator species per captures of *B. tropica* at the site. Emu Creek was the only site where both cattle and rufous bettongs co-occurred with *B. tropica*, with these species likely to compete with *B. tropica* for grass resources. Interestingly, current predation and competition pressure did not appear to significantly influence the fitness of *B. tropica*, with survival rates, body condition and number of females with young similar between sites. This was surprising since predation pressures appeared to strongly influence microhabitat selection by *B. tropica*. It is possible that the current predation and competitive pressure was not sufficiently different between sites to detect an influence on population density of *B. tropica* in this study. However, climate change may increase predation pressure, with PVA modelling showing that predation by feral species could have the greatest impact on the future viability of *B. tropica* populations. Managing the habitat to minimise the potential impacts of predators is thus of high conservation priority.

Current habitat management practices involve low-intensity mosaic burns undertaken every two to three years on the Lamb Range. The population on the Lamb Range is stable, indicating current fire regimes are generally adequate and not negatively impacting upon *B. tropica*. However, habitat management could be improved based on the results of this study. Specifically, it is recommended that burns be conducted at a 20 ha scale and at least six areas of approximately 0.70 ha be left unburned to provide sufficient post-fire nesting resources. Management practices should also focus on maintaining or increasing the density of the habitat parameters identified in this study that are important for both nesting (grass cover and grass trees) and foraging (cockatoo grasses and low tree basal area). This may assist in improving habitat quality and increasing the density and viability of *B. tropica* populations.

It is important that habitat quality be improved throughout the species distribution. The distribution of *B. tropica* has previously been modelled based on the distribution of their food resources projected from environmental variables. After my study, camera trapping can be used to survey for the presence/absence of *B. tropica* throughout that modelled distribution. Monitoring within *Eucalyptus* and wet sclerophyll woodlands on steep slopes and comprising an abundance of grass cover, grass trees and cockatoo grass and low tree basal area will maximise the detectability of *B. tropica*. Previous researchers have found that vegetation thickening can reduce grass cover. I determined that grass cover and cockatoo grass are important resources for *B. tropica*. Bettong individuals constructed poorly camouflaged nests within thickets of lantana. These nesting structures were not observed throughout the rest of the habitat, indicating that weedy and thickened vegetation provides sub-standard habitat for *B. tropica*. If *B. tropica* occurs within areas where vegetation thickening is occurring, low-intensity burns should be conducted to reduce thickening and promote a grassy understorey. Low-intensity fire management may assist in improving the habitat quality for *B. tropica* throughout their distribution.

It is also recommended that the number of known *B. tropica* populations be increased. *Bettongia tropica* is now only recorded from two populations (the Lamb Range and Mt. Carbine). The Mt. Carbine population is very small, with little research conducted on that population. As determined from Chapter 2, the Lamb Range population is resilient to a reduction in the number of individuals, making translocations a viable option at this time. Establishing additional populations would increase the population viability of the species and provide a safeguard for the species' survival if the Lamb Range population suffered a large population decline or one or more of the sub-populations went locally extinct. The population viability may also be improved by a better understanding of the ecology and fate of juveniles, as juveniles were the main drivers of the population viability of *B. tropica*. In Chapter 3, it was shown that the survival rates of adult bettongs were high throughout the year across all sites and females carried pouch young during both the wet and dry season. However, the fate of juveniles and sub-adults was not measured. It is recommended that future research assess the survival rates of sub-adults and juveniles and determine the main factors affecting their survival. This will assist in improving the conservation of *B. tropica*.

Bettongia tropica provide important ecosystem services within *Eucalyptus* woodlands, including fungal spore dispersal and possible nutrient recycling. These services can improve habitat quality by improving the growth of certain plant species, which in turn affects vegetation community composition. *Eucalyptus* woodlands are habitat for a diversity of native species and protecting *B. tropica* may thus improve the health of an entire ecosystem. This conservation of healthy *Eucalyptus* woodlands should also assist in maintaining the population viability of other native species within this habitat.

The concepts from this study can also be applied to research into other small mammal species. This study highlights the importance of consistent monitoring during the wet and dry seasons. My research also demonstrates that studying animals' movement patterns can determine their microhabitat requirements. Many small mammal species have cryptic behaviours and their microhabitats are often poorly understood. Previous studies have determined the habitat preferences of small mammals by comparing trap capture rates within different habitats. However, this method may be biased by many factors, including animals being attracted to an area due to baiting of traps or less sampling effort occurring within difficult to access habitats. Using species movement patterns thus provides a more accurate method and is recommended for ascertaining the microhabitat requirements of other small mammal species. This information is crucial for species conservation, as it enables management to focus on protecting important microhabitats.

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Whitehead, T., et al. Population trends and life-history traits of the endangered northern bettong.

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Thesis Chapter Five

Whitehead, T., et al. Nesting resources and microhabitat requirements of the northern bettong.

Whitehead, T., et al. Microhabitat use of the northern bettong whilst foraging.

Other publications in preparation

Whitehead, T., et al. Small mammal community composition within *Eucalyptus* woodlands.

Whitehead, T., et al. Does camera trapping accurately reflect the population density of small mammals within *Eucalyptus* woodlands?

Chapter 1: General Introduction

Australian terrestrial mammals have experienced the highest rate of mammal extinctions worldwide, accounting for a third of extinctions (Fisher et al. 2013). At the time of European settlement, an estimated 273 terrestrial mammals were endemic to Australia (Woinarski et al. 2015). Around 10% (30 species) of Australia's mammals are now extinct and 21% (56 species) are considered threatened, being classified as either critically endangered (10 species), endangered (10 species) or vulnerable (36 species) (Chapman 2009; Woinarski et al. 2015). An additional 15% (52 species) are near threatened (Chapman 2009; IUCN Standards and Petitions Subcommittee 2013; Woinarski et al. 2015). Mammals continue to suffer severe declines throughout Australia (Woinarski et al. 2010), with the extinction of one to two species per decade likely to continue (Woinarski et al. 2015).

Most Australian mammal declines have occurred within relatively unmodified semi-arid or arid habitats in southern Australia in areas away from human centres (Fisher et al. 2013; Woinarski et al. 2015). Within these regions, small to medium-sized mammals (35 g to 5.5 kg) have suffered the greatest declines (Burbidge & McKenzie 1989; Short & Smith 1994). More recently, species within tropical (northern) regions have started to decline (Fisher et al. 2013). Small ground-dwelling species that inhabit open vegetation with moderate rainfall have typically experienced substantial declines (Fisher et al. 2013; Woinarski et al. 2010). For example, the northern brush-tailed phascogale (*Phascogale pirata*), northern quoll (*Dasyurus hallucatus*) and fawn antechinus (*Antechinus bellus*), have experienced large range contractions and population declines of >90% (Fitzsimons et al. 2010; Woinarski et al. 2011a; Fisher et al. 2013). The cause of those declines is uncertain, although predation by feral species and habitat alteration are likely explanations, with poisoning by toads also affecting northern quoll populations (Fitzsimons et al. 2010; Woinarski et al. 2011a; Fisher et al. 2013).

Predation and inappropriate fire regimes are considered to be the two main causes of severe mammal declines across Australia (Woinarski et al. 2015). Predation by cats (*Felis catus*) is considered the main threat to native Australian mammals, with 97 species impacted (22 extinctions, 46 species threatened and 29 species near threatened) (Woinarski et al. 2015). Inappropriate fire regimes have also affected 63 mammal species (6 extinctions, 35 species threatened and 22 species near threatened), whilst predation from red foxes (*Vulpes vulpes*), thought absent from the tropics, has impacted 58 species (13 extinctions, 28 species threatened and 17 species near threatened) (Woinarski et al. 2015). Habitat transformation (Fisher et al. 2003), including habitat loss and fragmentation, grazing, competition with feral species and disease are also contributing to mammal declines (McKenzie et al. 2007; Fisher et al. 2013; Woinarski et al. 2010; Woinarski et al. 2011a; Woinarski et al. 2015; Preece et al. 2017).

Bettong species (*Potoroidae*) are endemic Australian marsupials that have experienced substantial population declines (Wayne et al. 2013b). Translocated populations of bettong species, including the Tasmanian bettong (*Bettongia gaimardi*) and burrowing bettong (*Bettongia lesueur*), have gone locally extinct due to predation by feral cats (Short & Turner 2000; Fancourt 2014). Brush-tailed bettongs (*Bettongia penicillata*) in particular have suffered severe population declines and range contractions and by the 1960s were restricted to three small areas within south-west Western Australia (Wayne et al. 2013b). Predation by invasive species, mainly foxes, was considered the main cause of the population decline (Start et al. 1995). To conserve the species, predators (foxes and cat) were controlled and bettong individuals translocated into predator free areas (Start et al. 1995). Populations recovered rapidly and the species was delisted from the threatened species list in 1996 (Start et al. 1995). However, between 1999 and 2006, populations suffered severe and rapid (75-90%) declines (Groom 2010; Wayne et al. 2013b; Thompson et al. 2014) and as of 2008, brush-tailed bettongs were re-listed by the International Union for Conservation of Nature (IUCN) as being critically endangered (Woinarski & Burbidge 2016). Disease is the leading hypothesis for the cause of this decline, although predation, a reduction in resources and direct human interference may have all contributed (Wayne et al. 2013b).

The northern bettong (*Bettongia tropica*) (Wakefield 1967) has also suffered large range contractions, although the extent of population declines is currently unknown (Burbidge & Woinarski 2016). *Bettongia tropica* is listed as Endangered according to the IUCN Red List of Threatened Species (Burbidge & Woinarski 2016) and the Environment Protection and Biodiversity Conservation Act 1999 (Australian Commonwealth) (Dennis 2001). Given the species endangered status and the vulnerability of bettong species to threats, research regarding the current population status and the ecology of *B. tropica* may assist in developing management strategies to conserve the species. It is important these strategies are devised and implemented before *B. tropica* experiences the severe population declines observed for other bettong species.

During surveys in the early 1990s, *B. tropica* was recorded at four sites within far north Queensland: the core population on the Lamb Range (with four sub-populations) and peripheral small, low-density populations at Mt. Carbine, Mt. Windsor and Mt. Zero (Dennis 2001) (Figure 1.1). As of 2003, persistence of these peripheral populations has been uncertain. Extensive cage trapping (>3,600 trap nights) conducted between 2006 and 2007 failed to detect *B. tropica* at Mt. Zero (Bateman 2010), with the population considered locally extinct (Burbidge & Woinarski 2016). At Mt. Windsor, only one individual was ever detected from a total of 520 cage trap nights and 44 hours of spotlighting during the 1990s (Winter 1992; Winter 1997; Dennis 2001) and 2,800 camera trap nights in 2017 (Koleck et al. 2017, unpublished data). However, sampling at Mt. Windsor has only previously been conducted during the wet season (Winter 1997; Koleck et al. 2017, unpublished data). Trap success is generally lower during the wet season (McClearn et al. 1994) and surveying during the dry season may increase the chance of detecting *B. tropica*. Camera trapping (2,800 trap nights) conducted in February 2017 detected three individuals at Mt. Carbine (Koleck et al. 2017, unpublished data). This means there may have been a 50% reduction in the number of *B. tropica* populations, with the species only now recorded from two populations; the core population on the Lamb Range and the smaller and potentially disconnected population at Mt. Carbine.

All populations (both extinct and extant) of *B. tropica* are restricted to a narrow band of transitional forests from dry sclerophyll to *Allocasuarina* on the western margin of the Wet Tropics World Heritage Area (Winter 1992). The diet of *B. tropica* appears to be the main factor restricting the species' distribution (Abell et al. 2006; Bateman et al. 2011). Throughout the year, *B. tropica* predominately consumes ectomycorrhizal hypogeous fungal sporocarps (underground fruiting bodies), commonly known as truffles (Johnson & McIlwee 1997; Abell et al. 2006). Lilies, forbs and grasses, particularly the shoot base of cockatoo grass (*Alloteropsis semialata*), comprise around half the species' diet during the dry season when truffle abundance declines (Johnson & McIlwee 1997; McIlwee & Johnson 1998). Therefore, *B. tropica* is confined to areas where truffles occur for the majority of the year and cockatoo grass grows in abundance during the dry season when truffle abundance declines (Johnson & McIlwee 1997; McIlwee & Johnson 1998; Abell et al. 2006).

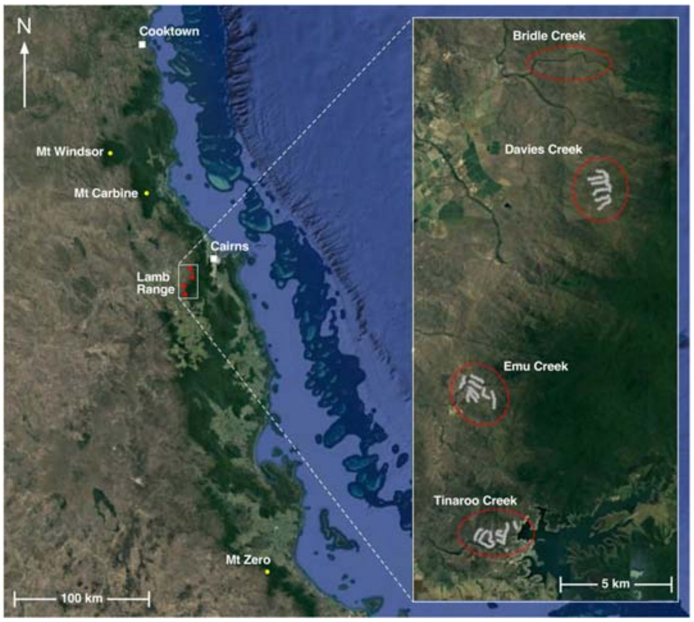

Figure 1.1. Location of *Bettongia tropica* peripheral populations (Mt. Windsor, Mt. Carbine and Mt. Zero) shown by yellow dots and the core Lamb Range sub-populations (Bridle Creek, Davies Creek, Emu Creek and Tinaroo Creek) indicated by red dots. Inset shows the study sites at Davies Creek, Emu Creek and Tinaroo Creek (red circles), with the white lines showing the locations of cage trap transects within the study sites. The location of Bridle Creek is also shown (Google Earth®, adapted from Vernes and Pope (2006)).

The presence of *B. tropica* may be vital for maintaining ecosystem functioning within *Eucalyptus* woodlands on the Lamb Range. *Bettongia tropica* is a specialist disperser of truffles in north-eastern Queensland, Australia (Reddell et al. 1997; Nuske 2017). Truffles are important for forest health, as they form a symbiotic relationship with certain plant species, usually woody trees (Sharma 2017). This relationship can increase plant growth and survival (Fellbaum et al. 2011), improve seedling establishment and/or influence plant community dynamics (Nara 2006). Dispersing truffle spores may also contribute to maintaining fungal diversity within the landscape (Danks 2012; Fleming et al. 2014a), with fungi being important for nutrient recycling and other ecosystem functions (Hodge & Fitter 2010). *Bettongia tropica* potentially assist with nutrient cycling by bioturbation when digging for truffles and the shoot base of cockatoo grass (Vernes & Dunn 2009; Fleming et al. 2014a). Truffle dispersal and nutrient cycling are important ecosystem services, with *B. tropica* being classified as a keystone species within *Eucalyptus* woodlands (Nuske 2017; Nuske et al. 2017).

Given their endangered status, a recovery plan was established in 2000 to conserve *B. tropica* (Dennis 2001). An updated but unpublished recovery plan was then developed by the Department of Environment and Heritage Protection in 2012 (Burbidge et al. 2014). The overarching goal of both recovery plans is to conserve *B. tropica* by maintaining or expanding current wild populations and to establish new wild populations (Dennis 2001; Burbidge et al. 2014). The species will be considered stable when *B. tropica* populations occur within five areas containing suitable habitat and populations are stable over the long term.

My project was aligned with addressing the first objective of the northern bettong recovery plan, which is to manage the habitat of known populations of *B. tropica* (Dennis 2001; Burbidge et al. 2014). To achieve this, the recovery plan lists four sub-objectives, which involve:
1) mapping the distribution, population density and habitat requirements of *B. tropica*,
2) obtaining a memorandum of understanding between management agencies to conserve *B. tropica* habitat,
3) developing appropriate fire management regimes, and
4) understanding population trends within the Lamb Range and peripheral populations.

1.1 Thesis aims and structure

The overarching aims of my project were to determine the (1) population trends (fourth sub-objective of the recovery plan) and (2) habitat requirements of *B. tropica* (first sub-objective), with the overall goal of improving the conservation management of the species. This work was divided into four aims corresponding to each chapter.

1.1.1 Chapter 2: Influence of potential threats to population viability

I aimed to determine the impacts of potential future threats on the population viability of *B. tropica*. It is often difficult to establish the cause of population declines, as multiple threats may simultaneously affect populations (Evans et al. 2011). *Bettongia tropica* populations are potentially under pressure from various threats, including invasive predators, inappropriate fire regimes and habitat alteration (Burbidge & Woinarski 2016). Climate change could also substantially impact upon the species' viability in the future. Both increased drought frequency and/or intensity and range expansions of invasive predators (cats and foxes) further into *B. tropica* habitat could impact upon *B. tropica* (Burbidge & Woinarski 2016). Predation is a leading cause of mammal declines and it was hypothesised that predation by invasive species, in particular feral cats, would have the greatest impact upon the population viability of *B. tropica*.

Population viability analysis (PVA) was used to model how *B. tropica* populations respond to these potential future threats, including evaluating the extent of possible population declines (Heinsohn et al. 2015). PVA uses simulation models to make projections of how threats will impact populations and can highlight the threat/s most likely to have the greatest impact upon population viability (Ferguson & Ponciano 2014). The model is particularly useful for species that are difficult to monitor, as it provides a starting point for managing a population (Heinsohn et al. 2015). Managers can devise appropriate preemptive conservation strategies to minimise the likely impacts of threats (Norris & Harper 2003). Proactive management is crucial for conserving species that are already threatened and vulnerable to extinction (Norris & Harper 2003). Following desktop PVA modelling, which was used to determine the factors that could result in population declines, I assessed the current population trends by undertaking fieldwork at each site.

1.1.2 Chapter 3: Population trends

The aim for Chapter 3 was to determine the population density and to assess the population trends of *B. tropica* within the three main sub-populations (Davies Creek, Emu Creek and Tinaroo Creek) on the Lamb Range. To effectively manage populations, it is crucial to examine population trends in the field (Wayne et al. 2006; Rinehart et al. 2014). Observed population declines similar to those modelled in Chapter 2 would warrant further investigation into the cause (Kuker & Barrett-Lennard 2010) and identified threats would need to be managed to avoid or minimise further declines (Woinarski et al. 2010). For example, regular monitoring of the brush-tailed bettongs (*Bettongia penicillata*) populations enabled management to determine the likely causes of the species multiple population declines, with management actions then undertaken to reduce the threats (Thompson et al. 2015). Brush-tailed bettongs rapidly declined in the 1970s due to predation by foxes, with fox baiting programs then undertaken and the population of brush-tailed bettongs subsequently recovering to around 200,000 individuals (Marlow et al. 2015; Thompson et al. 2015). The population continued to be monitored, with a rapid decline again occurring between 1999 and 2006 (Marlow et al. 2015; Thompson et al. 2015). Monitoring the trend of decline showed that predation by feral cats was the most likely cause, prompting translocations of brush-tailed bettongs into cat and fox controlled areas (de Tores and Marlow 2012). There is also increasing evidence to suggest disease also was a critical factor in the decline (Marlow et al. 2015; Thompson et al. 2015).

Assessing population trends is especially important for species such as *B. tropica* that are rare, already threatened (Brook et al. 2000) or occur within a small geographic range (Williams et al. 2009). These species often have small population sizes and are particularly vulnerable to threatening processes and stochastic population fluctuations (Williams et al. 2009; Furlan et al. 2012). Even small changes have the potential to result in vulnerable populations declining to extinction (Hoffmann & Parsons 1997; Duncan et al. 2012).

For *B. tropica*, the population density had been previously estimated within the core population on the Lamb Range. Vernes and Pope (2006) estimated the population density at the four sub-populations on the Lamb Range between November 1994 and May 1996, although only one sub-population (Davies Creek) was assessed and monitored thoroughly. A decline within the core population would likely be dire for the species' survival, given the already restricted distribution and few extant populations (Burbidge & Woinarski 2016).

A re-assessment of the population was thus required to determine the current population trends of *B. tropica*. Cage trapping was conducted over nine trapping sessions between November 2014 and November 2016 and all *B. tropica* were microchipped to distinguish individuals. Pollock's robust design multi-season mark-recapture analysis was conducted to estimate the population abundance at each trapping session, which enabled population trends over the two years to be assessed. Drier habitats support fewer food resources for *B. tropica* and it was predicted that the driest site would support the lowest population density and therefore be more vulnerable to decline.

1.1.3 Chapter 4: Fine-scale movement patterns

The third aim of my study was to assess the seasonal movement patterns, including home ranges and social interactions, of *B. tropica* within the three main sub-populations. Gaillard et al. (2010) proposed that the most limiting factors at broad- and fine-scales should theoretically dictate spatial ecology and habitat selection. An understanding of a species' movement patterns can provide an insight into the habitat resources that are crucial for the species (McLoughlin et al. 2000; Powell 2012) and the fine-scale distribution of these resources (Allen & Singh 2016). For example, Finlayson and Moseby (2004) radio-tracked female burrowing bettongs (*Bettongia lesueur*) and used the location fixes to determine the habitat that individuals preferred. Movement patterns can vary between sub-populations due to various factors, including differences in resource distribution, habitat quality, competition or predation between locations (Holyoak et al. 2008; Nathan et al. 2008; Davies et al. 2013). It is thus important to assess a species' home range and movement patterns across multiple locations (Davies et al. 2013). Both truffles and cockatoo grass (main food resources) are sparsely distributed and it was predicted that *B. tropica* would require large home ranges and travel large distances each night to source sufficient food.

Prior to this study there were limited data on the seasonal movement patterns of individuals of *B. tropica*. Vernes and Pope (2001) radio-tracked 23 *B. tropica* individuals at Davies Creek and estimated broad-scale movement patterns and home range size based on fixes recorded every two hours during the night. Due to *B. tropica* travelling relatively large distances each hour (Vernes & Pope 2001), the specific location where *B. tropica* foraged could not be assessed using that methodology. The fine-scale distribution of resources and the specific habitat requirements of *B. tropica* also could not be investigated. In contrast, I determined the fine-scale movement patterns by GPS tracking 41 bettongs. I created maps, determined the size of home ranges and examined them for potential social interactions. I also determined the movement trajectory and speed that *B. tropica* travelled to understand how bettongs move throughout their habitat to access resources. It was predicted that *B. tropica* within populations would have large home ranges and that the home ranges of individuals would substantially overlap with others, due to food resources (truffles and cockatoo grass) being sparsely distributed.

1.1.4 Chapter 5: Fine-scale habitat requirements

The final aim of this study was to identify the fine-scale habitat requirements of *B. tropica* at their nesting and foraging areas and the presence of their potential predators and competitors. The interaction between animals and their environment results in non-random habitat use (Börger et al. 2008; Signer et al. 2015), with habitat selection varying between species due to differences in niche and habitat requirements (Kingston & Morris 2000; Luza et al. 2016). Species often concentrate a larger proportion of their movements within certain areas (core areas), with these areas usually containing a high density of important resources (Asensio et al. 2012; Feldhamer et al. 2015). Vegetation surveys can be targeted to core areas, enabling the important habitat requirements of species to be determined (Bingham & Noon 1997). Management can then focus on improving habitat quality to increase the presence of important resources.

For *B. tropica*, the species broad-scale habitat requirements are known. *Bettongia tropica* attain higher density within *Eucalyptus* woodlands with a grassy understorey (3.7 to 7.5 bettongs/km^2) compared to drier or wetter habitats, such as *Allocasuarina* forest (1.5 bettongs/km^2) (Vernes & Pope 2006). *Eucalyptus* woodland close to rainforest receives sufficient rainfall to support truffles almost all year round and the canopy is open enough for cockatoo grass to grow in the understorey (Abell et al. 2006). In contrast, wetter habitats (rainforest to *Allocasuarina*) largely shade out grasses (Harrington & Sanderson 1994) and rainforest trees are not appropriate host trees for ectomycorrhizal truffles (Smith et al. 2013b).

Prior to my study, there was limited information on the fine-scale habitat preferences of *B. tropica* and it was unknown whether preferences differed across the landscape. Vernes and Pope (2001) radio-tracked *B. tropica* to their nests and determined the materials used for nest construction at one sub-population (Davies Creek). However, the fine-scale habitat preferences at nesting areas were not surveyed. Additionally, there was minimal information of habitat requirements when foraging. Vernes (2003) surveyed the habitat at cage trap locations and inferred the habitat preferences of *B. tropica* whilst foraging based on the number of captures at each cage trap. *Bettongia tropica* were caught more frequently within cages placed along open ridgelines compared to denser mid-slopes and gullies (Vernes 2003). However, this result may have been biased by non-random trap placement (Cusack et al. 2015; Hotfmeester et al. 2016). Habitat requirements of *B. tropica* thus needed to be re-assessed without bias and with habitat surveys conducted at multiple sub-populations. This should provide a more comprehensive insight into the habitat resources that are important for the species across the landscape (de Knegta et al. 2007; Hebblewhite & Haydon 2010; Allen & Singh 2016). To determine the microhabitat requirements of *B. tropica*, I analysed the movement patterns of *B. tropica* (obtained in Chapter 4) to determine where bettongs nested and foraged. I then conducted vegetation surveys at five nesting and foraging areas for six individuals (three males and three females) at each study site. I also radio-tracked collared *B. tropica* to their nests and recorded the nesting material that each individual had used. It was expected that nesting and foraging areas would comprise of variables that maximised camouflage from predators.

Additionally, the presence of potential competitors and predators had not been ascertained across the populations on the Lamb Range. Vernes (2000) undertook the only previous research into predator species on the Lamb Range by analysing dingo scats for the presence of bettongs. The presence of other predator species had not been assessed. Prior to my study, no research had determined whether potential competitor species occupied the same area as *B. tropica*. I conducted 12,960 camera trap nights to detect the presence of predator and competitor species.

1.1.5 Chapter 6: Synthesis and management recommendations

In Chapter 6, I synthesised the results of chapters 2 to 5 and discussed the implications of the study regarding the ecology of *B. tropica* and how this new information can contribute to the management of *B. tropica* populations. My research provides baseline information on multiple aspects of *B. tropica* ecology across the Lamb Range. Recommendations from my research will enable managers to develop and improve management strategies to conserve *B. tropica*. I also outline how my research contributes to addressing the management actions listed in the *B. tropica* recovery plan and recommend future research priorities. Future studies can build upon this research to provide a greater insight into the distribution and movements of *B. tropica*, with spatial and temporal replication recommended to provide an insight into the trends of *B. tropica* across the species distribution and through time.

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Chapter 2: Influence of predation, drought and fire on the population viability of *Bettongia tropica*

2.1 Abstract

Context. Identification of key threats to endangered species is vital for devising effective management strategies but may be hindered when relevant data is limited. A population viability analysis (PVA) may overcome this problem by using simulation models to make projections of the future impacts of factors under various scenarios.

Aims. This chapter aimed to determine population viability of endangered northern bettongs (*Bettongia tropica*) in north-eastern Australia and investigate key threats to population resilience including increases in mortality rates and changes in fire and drought frequency.

Methods. Using population viability analysis (PVA) I modelled survival probability of *B. tropica* populations under likely scenarios including: 1) increased predation; 2) changes in drought and fire frequency predicted with anthropogenic climate change; and 3) synergistic effects of predation, fire, and drought.

Key results. Population viability models suggest that populations are highly vulnerable to increases in predation by feral cats, *Felis catus* (and potentially red fox, *Vulpes vulpes*, should they colonise the area), as juvenile mortality is the main age-class driving population viability. If *B. tropica* become more vulnerable to predators during post-fire vegetation recovery, more frequent fires could exacerbate effects of low-level cat predation. In contrast, populations were predicted to be resilient to the greater frequency of droughts expected with climate change, with high probabilities of extinctions only predicted under the unprecedented and unlikely scenario of 4 drought years in 10. However, since drought and fire are interlinked, the impacts of predation could be more severe with climate change should predation and fire interact to increase *B. tropica* mortality risk.

Conclusions. Like other Potoroids, *B. tropica* appear highly vulnerable to predation by introduced mammalian predators such as feral cats.

Implications. Managers need information allowing them to recognise scenarios when populations are most vulnerable to potential threats, such as drought, fire and predation. PVA modelling can assess scenarios and allow pro-active management based on predicted responses rather than requiring collection of extensive field data prior to management actions. My analysis suggests that assessing and controlling predator populations and thereby minimising predation, particularly of juveniles, should assist in maintaining stability of populations of the *B. tropica*.

2.2 Introduction

Widespread population declines of small mammals have occurred throughout Australia (Fisher et al. 2013). Predation by feral species, including foxes and cats, and habitat alteration through inappropriate fire regimes are the major factors contributing to the species declines (Fisher et al. 2003; Woinarski et al. 2011a; Fisher et al. 2013). Environmental changes may also severely threaten the survival of many vulnerable mammal species (Isaac 2009), particularly with increased frequency and intensity of extreme weather events (Hughes 2003). Predictions of drought frequency in north-eastern Australia have risen from 2 years in 10 (Kothavala 1999) to drought every two to four years (Quiggin 2010). Multiple threats may be operating on populations. Effectively reducing further declines depends on identifying and mitigating the main threatening process affecting a species (Evans et al. 2011). However, the rarity of threatened and endangered species makes it difficult to detect specific causes of declines and management decisions are often based on limited data. To ensure that the most appropriate decisions are made to conserve these species, such data must be applied effectively.

There are often insufficient replicate populations to accurately assess which conservation strategies maximise the probability of a population persisting (Coulson et al. 2001). Population viability analysis (PVA) is a simple method that can overcome this problem by estimating the probability of a population becoming extinct over a certain period of time (Coulson et al. 2001) using models of future life-history parameters, environmental events and identifiable population threats (Brook et al. 2000). Theoretical influences of ecological and life-history traits and threats on the viability of a population can also be predicted over time (Akcakaya & Sjogren-Gulve 2000). The risk of extinction, or of a population falling under a critical abundance level, can be assessed together with the relative importance of multiple potential threats to population growth (Ferguson & Ponciano 2014). PVAs have assisted in developing management strategies for various species (Lindenmayer & Possingham 1996; Heinsohn et al. 2004; Heinsohn et al. 2015). Additionally, PVAs may be used for guidance in prioritising the most effective strategy (Gerber & González-Suárez 2010) to minimise population declines before declines are irreversible (Wayne et al. 2006).

Small and endangered populations are particularly susceptible to altered population dynamics (Brook et al. 2000). In small populations it is unlikely that future rates of population change will remain similar to their current rate (Brook et al. 2000). This limits the accuracy of PVA to predict the future status of populations (Brook et al. 2000). However, PVA can still model the potential impacts of changes, including that of catastrophes or changes to vital rates (Coulson et al. 2001). Undertaking a PVA is only the first step in the process for assessing species' population trends. Field validation is later required to confirm whether the trends in the field follow the modelled trends (Wayne et al. 2006). *Bettongia tropica*, the northern bettong, provides an example of the use of PVA to supply information useful for conservation managers and alleviate the problems of limited data.

Bettongia tropica is restricted to dry sclerophyll forests on the western boundary of the Wet Tropics World Heritage rainforests (Vernes & Pope 2001) in north-eastern Australia (Burbidge & Woinarski 2016). Dietary requirements restrict *B. tropica* to these forests, as these habitats receive sufficient rainfall to support the preferred nutritious food source of truffles (fungal fruiting bodies) during the wet season, but are open enough for the dry season staple of the species, cockatoo grass (*Alloteropsis semialata*), to grow in the understorey (Abell et al. 2006). Due to their specialised diet, drought and changed fire regimes resulting in vegetation alteration (Hilbert et al. 2001; Bateman et al. 2012a), are likely to have a major impact on the population viability of *B. tropica*, as both reduce food abundance (Bateman et al. 2012a; Harrison & Congdon 2002; Short 1998).

Predation and competition may also threaten *B. tropica* populations. No known study has comprehensively assessed the influence of predation on *B. tropica*. However, other bettong species have suffered large population declines or local extinctions primarily due to predation, principally by feral cats (Short & Turner 1999; Priddel & Wheeler 2004; Bateman et al. 2011; Fancourt 2014). Therefore, predation is considered to be a major threat to *B. tropica*. Additionally, competition with rufous bettongs (*Aepyprymnus rufescens*) could possibly influence the population stability of *B. tropica*, particularly within drier areas (Bateman et al. 2012a). Rufous bettongs are adapted to a wider temperature and precipitation range and have colonised areas where *B. tropica* populations previously occurred (Bateman et al. 2012a).

These aforementioned threats, especially drought, changed fire regimes and predation, may have contributed to *B. tropica* disappearing from substantial areas of their former range (Maxwell et al. 1996; Pope et al. 2012), creating four disjunct populations: a core population on the Lamb Range (Vernes & Pope 2006), and three smaller, low-density populations (Laurance 1997; Dennis 2001; Bateman 2010). On the Lamb Range, four geographically close sub-populations occur at Bridle Creek, Davies Creek, Emu Creek and Tinaroo Creek (Pope et al. 2000), with greater densities in the southern sub-populations (Laurance 1997; Vernes & Pope 2006). However, current population size and viability of these populations was unknown (addressed in Chapter 3).

2.2.1 Aims

This analysis aimed to assess the population viability of *B. tropica* using pre-existing data (Vernes & Pope 2006) from four monitored sub-populations on the Lamb Range. Specifically, I aimed to assess how the viability of each sub-population was influenced by varying rates of juvenile, adult and dispersing sub-adult mortality, both with and without the potential synergistic effects of fire on *B. tropica* survivorship. I also aimed to model the response of each population to changes caused by drought, again with and without fire and predation effects.

2.3 Methods

2.3.1 Base model of bettong population viability

Data on life history characteristics, abundance and distribution of *B. tropica* were collated from mark-recapture studies undertaken between 1994 and 1997 (Appendix A) at Bridle Creek (16°58′S, 145°35′E), Davies Creek (17°01′S, 145°35′E), Emu Creek (17°06′S, 145°31′E) and Tinaroo Creek (17°10′S, 145°32′E) on the Lamb Range, in north-eastern Queensland, Australia. In particular, field data collected in 1994 on population density (Vernes & Pope 2006), adult fecundity and pouch young survivorship (Vernes & Pope 2002), population structure (Pope et al. 2000), mating system and local dispersal patterns (Pope et al. 2012) form the backbone of the model. Data from captive studies on reproduction in *B. tropica* by Johnson and Delean (2001) and on related potoroids were also used where required (Appendix A). I also modelled the frequency and severity of catastrophes (fire and drought) into the future, basing the scenarios on modelling by Quiggin (2010), Bateman (2010) and Bateman et al. (2011).

I predicted the probability of persistence of *B. tropica* populations over a 100-year period for each sub-population (Bridle Creek, Davies Creek, Emu Creek and Tinaroo Creek), as well as for the metapopulation. Modelling was undertaken using the PVA simulation computer program VORTEX (Version 10) and 1000 iterations of the model. Vortex determines a species probabilistic estimate of extinction (Beissinger et al. 2008) based on a random value from a specific distribution (Lacy 2000b). Simulations can then explore the sensitivity of population viability analysis to particular parameters. A base model of *B. tropica* populations was then developed from the parameter inputs determined from the literature (Appendix A). This enabled an evaluation of how changed population size and mortality rates influenced population viability. Genetic factors were not modelled as *B. tropica* populations have substantial genetic diversity (Pope et al. 2000), suggesting genetic factors are unlikely to be an important factor in their decline.

The base model assumed all dispersing individuals emigrated to other populations to the north or south (Appendix A). It was assumed that an equal percentage of individuals emigrated to the northern and southern populations from Davies and Emu Creek (the two populations within the centre of the metapopulation), whilst all dispersing individuals from Bridle Creek emigrated south to Davies Creek and those dispersing from Tinaroo Creek emigrated north to Emu Creek (Figure 1.1). However, it is possible that geographic or environmental features may result in the percentage of immigrating individuals being unevenly divided between northern or southern populations. The emigration rates to certain populations may potentially be an over or under-estimation.

2.3.2 Influence of declining population sizes on population viability

The influence of a decreased population size on population viability was also assessed over a 100-year period using 1000 iterations of the model. Using the same life history parameters as in the base model (Appendix A), the population size of each of the four sub-populations was constrained to be 25%, 50% and 75% lower than base model population estimates. Carrying capacity was also set at a lower limit to match the starting population size for each simulation.

2.3.3 Influence of increased mortality on population viability

Changes in juvenile mortality rates and the persistence of dispersing sub-adults were modelled using sensitivity analysis to determine how sensitive the model was to increasing mortality rates. It is noted that juvenile mortality is the component of the model for which the data is least robust. The analysis had three components; juvenile mortality (0-1 years), adult mortality (1+ years) and mortality of sub-adult dispersers. Juvenile mortality was allowed to increase from its approximate base value (45%) in 5% increments to a maximum of 85%, whilst adult and disperser mortality was increased from its base value (15%) in 5% increments to a maximum of 80%. Each component was modelled as a single factor that changed incrementally as the other two components were held constant.

2.3.4 Influence of cat predation on population viability

The base model was modified to create scenarios that simulated different levels of cat predation (low, moderate, and high) on bettong populations. Feral cats are known predators of small macropods and have been implicated in the decline of several populations (Fisher et al. 2013; Frank et al. 2014). Previous studies indicate that feral cats may pose a high to very high risk to *B. tropica* populations (Department of Environment 2015), despite feral cat populations currently being thought to be small on the Lamb Range (Harrison & Congdon 2002). A current assessment specifically on the impacts of feral cats within the Wet Tropics has not been undertaken. Cat predation rates of *B. tropica* were therefore estimated based on the impact of cats on other small mammal populations within Australia. Predation rates reported in the literature typically range from 40 to 60%; for example, Gibson et al. (1994) confirmed cats were responsible for 40 to 56% of mala (*Lagorchestes hirsutus*) mortality after reintroduction to the Tamami Desert, whilst Priddel and Wheeler (2004) reported 42% of reintroduced brush-tailed bettongs (*B. penicillata*) were killed by cats in western NSW. Additionally, Marlow et al. (2015) found that 65% of brush-tailed bettongs were killed by feral cats within two reserves in their Western Australia study site. Based on these and other studies (see Fisher et al 2015), 'high cat predation' was set as at 60%, and 'moderate cat predation' at 40% in the models (Table 2.1). Additionally, since low densities of cats should have less impact on bettongs, I created a 'low cat predation' scenario where cat predation was arbitrarily set at 20% (Table 2.1).

Table 2.1. Mortality rates of *Bettongia tropica* for different VORTEX models of low, medium and high cat predation, with and without the synergistic effects of fire, and the impact of fire.

Scenario	Cat predation	Severity factor of drought applied to adult survivorship	Juvenile mortality (%)	Adult mortality (%)	Survival of dispersers (%)
Base model	No cat predation, no fire effects on mortality	0.95	46.0	15.0	87.0
Scenario 1	Low cat predation (+20%), without fire effect	0.95	55.2	35.0	69.6
Scenario 2	Low cat predation (+20%), with fire effect	0.80	55.2	35.0	69.6
Scenario 3	Moderate cat predation (+40%), without fire effect	0.95	64.4	55.0	52.5
Scenario 4	Moderate cat predation (+40%), with fire effect	0.80	64.4	55.0	52.5
Scenario 5	High cat predation (+60%), without fire effect	0.95	73.6	75.0	34.8
Scenario 6	High cat predation (+60%), with fire effect	0.80	73.6	75.0	34.8

Dependent juveniles were linked to mothers in the models, so if a female bettong died, any dependent young (age 0-1) died with her. Predation rates were added to existing (base model) rates for adults (Table 2.1) (i.e. in the models, adult mortality is base+cat predation rate). Juvenile mortality rates were compounded to the existing mortality rates by 20, 40 and 60% (i.e. in the models, juvenile death is base+base*cat predation rate). This was intended to cover 1) any young in the pouch dying automatically if their mother was predated, and 2) some additional young also dying as either a sub-adult animal that was outside the pouch but still dependent on its mother, or still in the pouch but ejected by their mother as she escaped predation. Pouch ejection is a known contributor to pouch young mortality when mothers are stressed by predators (Morton 1990; Priddel & Wheeler 2004; Associate Professor Karl Vernes, personal observation), although the rate at which this occurs in the wild is unknown. It is acknowledged that the rate of pouch young and sub-adult deaths is unknown in real populations exposed to different levels of cat predation. However, it is reasonable to assume that the rate increases as cat predation increases.

Red foxes (*Vulpes vulpes*) are currently absent within the range of *B. tropica* (Harrison & Congdon 2002). However, foxes are likely to detrimentally affect *B. tropica* populations in the future if fox distribution expands into areas occupied by *B. tropica*. Other bettong species have suffered substantial declines or extinctions due to predation by foxes (Department of Sustainability, Environment, Population and Communities 1998; 2010). There is limited data on mortality and survival rates following fox incursion into areas occupied by bettongs. Therefore, the potential influence of foxes was not modelled separately.

2.3.5 Influence of fire on population viability

Previous studies have determined that predation post-fire, especially by foxes or cats, can be as high as 46% and cause large declines of bettong populations (Christensen 1980). There is limited data on predators on the Lamb Range, although one cat was captured on a camera trap at Tinaroo Creek (Chapter 5). If cats become a significant predator of *B. tropica* on the Lamb Range, it is reasonable to consider scenarios where predation and fire operate synergistically along the lines demonstrated by Christensen (1980). This would lead to increased mortality of bettongs following fire. Accordingly, the three cat predation scenarios each have two components: with and without the synergistic effect of fire (Table 2.1).

2.3.6 Influence of increased drought frequency on population viability

Drought in wet and dry sclerophyll forests has been classified in a number of ways. Bateman et al. (2011b) suggested that since >50 mm of rain was required for truffle fruiting, 14 days without this amount of rain constituted a drought. However, Abell et al. (2006) found that truffles occurred throughout the year at Davies Creek, despite 5 months of rainfall <50 mm and truffle abundance was largely influenced by rainfall in the previous one or two months. Expert opinion on climate and drought modelling (Professor Stephen Turton, pers. comm.) suggested that 60 days without rain (traces excepted) would constitute a dry period within the wetter sclerophyll habitat that is adjacent to the dry sclerophyll habitat of my study sites. The Bureau of Meteorology (2016) defines drought as a severe or serious deficiency in rainfall, where there are three or more consecutive months where rainfall is among the lowest 5% (severe) or 10% (serious) of historical totals. To account for high abundances of truffles only occurring when rainfall was above 50 mm, drought was defined as a three-month or longer period with less than 50 mm of rain. Drought was classified to have ceased when rainfall during the following three months was above 70% of historical records (Bureau of Meteorology (BOM) 2016).

The number of droughts was totalled for the last 10 years (2007 until 2016) using the weather station at Tinaroo Falls Dam ((BOM) 2016). This weather station is close to the wettest study site (Tinaroo Creek) and thus the rainfall data is the best-case scenario for all three sub-populations. Rainfall estimates from Walkamin weather station were used when estimates were unavailable from Tinaroo Falls Dam.

One drought, lasting 3 months, occurred within the 10 years. Drought frequencies were thus modelled between 10% (one in 10 years) to 50% (every other year) to determine how this impacted population abundance and population viability of *B. tropica* over a 100-year period. Drought was defined as a ‘catastrophe’ in the base model, with a strong negative effect on reproduction (impact = 0.66, as in drought years reproduction was 66% of the rate in non-drought years), but was modelled as having a relatively minor effect on persistence (impact = 0.9, as survival of bettongs was 90% of the rate in non-drought years). The impact factor for the models was based on the results of Priddel and Wheeler (2004). Priddel and Wheeler (2004) assessed the impact of a severe drought (<75 mm rain over 9 months) on reproduction and juvenile mortality of brush-tailed bettongs in mallee habitat in western New South Wales, Australia. Priddel and Wheeler (2004) found that during drought years, reproduction was 33% of the rate in non-drought years. The climate in western New South Wales is drier than on the Lamb Range and thus droughts in north-eastern Queensland are likely to be less severe and shorter in duration compared to those experienced in drier climates (Kirono et al. 2012). It is thus unlikely that *B. tropica* would experience as severe a drought as reported by Priddel and Wheeler (2004). I therefore reduced the impact of drought on reproduction by half that observed by Priddel and Wheeler (2004), from 0.33 (Priddel & Wheeler 2004) to 0.66. It is noted that *B. tropica* may be less resilient to greater variations in temperature and precipitation than species adapted to drier climates (Bateman et al. 2011). The models may thus somewhat underestimate the impact on the reproduction and survival bettongs. However, cockatoo grass (dry season food resource) may be able to persist and sustain *B. tropica* populations during dry periods (Johnson & McIlwee 1997). For the sensitivity analysis, drought was allowed to increase from its base value in 10% increments to 50%.

Because droughts and fire are usually correlated (Lucas et al. 2007), I increased the probability of fire occurring in a drought year. I modelled fire as having a 50% chance of occurring in a drought year, versus a 25% chance in non-drought years. I also modelled increasing drought combined with an increased incidence of fire with the Base Model, Scenario 1 (low cat predation, without fire effects) and Scenario 2 (low cat predation, with fire effects). This provided an assessment of the impact that increasing drought frequency might have on the population viability of *B. tropica* under low levels of cat predation. I did not model higher predation scenarios with increasing drought frequency because these scenarios already predicted rapid extinction of bettongs under current drought and fire frequencies.

2.4 Results

2.4.1 Base model of bettong population viability

The probability of persistence in the Base Model was 1 (based on the life-history parameters shown in Appendix A), with all four sub-populations fluctuating around carrying capacity and with population viability not declining over a 100-year period (Figure 2.1; Table 2.2). It is acknowledged that potential model inaccuracies resulting from gaps in knowledge could affect the conclusions.

Table 2.2. Population prognosis of *Bettongia tropica* in terms of population size and probability of extinction at the end of a 100 year-long simulation, under scenarios of low and high cat predation, with and without the synergistic effects of fire. Mean time to extinction from commencement of simulation is also shown.

Scenario	Population	Number Extant (± SD)	Probability of Extinction	Mean Time to Extinction ± SD (Years)
Base Model	Meta	1067 ± 73	0	–
	Bridle	104 ± 10	0	–
	Davies	226 ± 20	0	–
	Emu	302 ± 27	0	–
	Tinaroo	433 ± 37	0	–
Scenario 1 (Low Cat)	Meta	926 ± 96	0	–
	Bridle	91 ± 12	0	–
	Davies	208 ± 20	0	–
	Emu	275 ± 28	0	–
	Tinaroo	353 ± 61	0	–
Scenario 2 (Low Cat, with Fire Effect)	Meta	572 ± 225	0.003	91 ± 4
	Bridle	63 ± 25	0.002	84 ± 18
	Davies	158 ± 52	0.004	82 ±10
	Emu	189 ± 76	0.007	90 ± 6
	Tinaroo	163 ± 104	0.002	86 ± 3
Scenario 3 (Medium Cat)	Meta	0	1.0	24 ± 5
	Bridle	0	1.0	16 ± 4
	Davies	0	1.0	21 ± 5
	Emu	0	1.0	22 ± 5
	Tinaroo	0	1.0	20 ± 4
Scenario 4 (Medium Cat, with Fire Effect)	Meta	0	1.0	20 ± 4
	Bridle	0	1.0	13 ± 4
	Davies	0	1.0	17 ± 4
	Emu	0	1.0	18 ± 4
	Tinaroo	0	1.0	17 ± 4
Scenario 5 (High Cat)	Meta	0	1.0	9 ± 1
	Bridle	0	1.0	6 ± 1
	Davies	0	1.0	7 ± 2
	Emu	0	1.0	8 ± 2
	Tinaroo	0	1.0	8 ± 2
Scenario 6 (High Cat, with Fire Effect)	Meta	0	1.0	8 ± 1
	Bridle	0	1.0	6 ± 1
	Davies	0	1.0	7 ± 1
	Emu	0	1.0	7 ± 1
	Tinaroo	0	1.0	7 ± 1

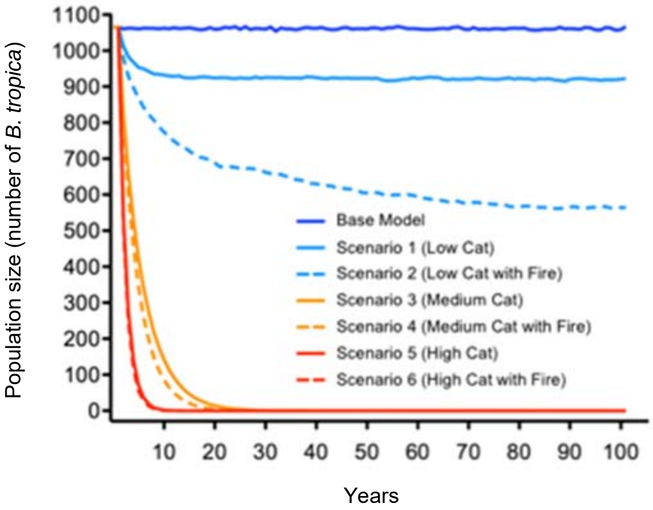

Figure 2.1. Changes in *Bettongia tropica* metapopulation size and probability of extinction under low, medium and high cat predation, with and without the synergistic effects of fire.

2.4.2 Influence of declining population sizes on population viability

Populations were resilient to reduced population sizes. All sub-populations remained viable when starting population sizes were 25% and 50% less than the base model population. Only the Bridle Creek sub-population had a slightly lower probability of persistence when the population size was reduced by 75%. Despite the lower starting population sizes, all populations returned to carrying capacity within 10 years when the carrying capacity was held at the level used in the base model.

2.4.3 Influence of increased mortality on population viability

When changes in juvenile, adult, and sub-adult disperser mortality rates were individually modelled using sensitivity analyses, changes in juvenile mortality had the greatest influence on population viability. Increases in juvenile mortality from 45% (base level) to 65% had minimal effect on population viability. However, the probability of extinction within 100 years began to increase above zero when juvenile mortality was 75% and was assured ($p = 1$) when juvenile mortality was 80% or greater (Figure 2.2a). Increases in adult mortality from 15% (base level) to 55% had no effect on the population viability, but from 60% to 65%, probability of extinction increased greatly, and beyond 65% extinction was assured (Figure 2.2b). Thus, adult mortality had to increase by >50% before extinction was assured, whereas juvenile mortality only had to increase by 35% above the base level before extinction was assured. The mortality rate of dispersing sub-adults did not influence any of the four sub-populations or the population size or risk of extinction of the metapopulation. Even when 100% of dispersing individuals died, all sub-populations remained viable and at their carrying capacity (over a 100-year projection). Additionally, the probability of extinction did not change if the mortality rate of dispersing individuals fluctuated.

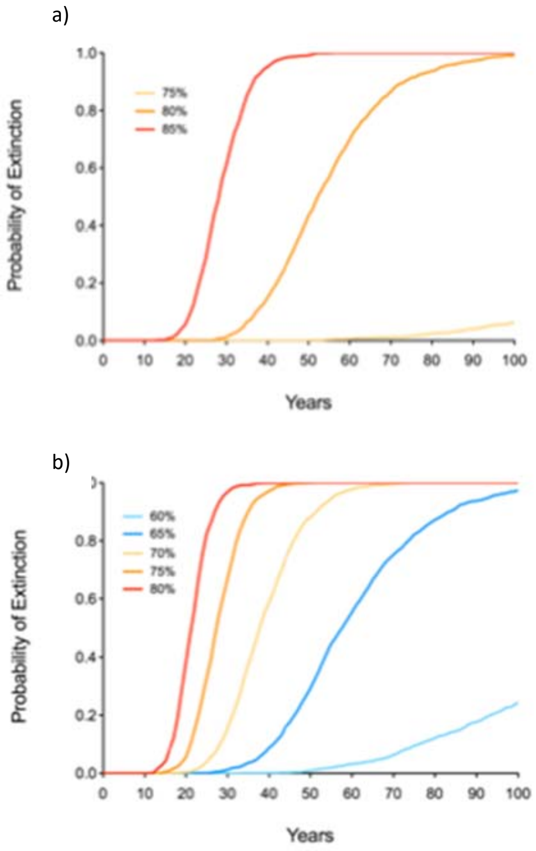

Figure 2.2. Simulation of sensitivity of the *Bettongia tropica* metapopulation to extinction from fluctuating (a) juvenile and (b) adult mortality. Only scenarios that had a probability of extinction >0 are included.

2.4.4 Influence of cat predation and fire effects on population viability

The bettong metapopulation persisted under scenarios of low cat predation and low cat predation with a fire effect (Table 2.2; Figure 2.1). However, moderate and high cat predation scenarios led to rapid extinction of the population, regardless of whether fire was operating in synergy with predation (Table 2.2; Figure 2.1). Bettong populations went extinct within about 10 years when cat predation was high (regardless of fire effects) and within about 25 years when cat predation was moderate (regardless of fire effects) (Table 2.2; Figure 2.3a, b, c and d).

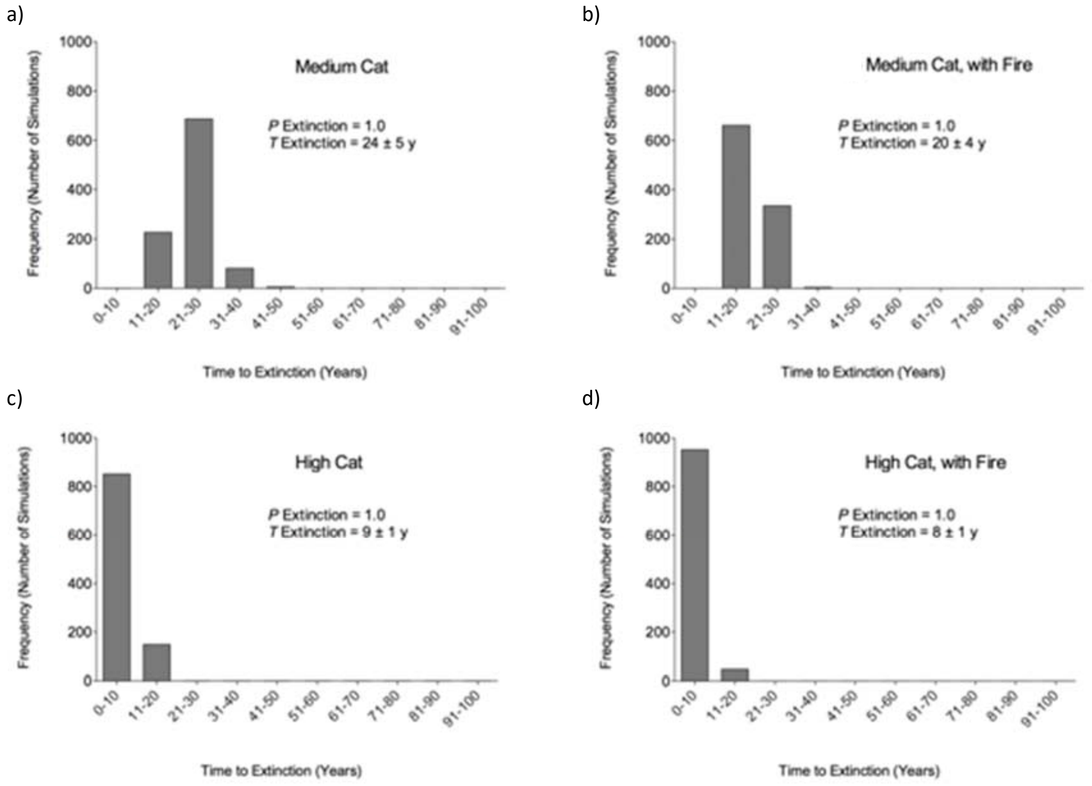

Figure 2.3. Simulation of changes in the probability of extinction with time, for *Bettongia tropica* on the Lamb Range under scenarios of medium and high cat predation, with and without the synergistic effects of fire. Only scenarios that had a probability of extinction >0.01 are shown.

2.4.5 Influence of increased drought frequency on population viability

Drought did not affect the viability of the *B. tropica* population (Figure 2.4a) until there was a 40% or greater chance of drought occurring (i.e. two droughts every 5 years). This frequency has not occurred (BOM 2014) nor is predicted to occur in north-eastern Queensland under current climate change models (Kirono et al. 2012). When there was low cat predation linked with fire and coupled with increasing drought, the probability of extinction increased post-fire (Figure 2.4b and c). Low cat predation combined with fire and a high likelihood of drought (30% or greater) resulted in a high probability of extinction (Figure 2.4c). Low cat predation under increasing drought scenarios had minimal influence on population viability when survivorship was independent of fire (i.e. low cat predation without a fire effect; Figure 2.4b). When cat predation was low and coupled with drought (but not fire), the population probability of extinction only increased above zero under the unlikely scenario of a 40% chance of drought in any one year (Figure 2.4c).

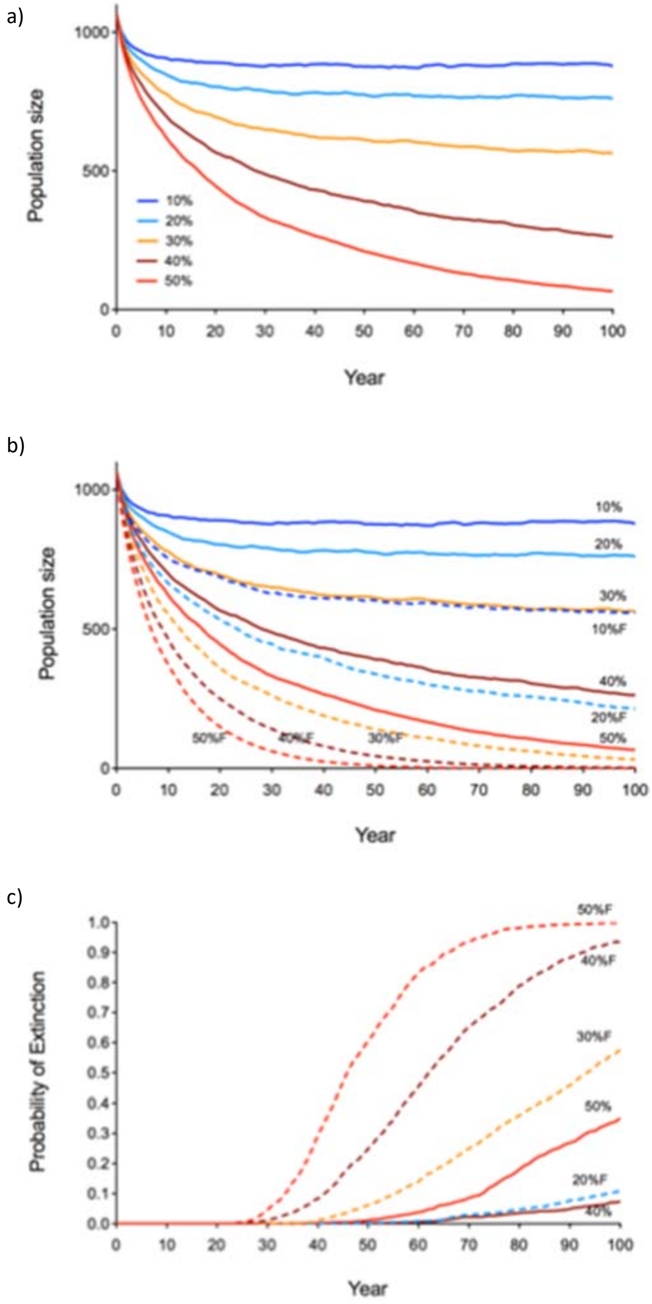

Figure 2.4. (a) Predicted metapopulation size of *Bettongia tropica* with increasing drought frequency; (b) predicted metapopulation size with increasing drought frequency under low rates (20%) of cat predation both with and without the effects of fire; and (c) probability of extinction with increasing drought frequency under low rates (20%) of cat predation both with and without the effects of fire. For (b) and (c) 'F' denotes a synergistic effect between predation and fire. Only scenarios that had a probability of extinction >0 are included.

2.5 Discussion

The PVA models assessed how varying rates of juvenile, adult and dispersing sub-adult mortality influenced the viability of *B. tropica* sub-populations. Models were constructed both with and without the potential synergistic effects of fire as well as drought. The models indicated populations were highly vulnerable to increases in cat predation, whilst fire and drought had less of an influence.

2.5.1 Influence of declining population sizes on population viability

Simulations suggested that without external influences, *B. tropica* populations should remain stable. Additionally, if population sizes severely declined, they would have a strong capacity to recover following cessation of the factor responsible for the initial decline. However, it is recognised that many species are unable to regain their original population size immediately after a catastrophe (Yarrow 2009). New, lower carrying capacities (Berg 2007) or small population sizes may be unable to withstand environmental or stochastic events and may fail to recover (Hoffmann & Parsons 1997) and subsequently decline towards extinction (Duncan et al. 2012).

2.5.2 Influence of increased mortality on population viability

Both adult and juvenile mortality affected population viability, with increases in either mortality rate causing substantial population declines or limiting population size. Unexpectedly, increased juvenile mortality was the greatest concern. Although juvenile mortality needed to almost double (from 45% to 80%) before the population declined to extinction, this was substantially less than the 4.5-fold increase in adult mortality (15% to 70%) that would cause a similar outcome. Wildlife populations that support substantially higher proportions of adults than young often decline over time as few new individuals become reproductive each year (Yarrow 2009). Declines can be exacerbated by threats that affect mortality rates and have long-lasting effects on populations, such as predation, disease, environmental change or catastrophes such as drought and large wildfires (Hughes 2003; Yarrow 2009).

Interestingly, mortality resulting from dispersal appears likely to have little impact on the metapopulation viability of *B. tropica*. Dispersing to more climatically suitable areas or foraging over larger areas during times of environmental stress may thus be expected to be integral to survival of the species (Harris & Leitner 2004). Threatening factors, including predation and environmental stressors (drought with fire), appeared to impact *B. tropica* population viability and thus *B. tropica* may need to disperse to more suitable areas when under environmental stress. *Bettongia tropica* displays high site fidelity (Vernes & Pope 2001), with limited dispersal from their home range (Pope et al. 2000) and only 20% of males dispersing (Pope et al. 2012). This may impede their ability to move to more climatically suitable areas or lengthen the time taken to do so (Harris & Leitner 2004).

Predation by feral species, habitat changes or environmental events, including severe drought and fire, can increase mortality rates of bettong species and cause population declines (Short & Turner 1999; Priddle & Wheeler 2004; Yeatman & Groom 2012; Fancourt 2014). Modelling indicates that increased mortality rates due to predation could impact severely upon the viability of *B. tropica* populations. Modelling also suggests that under low cat predation (with and without fire), bettong populations could remain viable over 100 years but stabilise at a lower population size. However, under moderate and high predation rates, the population will probably decline drastically to extinction.

Predation has been implicated as the major cause of population declines in many other small mammal species across Australia (Risbey et al. 2000; Woinarski et al. 2010). Smaller species of macropods are usually largely regulated by predation, whilst larger species are regulated by the effect of food supply on juvenile mortality or fecundity (Sinclair 1996). Limited research has been conducted on populations of potential predators of *B. tropica* and thus the impact of predators on *B. tropica* populations is currently unknown. Other bettong populations have proven vulnerable to predation by cats and foxes, with predation rapidly increasing mortality rates, reducing reproductive success and triggering population declines of several species (Short & Turner 1999; Short & Turner 2000; Priddel & Wheeler 2004; Fancourt 2014). For example, a population of Tasmanian bettongs (*Bettongia gaimardi*) declined to extinction within six months of at least three feral cats colonising the area (Fancourt 2014). Additionally, Short and Turner (2000) determined that feral cats had a disproportionate impact on juvenile burrowing bettongs (*Bettongia lesueur*), with little or no recruitment during years when feral cats occupied habitat in Western Australia.

Due to the severe impact of invasive predators, it is thought unlikely that bettongs could survive for any length of time when density is >1 cat/km^2 (Short & Turner 2000) or when a few aggressive cats occupy an area (Fancourt 2014). If invasive predators on the Lamb Range were to increase to medium or high levels, modelling indicates that the metapopulation of *B. tropica* is very likely to become extinct. Determining the factors that could enable predator populations to increase from low levels is thus of great importance for the conservation of *B. tropica* populations.

2.5.3 Influence of fire on population viability

Reduced cover from fire coupled with cat predation, has been proposed as a contributor to the recent declines in mammals more broadly across northern Australia (Fisher et al. 2014). High intensity fire usually results in widespread loss of vegetation (Williams et al. 1999) and the habitat being less suitable until vegetation regenerates (Monany & Fox 2000). Vegetation loss is likely to increase the risk of predation for bettongs because bettongs primarily nest in vegetation both for protection from predators and for shelter (Taylor 1993b; Vernes & Pope 2001). Increased predation rates following high intensity fires have substantially impacted other bettong populations. For example, Christensen

(1980) showed that wildfire within his Western Australian study site profoundly affected the survivorship of brush-tailed bettongs. Prior to a fire, bettongs could persist at the site despite predation (principally by foxes), but immediately after fire, predation rates by foxes, cats, and native quolls (*Dasyurus geoffroyi*) increased greatly (Christensen 1980). As a consequence, 46% of 24 radio-collared animals succumbed to predation, mostly within the six weeks following the burn (Christensen 1980). In areas of high wildfire frequency, nesting sites that withstand fire, such as those located amongst boulders, may become crucial resources (Vernes & Pope 2001). Fire-resistant nesting sites may be particularly important as fire frequency and intensity is expected to increase under changed climatic conditions (Hughes 2003; Brook et al. 2008).

However, in my models, the population size of *B. tropica* declined after fire, due to an increase in predation rates resulting from vegetation loss. This was even when predator populations were low. Interestingly, population viability was not affected, with the population still occurring after 100 years, but at a lower population size. These model findings are supported by evidence from experimental fires conducted at Davies Creek by Vernes (2000), when much of the ground-layer vegetation was removed. In that experiment, none of the 21 radio-collared bettongs died during the post-fire vegetation recovery phase. Vernes (2000) attributed this to few cats and no foxes being present at the site, and the main predator being the native dingo (*Canis familaris*), which preys infrequently on bettongs. Unexpectedly, when moderate and high levels of cat predation, in combination with fire, were modelled, fire effects were relatively unimportant. This was because predation pressure alone was already too great for long-term population viability.

2.5.4 Influence of increased drought frequency on population viability

It was expected that *B. tropica* populations would become less viable after longer periods of drought conditions. Drought decreased population viability, although current climate change models do not predict that droughts will occur at the frequency required to cause severe effects (Kirono et al. 2012). However, when low cat predation and fire were combined with the effects of drought, the probability of extinction increased. Drought may also impact upon *B. tropica* populations by reducing the time truffles are available (Bateman et al. 2012a), resulting in a longer reliance on less nutritious cockatoo grass (Johnson & McIlwee 1997). Additionally, other environmental or climate changes may also impact upon *B. tropica* populations. Environmental and climate changes are predicted to result in native specialist and endemic species suffering range and population contractions, whilst the distribution or density of invasive predatory species may increase (Didham et al. 2007; Brook et al. 2008; Isaac 2009). Future changes may also exacerbate threatening processes (Didham et al. 2007). The influence of other potential environmental or climate changes could not be modelled based on the available data. Incorporating the influence of other environmental factors would increase the accuracy of models and is an avenue for further research.

2.6 Management implications

Population viability analysis provides an important tool for management, by providing information on how viability is influenced by changes in population size and mortality rates. Modelling suggests predation could be the major driver of population decline of *B. tropica*. Field verification is still required to confirm these results (Wayne et al. 2006). The results from the PVA provide a starting point for further research to be undertaken.

It is proposed that management actions of top conservation priority include:
1) assessing whether the population has declined since previous studies were conducted by Vernes and Pope (2006),
2) determining the density of predator populations, with a focus on the core habitat,
3) measuring the mortality rates, especially of juvenile and sub-adult animals, and the cause of mortality, and
4) implementing control measures (e.g. predator control) to minimise mortality, especially of juveniles.
These actions have the potential to increase viability and minimise, stabilise or even reverse potential population declines of the endangered *B. tropica*.

The modelled declines of *B. tropica* populations are consistent with population declines of other mammals throughout Australia (Risbey et al. 2000; Woinarski et al. 2010). However, most previous studies have not specifically identified the age class most responsible in driving the population decline. By identifying juvenile mortality as the main factor driving population viability, conservation managers can focus on minimising predation to this age class. This study suggests that increases in juvenile mortality, resulting from predation, should be investigated as being a potential cause of substantial declines for other small Australian mammals. Models with varying mortality rates provide an indication of the severity of declines that could occur on the ground. Managers can then implement measures to minimise mortality and population declines.

Between 2000 and 2009, inconsistent monitoring was conducted at Davies Creek, with sampling conducted along different transect lines (with cages closed if there were infrequent captures), at different times of year and sampling did not occur during some years (Parks and Wildlife 2009, unpublished data). Based on the cage trapping records, there appeared to be a decline in the number of captures of *B. tropica* (Figure 2.5). Due to this potential decline, a re-assessment of the population needed to be undertaken using consistent monitoring. I therefore assessed the current population status of *B. tropica*, which is presented in the following chapter.

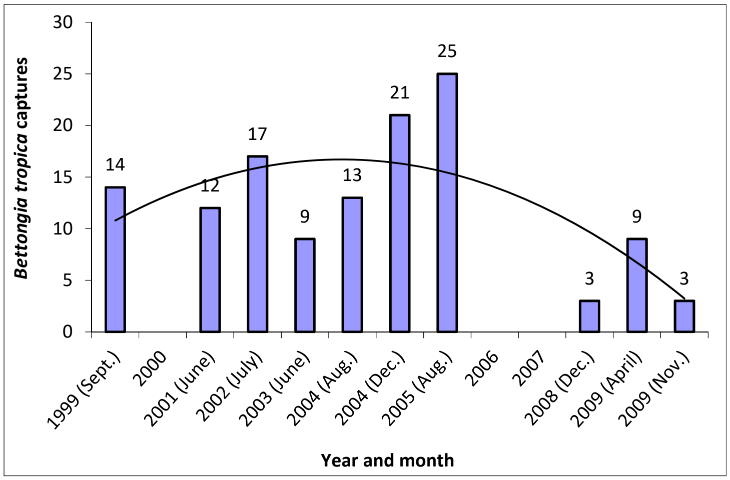

Figure 2.5. Captures (and the trend line of captures) of *Bettongia tropica* between 1999 and 2009 at Davies Creek. (Source: Queensland Parks and Wildlife 2009, unpublished data).

Chapter 3: Population trends and life-history traits of *Bettongia tropica*

3.1 Abstract

Context. A decline of a keystone species is likely to substantially impact upon ecosystem functioning and may threaten the population viability of other species dependent upon the ecosystem. It is therefore crucial to determine the population trends of keystone species and to understand the factors that influence the population trends, including seasonal and spatial variations. *Bettongia tropica* is a keystone species within *Eucalyptus* woodlands and ensuring the species' population is stable is important for maintaining the health of this ecosystem.

Aim. This chapter aimed to assess the influence of study site (spatial differences) and season (wet and dry) on population density, fitness (including survival rates, body condition and proportion of females with dependent young) and trap success of the northern bettong (*Bettongia tropica*) within the species' three main sub-populations on the Lamb Range, far north Queensland. I also compared new density estimates (2014 to 2016) to those obtained 20 years earlier (1994-1996).

Method. Nine four-night cage-trapping sessions were conducted every two to three months between November 2014 and 2016. Fifty-three cage traps were deployed each session. Trapped *B. tropica* were microchipped to distinguish individuals and morphometrics taken upon each capture. The population density and survival probabilities of *B. tropica* at each sub-population were estimated using Pollock's robust design multi-season mark-recapture analysis based on the presence/absence of *B. tropica* individuals during each trapping session. Trap success, body condition and the proportion of females with dependent young were calculated.

Key results. Across the Lamb Range, population density estimates varied between 5.90 and 12.82 bettongs/km^2 and appeared stable compared with estimates from 20 years earlier. At Davies Creek, Emu Creek and Tinaroo Creek, population density averaged 7.17 bettongs/km^2, 8.82 bettongs/km^2 and 13.00 bettongs/km^2 respectively. Density estimates at Tinaroo Creek were substantially higher than the other sites, likely due to higher rainfall, which presumably increased the abundance of food resources. During the wet season, trap success was lower than during the dry season, whilst population density was similar between seasons. Body condition, survival rates of adults (>80%) and the number of females with young (>70%) were similar across all sub-populations and seasons.

Management implications. A stable *B. tropica* population indicates that fire management conducted on the Lamb Range has been successful in maintaining suitable habitat for *B. tropica*. Population density estimates varied between trapping sessions, whilst trap success estimates fluctuated seasonally. Future monitoring surveys need to be devised to minimise seasonal bias to ensure long-term population trends are accurately assessed. Consistent and regular monitoring is required for early detection of potential future declines.

3.2 Introduction

With the decline of native species worldwide, it is increasingly important to develop effective and efficient conservation strategies (Rands et al. 2010). Conservation management strategies have often focused on either single-species conservation (conserving one species) or ecosystem management (Simberloff 1998; Lindenmayer et al. 2007). Ecosystem management focuses on improving the health of the ecosystem, with the assumption that a healthy ecosystem will conserve species within the ecosystem (Simberloff 1998). However, both management strategies can pose problems. Management actions designed to benefit a single species may detrimentally impact other native species (Committee on Scientific Issues in the Endangered Species Act 1995; Lindenmayer et al. 2007). Ecosystem management tends to focus on processes, such as nutrient cycling, and thus could allow the loss of species that do not substantially impact important processes (Simberloff 1998) or potentially overlook or undervalue specialists or wide-ranging species (Lindenmayer et al. 2007). Additionally, the goals of ecosystem management are often variously defined (Simberloff 1998) and may lack specific conservation goals (Lindenmayer et al. 2007).

Simberloff (1998) proposed the conservation of keystone species as a strategy for combining beneficial features of both single-species and ecosystem management. Keystone species (Paine 1969) are species that have a disproportionate impact on the ecosystem in which they live and whose activities impact upon the well-being of many other species within the ecosystem (Power et al. 1996). Keystone species undertake important functions such as fungal dispersal (Vernes & Dunn 2009), seed dispersal (Vander Wall et al. 2005) and/or bioturbation (Fleming et al. 2014a), and the loss of these species may have severe impacts on the ecosystem function and community structure (Sinclair 2003; O'Connor & Crowe 2005). By focusing on keystone species, managers only need to devise specific conservation goals for one species. The conservation of this species should potentially improve the overall health of the ecosystem and thus achieve the goal of ecosystem management (Lindenmayer et al. 2007; Simberloff 1998).

The northern bettong, *Bettongia tropica*, is a keystone species within wet *Eucalyptus* woodlands, consuming and dispersing more truffle species than other small mammals within the ecosystem (Nuske et al. 2017). Truffle diversity can be important for shaping vegetation community composition (Nara 2006) and maintaining ecosystem functioning (Johnson et al. 2012). Because *B. tropica* provides these important dispersal services, changes in *B. tropica* populations are likely to affect the ecosystem (Davic 2003). Understanding the population trends of *B. tropica* may provide an insight into ecosystem health.

Vernes and Pope (2006) estimated population density of *B. tropica* for the four sub-populations on the Lamb Range between 1994 and 1996. The population density was estimated as 1.0-3.5 *B. tropica*/km^2

at the Bridle Creek sub-population, 1.3-7.5 *B. tropica*/km^2 at Davies Creek, 7-10 *B. tropica*/km^2 at Emu Creek and 6.5-14.5 *B. tropica*/km^2 at Tinaroo Creek (Vernes & Pope 2006). Extensive cage trapping (4,267 trap nights) occurred at Davies Creek to calculate the population density (Vernes & Pope 2006). Trap nights is the trapping effort (number of traps by number of trapping nights) (Widmer et al. 2017). Only limited sampling occurred at the other sub-populations (125, 130 and 334 trap nights at Bridle Creek, Emu Creek and Tinaroo Creek respectively) (Vernes & Pope 2006). Few trap nights potentially limits the accuracy of population estimates (Kowalewski et al. 2015). A comprehensive assessment of the density of *B. tropica* within its multiple sub-populations was thus required. Ascertaining the current population density will enable comparisons that assess population trends and stability.

When managing populations, it is also important to assess the factors that influence population dynamics, including fitness measures (McCleery et al. 2013) such as body condition, and survival and reproductive rates (Ballesteros et al. 2013). Changes in food abundance between sites or seasons can also affect the fitness of species (Wirminghaus & Perrin 1993; Murray 2002; Korpimäki et al. 2004; Rocha et al. 2017). A change in fitness can ultimately influence population density (Hanya & Chapman 2013; Prevedello et al. 2013). For *B. tropica*, the effect of seasonality on population estimates, fitness and trap success had not previously been assessed across all populations.

Trap success is often used to indicate population density (e.g. Woinarski et al. 2011b; Fancourt et al. 2013; Wayne et al. 2017) and is an important measure to assess. Trap success is the number of animal captures relative to trapping effort (Widmer et al. 2017) and can vary seasonally (Cunningham et al. 2005). However, short-term seasonal fluctuations do not necessarily reflect the long-term trends in population abundance or density (de Andreazzi et al. 2011; Rocha et al. 2017). It is thus important to understand how seasonal variations can influence trap success estimates (Plumptre 2000; Lee & Bond 2016; Proença et al. 2016).

3.2.1 Aims

In this chapter I estimated population density, dynamics and trap success of *B. tropica* at three sites within the Lamb Range, aiming to assess:

1) population density and trap success between sites, between wet and dry seasons and between time periods (1994-1996 vs. 2014-2016),
2) survival between sites and between seasons,
3) influence of site, season and gender on body condition, and
4) influence of site and season on proportion of females with young.

Truffles occur at higher abundance in wet compared to dry areas (Abell et al. 2006). I expected that the population density, trap success, survival rates, body condition and numbers of females with young would be higher during the wet season and at the wettest site. Based on the decline in trap success observed from 1999 to 2009 (see Figure 2.5), it was predicted that the population density would have declined between the two time periods.

3.3 Methods

3.3.1 Study sites

This study was conducted in the three main *B. tropica* sub-populations (referred to as sites) within the Lamb Range (Figure 1.1): Davies Creek (17º01'S, 145º35'E, altitude 670 m above sea level (a.s.l.)), Emu Creek (17º06'S, 145º31'E, altitude 670 m a.s.l.) and Tinaroo Creek (17º09'S, 145º32'E, altitude 680 m a.s.l.). Davies Creek is the northernmost of these three sites, being approximately 10 km north of Emu Creek and 15 km north of Tinaroo Creek (Vernes & Pope 2006). Emu Creek occurs at the drier limits of the species' range and has the driest habitat type (Johnson & McIlwee 1997; Bateman et al. 2012b), whilst Tinaroo Creek is the wettest site and Davies Creek is an intermediate between Tinaroo Creek and Emu Creek (Johnson & McIlwee 1997). All sites have a similar geology, with predominantly granitic bedrock containing minor outcrops of hornfelsed meta-sedimentary rocks (schist and quartzite) (P. Whitehead, pers. comm.). Tinaroo Creek also contains a small (≈ 0.2 km^2) region of basalt (P. Whitehead, pers. comm.).

The habitat at each site comprised open *Eucalyptus* woodland with low to medium density of trees. The dominant tree species were *Eucalyptus crebra* and *E. citriodora*, *Corymbia dorlesomona*/*intermedia*, and *Acacia flavescens* (Wet Tropics Management Authority 2015). Plate 3.1 shows the habitat at each study site. The shrub layer across all sites included *Grevillea glauca, Acacia flavescens, Allocasuarina littoralis* and *Hakea macrocarpa*, whilst the understorey was dominated by kangaroo grass (*Themeda triandra*) (Vernes & Pope 2006), with cockatoo grass (*Alloteropsis semialata*) and grass trees (*Xanthorrhoea johnsonii*) also present (pers. obs.) (Plate 3.2). Blady grass (*Imperata cylindrica*) was common along gullies and creek beds (pers. obs.). There were slight differences in the broad-scale habitat between the sites. Emu Creek, the driest site, had more *E. citriodora* than the other sites, with stands of *Melaleuca* occurring on the lower slopes (pers. obs.) (Plate 3.3). The lower slopes of Emu Creek also had lower grass density than Davies Creek and Tinaroo Creek. At Tinaroo Creek, *Lantana camara* occurred in patches on the lower slopes and there were areas where *Allocasuarina* spp. dominated (Plate 3.4).

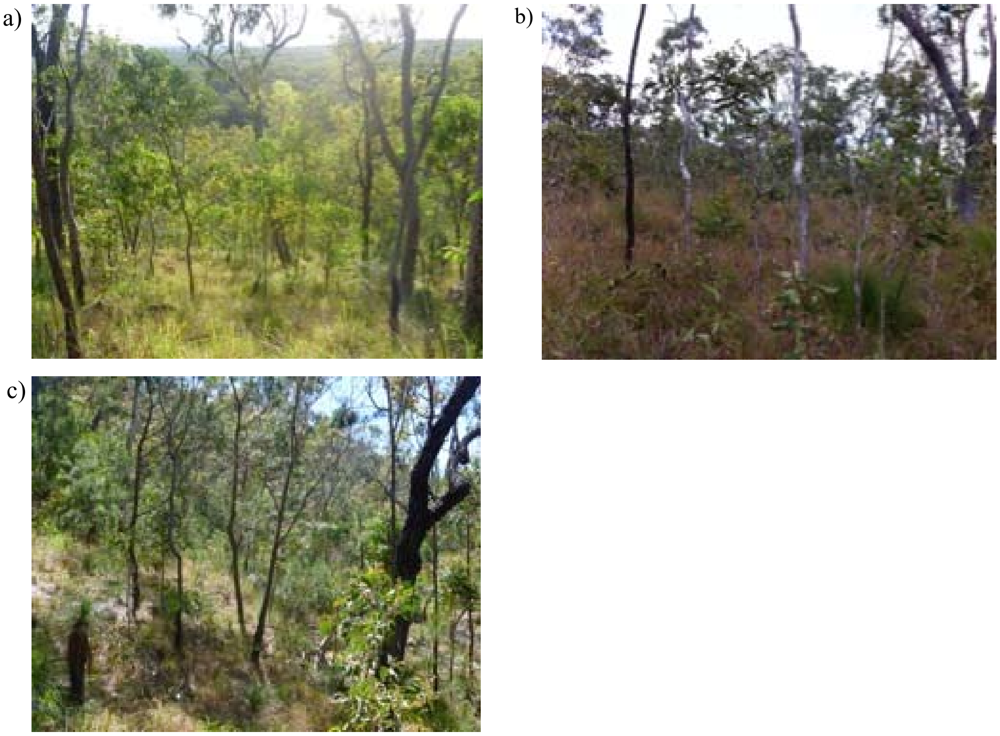

Plate 3.1. Habitat at (a) Davies Creek, (b) Emu Creek, and (c) Tinaroo Creek.

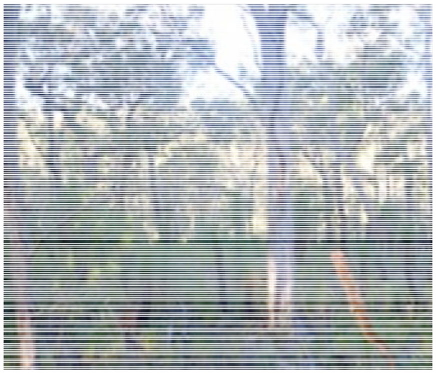

Plate 3.2. Understorey at Tinaroo Creek dominated by grass trees (*Xanthorrhoea johnsonii*).

Plate 3.3. Low density stands of *Melaleuca* trees on the lower slopes at Emu Creek.

Plate 3.4. Dense stands of *Lantana* within the understorey on the lower slopes at Tinaroo Creek. The sub-canopy was dominated by *Allocasuarina* spp. and there was minimal to no grass cover.

3.3.2 Cage trapping

A pilot study was conducted in July 2014 for four consecutive nights at each site to habituate *B. tropica* to cage traps. Trapping was undertaken for four nights in November 2014, February, May, August and November 2015, and February, May, August and November 2016 at each site.

At Davies Creek, the trapping grid comprised four 800 m and three 700 m transects, whilst at Emu Creek and Tinaroo Creek, the trapping grid comprised one 400 m transect, and seven 700 m transects (Figure 3.1). Emu Creek and Tinaroo Creek had shorter ridgelines within *Eucalyptus* woodland than Davies Creek, resulting in the difference in grid configuration between sites. Five transects at Davies Creek and six transects at Emu Creek and Tinaroo Creek were positioned 200 m to 350 m apart along roughly parallel ridgelines. Transects started 100 m from a dirt road that carried very low traffic levels (an estimated maximum of ten cars per day (pers. obs.)). At all sites, two transects were 20 m to 40 m from the road and followed the road contour. These transects were positioned perpendicular to the other transects to increase trap success (Winter 2002).

Each site contained 53 medium-sized collapsible cage traps (60 cm x 24 cm x 26 cm). Cages were placed every 100 m along each transect (Figure 3.1). Between 5 cm and 10 cm of grass was placed on the top and on the sides of the cages to provide shelter for animals. The inside of the cages (except the bottom) were lined with plastic woven mesh to minimise abrasions to animals.

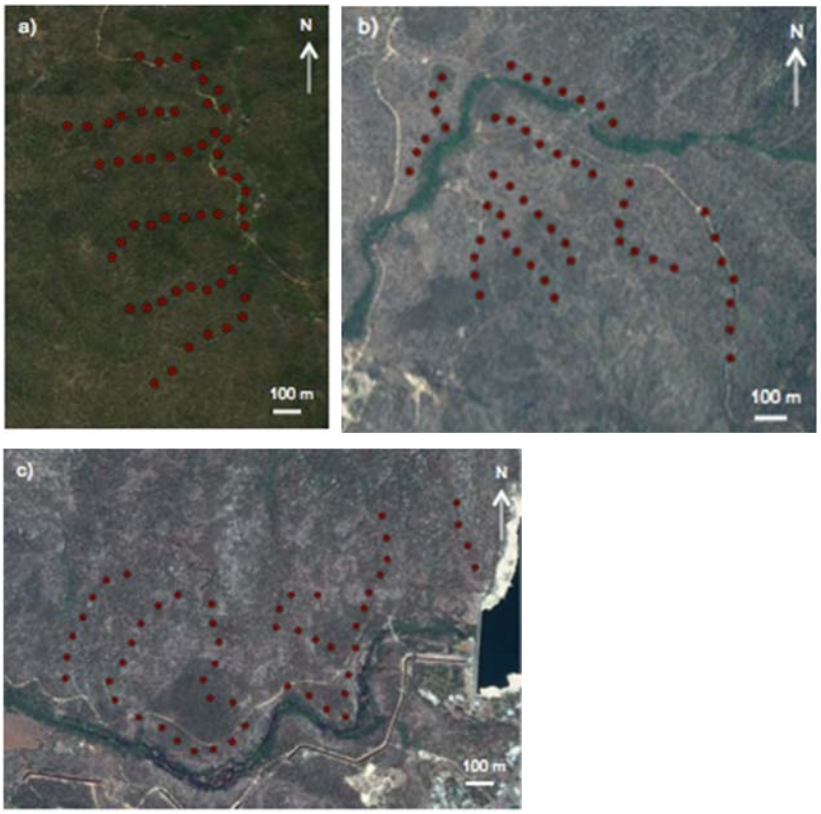

Figure 3.1. Trapping grid configuration at (a) Davies Creek, (b) Emu Creek and (c) Tinaroo Creek on the Lamb Range, showing the location of the 53 cage traps (red circles), positioned 100 m apart along seven transect lines at Davies Creek and eight transect lines at Emu Creek and Tinaroo Creek. (Source: Google Earth®, 2017).

Cages were baited and opened in the mid-afternoon with a 2.5 cm ball of bait containing rolled oats, honey, peanut butter, vanilla essence and sardines. Bait was replaced each day. Traps were checked between midnight and 4 am to ensure *B. tropica* were released before dawn to minimise their stress levels (Vernes 1999; Winter 2000, 2002).

When *B. tropica* were captured, they were removed from the cage and placed in a cloth bag. Bettongs were scanned with a microchip reader to detect the presence of a Passive Integrated Transponder (PIT) tag (Trovan Unique ID100 (1.4) Midi-Chip), and the tag number recorded (Vernes & Pope 2006). PIT tags have a unique number, enabling individuals to be identified (Gibbons & Andrews 2004). If no tag was present, one was inserted into the scruff of the bettong's neck between the shoulder blades (Vernes & Pope 2006). *Bettongia tropica* were weighed and their hind foot length (excluding claw), head length (back of head to nose) and hind leg length measured using calipers (Plate 3.1). These are standard measures for small mammals (Hoffmann et al. 2010), including *B. tropica* (Vernes 1999). Sex, maturity and presence of pouch young were also recorded (Vernes & Pope 2002). Maturity for males was based on a scale of 0 to 3 for the size of epididymis and testes (Fleming 1974; McCravy & Rose 1992), with 0 indicating not visible and 3 being large and pronounced (M. Goosem, pers. comm.). A male with a rating of 2 or higher for both the epididymis and testes was classified as an adult (M. Goosem, pers. comm.). Female maturity was inferred from presence of young or by weight (>950g) (Vernes & Pope 2002). A 3 mm ear tissue sliver was taken on the first capture, and scat samples were collected with every capture, with this information used for future studies. Animals were released where they were captured.

The length of pouch young was taken by measuring the bulge in the pouch using calipers. Bettongs often eject pouch young when stressed (Thompson et al. 2015). To prevent this, the pouch of all females was taped. This was done by placing three 8 cm strips of rigid sports strapping tape vertically and two 8 cm pieces horizontally over the pouch. If pouch young were very small (<2 cm), only three pieces of tape (two vertical and one horizontal) were used.

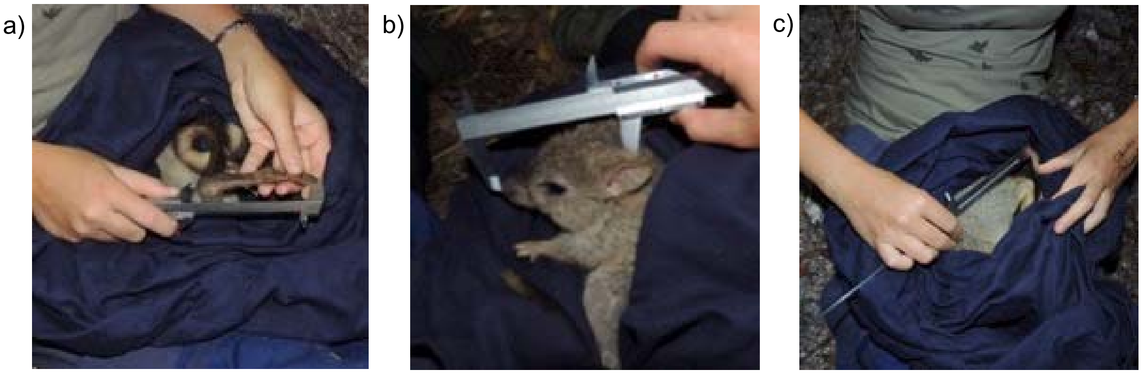

Plate 3.5. Measuring (a) hind foot length, (b) head length and (c) hind leg length of *Bettongia tropica*. (Photograph by Maree Baade).

<u>*3.3.3 Data analysis*</u>

The methodology for calculating the population density, which is the estimated population abundance/effective trapping area (Vernes & Pope 2006), is presented in three sections;

1) calculating the population abundance of each site, involving constructing capture-recapture matrices and validating model assumptions,
2) calculating the effective trapping area for each site, and
3) statistical analysis to determine differences in population density between sites and seasons (wet and dry season) and from 20 years previously (1994-1996 vs. 2014-2016).

3.3.3.1 Calculating population abundance

The population abundance within each site was calculated for each trapping session using Pollock's robust design multi-season mark-recapture analysis (hereafter referred to as robust design) (Pollock et al. 1989). Robust design enables population abundance, survival probabilities, emigration and immigration to be simultaneously estimated (McClintock & White 2009). Robust design uses capture-recapture data sampled at two time intervals: primary and secondary sampling periods (Pollock 1982; Silva et al. 2009). A primary sampling period is long enough for population change to occur (open population), whilst a secondary period is sufficiently short to assume no immigration or emigration (closed population) (Kendall et al. 1997; Silva et al. 2009). Using information from both open and closed populations means the methodology is more precise and has lower bias than implementing open or closed population models separately (Kendall et al. 1995; Kendall et al. 1997; McClintock & White 2009). Abundance estimates were derived for all sampling periods and for the entire sampling session (Baillargeon & Rivest 2007; Smith et al. 2013a).

For my study, primary periods were the two to three months between trapping sessions, whilst the secondary periods were the four nights of consecutive cage trapping in each session. Capture-recapture data of *B. tropica* for each night of trapping was imported into RStudio in a capture matrix (see methodology below) (Santostasi et al. 2016). Robust design analyses were undertaken separately for each site, with analysis conducted using package Rcapture (Baillargeon & Rivest 2007) in RStudio (version 3.2.2) (RStudio Team 2015).

3.3.3.1.1 Constructing capture-recapture matrices

A capture matrix was constructed for each site. The matrix comprised the presence/absence of each *B. tropica* individual for each night of cage trapping (Santostasi et al. 2016). Each matrix comprised a binary table with individuals in rows and sampling occasions in columns (Santostasi et al. 2016). Sampling occasions were labelled so that the nine trapping sessions were distinct from each other, with each of the four nights within the session also labelled (nights one to four). Within the matrix, a 1 was entered if the individual was detected and a 0 if the individual was absent (Santostasi et al. 2016). Table B.1, B.2 and B.3 in Appendix B show the capture matrix for Davies Creek, Emu Creek and Tinaroo Creek.

3.3.3.1.2 Validating model assumptions

Fundamental assumptions of live capture sampling, such as cage trapping data, are (1) the trapped population represents the target population, and (2) there is an equal probability of capturing individuals (Bisi et al. 2011). Individuals that are caught too frequently or considered transitory (only caught once when others were frequently captured) may produce large residuals that result in poor fitting models (Baillargeon & Rivest 2007). This may mean the model is not representative of the population (assumption 1). If *B. tropica* individuals were trap-happy or trap-shy this could result in an unequal probability of capturing individuals (assumption 2) (Nichols et al. 1984) and poorly fitting models (Baillargeon & Rivest 2007). Demographic estimates of open populations can also be skewed by the influence of trap effect, which is where animal behaviours are substantially influenced by the presence of traps (Baillargeon & Rivest 2007). The bias associated with a significant trap effect can be overcome by removing large residuals to ensure the model has a high goodness of fit (Baillargeon & Rivest 2007). To test whether these assumptions were met, preliminary robust design models were undertaken in RStudio (Baillargeon & Rivest 2007), with population abundance models considered valid and accurate. The methodology and results of that analysis are detailed in Appendix C.

3.3.3.2 Calculating effective trapping area of each site

To calculate density estimates, the area that individuals occupied needs to be calculated (Vernes & Pope 2006). The effective trapping area, which is the spatial extent of the trappable population (Efford 2004), was calculated by adding the mean home range radius of a male bettong (431 m, Chapter 4) to all sides of each cage trap location following a similar methodology as used by Vernes and Pope (2006). Slight alterations were necessary for Tinaroo Creek due to the presence of a wide river barrier on one side. The effective trapping area of the three sites was calculated as 324 ha for Davies Creek, 331 ha for Emu Creek and 261 ha for Tinaroo Creek (Figure 3.2). Appendix D details the methodology for calculating the effective trapping area.

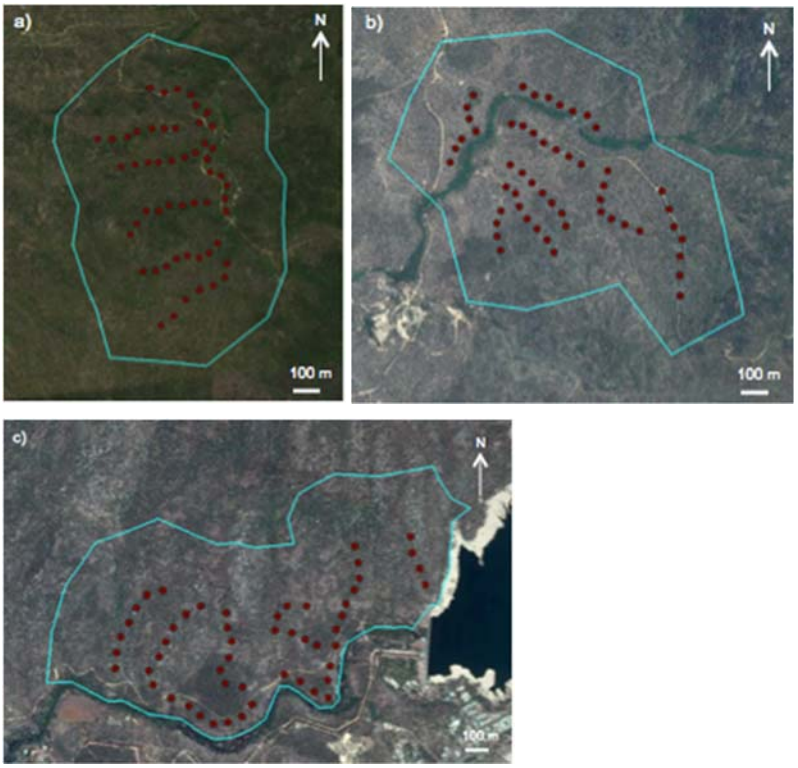

Figure 3.2. Effective trapping area (delineated by the blue outline) with the trap locations (red circles) for (a) Davies Creek, (b) Emu Creek and (c) Tinaroo Creek, also showing the dark green vegetation of the river just below the lower boundary at this site. (Source: Google Earth®, 2017).

3.3.3.3 Assessing population density

3.3.3.3.1 Comparison between sites and seasons

Baiting cage traps can also influence population estimates over time, with studies on other mammal species determining that bait consumption varies with season, which in turn, affects population density estimates (Fitch 1954; Vieira 1997; Rocha et al. 2017). I therefore examined whether the population density estimated for a trapping session was an outlier, with outliers classified as two standard deviations from the mean (Heard et al. 2012). The first trapping session at Davies Creek was an outlier, so was removed.

A repeated measures analysis of variance (ANOVA) was performed to assess whether population density varied with site or season (wet or dry). Season was used as a proxy for truffle (food) abundance, as truffle abundance is positively related to rain falling during the prior one to two months (Abell et al. 2006). Trapping sessions with less than 50 mm of rainfall in the three months prior were classified as occurring within dry seasons (Chapter 2). Sessions with over 50 mm of rainfall in the prior three months were classified as occurring within wet seasons.

Rainfall data for each site were obtained from weather stations located at Mareeba for Emu Creek and Tinaroo Falls Dam for Tinaroo Creek (Bureau of Meteorology (BOM) 2016). The Tinaroo Falls Dam weather station is around 1 km from the Tinaroo Creek site, whilst the Mareeba weather station is approximately 11 km from the Emu Creek site (measured from Google Earth®, 2017). Rainfall for Davies Creek was averaged from the two closest BOM weather stations, Walkamin (20.5 km to the south-west) and Mareeba (16 km to the west, north-west). Walkamin has a wetter habitat (*Eucalyptus* woodland with *Allocasuarina* encroachment) than at Davies Creek (*Eucalyptus* woodland), whilst Mareeba has a drier habitat (dry woodland) (pers. obs.). Data provided by a non-professional weather station, located only 7 km from Davies Creek, recorded similar rainfall data as calculated from the two weather stations (3 mm less than the rainfall averaged from the BOM stations) (R. Miller and Lloyd, 2017). Using mean data from the Walkamin and Mareeba weather stations was thus an appropriate measure. A repeated measures ANOVA assessed whether rainfall varied between sites and seasons, with Tukey honest significance difference (HSD) post-hoc tests undertaken to compare differences within factors.

3.3.3.3.2 Comparison to 20 years prior

To assess whether trap success differed between time periods, a t-test was used to compare estimates from previous research in 1994-1996 (Vernes & Pope 2006) with my estimates (2014-2016). Vernes and Pope (2006) conducted 12 three-night cage trapping sessions between November 1994 and May 1996 (1,944 trap nights) at Davies Creek within a *Eucalyptus* woodland grid with an effective trapping area of 173 ha. Vernes and Pope (2006) did not assess for the trap effect on their estimates and so I used all my estimates (no outliers removed) to enable fair comparisons between studies.

Vernes and Pope (2006) calculated population abundance using the Jolly-Seber methodology. To enable fair comparisons between studies, I only included trapping sessions that were undertaken during the same month and calculated the population abundance at my sites using the Jolly-Seber method. Analysis was computed in package Rcapture (Baillargeon & Rivest 2007), with density estimates again calculated by dividing by the effective trapping area.

For Emu Creek and Tinaroo Creek, there were insufficient data for statistical comparisons, as Vernes and Pope (2006) only undertook one trapping session at Emu Creek and three at Tinaroo Creek (Whitlock & Schluter 2009). Therefore, I qualitatively compared the average of my nine trapping sessions of data from Emu Creek and Tinaroo Creek with the data from Vernes and Pope (2006).

Food abundance can influence the population density of small mammals (Flowerdew et al. 2017), with rainfall influencing food abundance (Abell et al. 2006). I therefore assessed whether rainfall differed between the 1994-1996 and my study period using a Kruskal-Wallis and ANOVA. I compared the rainfall from two months prior to each cage trapping session for both studies. Rainfall data were sourced from BOM weather stations positioned at Walkamin and Tinaroo Falls Dam. Rainfall data were not available from the Mareeba BOM weather stations prior to 2000.

3.3.4 Differences in survival between sites and between seasons

Survival estimates were compared between sites and seasons (wet and dry) using a repeated measures ANOVA. Trapping sessions were classified as wet and dry seasons based on rainfall. Survival estimates were calculated using robust design analysis in RStudio (McClintock & White 2009; Smith et al. 2013a). Survival estimates were generated over the entire trapping session and for each trapping session, except the first (Smith et al. 2013a; Ergon & Gardner 2014).

3.3.5 Influence of site, season and gender on body condition

A repeated measures ANOVA assessed the influence of site, season and gender (nested in site) on body condition. An index for body condition was calculated as weight divided by hind foot length (Wauters et al. 2007). Hind foot length does not change with age (once adult) and has been used by Wauters et al. (2007) to correct for the variation in body mass of mammals resulting from differences in skeletal size. If an individual was trapped during both seasons, average weight was calculated separately for wet and dry seasons. Only adults were included in the analysis.

3.3.6 Influence of site and season on proportion of females with young

The proportion of females with young was used as a measure of reproductive rates (Gilfillan 2001; Hayward et al. 2003). The number of females with pouch young or small young at foot (<250 g, not microchipped) was compared between sites and seasons using a repeated measures ANOVA. The number of females with young per trapping session was tallied and the proportion with young then calculated (females with young/total females per trapping session).

3.3.7 Differences in trap success between sites, seasons and to 20 years prior

The influence of site and season on trap success was analysed using a repeated measures two-way ANOVA. Trap success (captures/trap nights) (Widmer et al. 2017) was calculated at each site for each trapping session, with trapping sessions classified by season.

A one-way ANOVA compared trap success at Davies Creek between 1994-1996 (Vernes & Pope 2006) and my estimates (2014-2016)). At Emu Creek and Tinaroo Creek, trap success was compared graphically, but statistical analyses were not possible due to limited data from 1994 to 1996.

3.4 Results

Between 2014 and 2016, I recorded 1,094 captures of 188 *B. tropica* individuals (Table 3.1). Most individuals and captures were recorded at Tinaroo Creek, with the least at Davies Creek (Table 3.1; Appendix E). The number of individuals and captures of *B. tropica* for each trapping session and the influence of site and gender on individuals and captures are presented in Appendix E.

Table 3.1. Number of individual *Bettongia tropica* caught and total number of captures of males and females at Davies Creek, Emu Creek and Tinaroo Creek.

	Male individuals	Female individuals	Total individuals	Male captures	Female captures	Total captures
Davies Creek	27	16	43	138	111	251
Emu Creek	36	28	64	210	160	370
Tinaroo Creek	38	43	81	209	264	473
All sites (total)	101	87	188	557	535	1094

Individuals at Davies Creek, Emu Creek and Tinaroo Creek were caught up to 25, 25 and 27 times respectively (Figure 3.3). Across all sites, >70% of individuals (132 out of 188 individuals) were captured more than once, with approximately 74% of individuals (32/43) at Davies Creek, 76% (49/64) at Emu Creek and 63% (51/81) at Tinaroo Creek (Figure 3.3). Recapture rates were similar between sites (KW test, $\chi^2 = 1.17$, df = 2, p = 0.56). On average, individuals were caught six times, with 22% of individuals (43/188 individuals) caught ≥9 times, or a mean of once per trapping session

(Figure 3.3). Individuals were captured multiple times, indicating they live within the area instead of dispersing through the site.

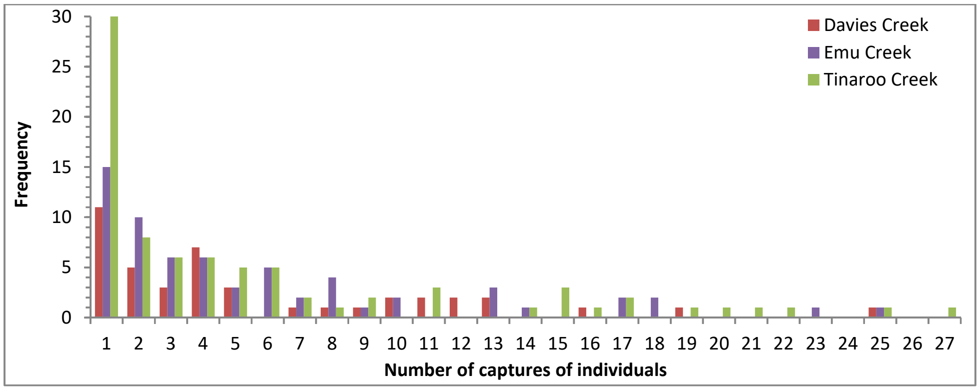

Figure 3.3. Capture frequency of *Bettongia tropica* individuals at Davies Creek, Emu Creek and Tinaroo Creek.

3.4.1 Assessing population density

3.4.1.1 Comparison between sites

The mean number of individuals estimated to occur across the entire trapping program was 33.23± 2.14 bettongs (mean ± SE) at Davies Creek, 29.21 ± 2.72 bettongs at Emu Creek and 34.99 ± 1.95 bettongs at Tinaroo Creek. The average population density per trapping session differed between sites ($F_{2,20} = 18.44$, $p<0.0001$). *Bettongia tropica* had a higher density at Tinaroo Creek ($\bar{x} = 13.40 \pm 0.74$ *B. tropica*/km^2) compared with Davies Creek ($p<0.001$, $\bar{x} = 7.92 \pm 0.67$ *B. tropica*/km^2) and Emu Creek ($p<0.001$, $\bar{x}= 8.82 \pm 0.82$ *B. tropica*/km^2). Similar population densities occurred at Davies Creek and Emu Creek ($p = 0.305$). The estimated population abundance and density for each trapping session is shown in Table 3.2.

Table 3.2. Trap success, capture and survival probabilities and population abundance and density estimates (with associated standard errors (SE)) for *Bettongia tropica* sub-populations at Davies Creek, Emu Creek and Tinaroo Creek from nine cage trapping sessions. Population abundance and density for the first trapping session at Davies Creek was an outlier (indicated by an asterisk) and removed from the mean density estimate. Survival estimates are unable to be computed for the first trapping session.

	Season	Trap nights	Trap success (%)	Capture probabilities	Survival probability (%) (± SE)	Population abundance (± SE)	Density estimates (individuals/km^2) (± SE)
Davies Creek							
November 2014	Wet	212	7.1	71.0 ± 14.5	(not computable)	14.1 ± 3.8*	4.4 ± 1.2*
February 2015	Wet	209^	5.7	41.2 ± 9.6	100 ± 0.0	24.1 ± 2.4	7.5 ± 0.74
May 2015	Dry	212	9.9	68.4 ± 9.0	91.2 ± 9.2	22.0 ± 2.3	6.8 ± 0.72
August 2015	Dry	212	19.8	89.5 ± 4.0	87.1 ± 8.8	23.8 ±1.0	7.3 ± 0.30
November 2015	Dry	212	17.9	80.6 ± 5.8	99.8 ± 5.4	26.8 ± 1.6	8.3 ± 0.50
February 2016	Wet	212	7.1	45.6 ± 10.2	93.7 ± 15.0	26.6 ± 4.1	8.2 ± 1.3
May 2016	Wet	212	10.4	73.0 ± 7.6	70.0 ± 13.9	26.0 ± 2.3	8.0 ± 0.71
August 2016	Dry	212	25.5	91.5 ± 3.4	86.8 ± 8.7	25.0 ± 1.1	7.7 ± 0.40
November 2016	Dry	212	16.0	86.9 ± 6.1	74.8 ± 12.5	20.7 ± 2.3	6.4 ± 0.70
Mean		**211.7 ± 0.33**	**13.2 ± 2.3**	**72.0 ± 7.8**	**87.9 ± 9.2**	**25.5 ± 1.9**	**7.9 ± 0.67**
Emu Creek							
November 2014	Dry	200^	6.0	56.8 ± 19.5	(not computable)	15.8 ± 6.4	4.8 ± 1.9
February 2015	Wet	212	9.0	69.5 ± 10.5	83.1 ± 15.3	20.4 ± 3.3	6.2 ± 1.0
May 2015	Wet	212	15.6	78.5 ± 7.0	82.5 ± 11.4	25.5 ± 2.5	7.6 ± 0.70
August 2015	Dry	212	21.7	88.0 ± 4.2	80.9 ± 9.2	27.4 ± 1.4	8.3 ± 0.41
November 2015	Dry	212	23.6	86.1 ± 4.4	91.2 ± 7.2	32.1 ± 1.7	9.7 ± 0.52
February 2016	Wet	212	9.9	49.9 ± 9.0	75.9 ± 9.8	31.5 ± 3.8	9.5 ± 1.2
May 2016	Wet	212	24.1	81.6 ± 5.0	89.0 ± 8.6	35.5 ± 1.9	10.7 ± 0.58
August 2016	Dry	212	34.0	94.4 ± 2.0	90.2 ± 5.7	35.5 ± 0.74	10.7 ± 0.22
November 2016	Dry	212	31.1	88.4 ± 3.9	99.6 ± 7.7	39.6 ± 2.9	12.0 ± 0.87
Mean		**210.5 ± 1.3**	**19.5 ± 3.3**	**77.0 ± 7.2**	**86.6 ± 9.4**	**29.2 ± 2.7**	**8.8 ± 0.82**

Tinaroo Creek							
November 2014	Dry	212	8.02	64.7 ± 15.1	(not computable)	18.6 ± 5.4	7.1± 2.1
February 2015	Wet	212	14.62	76.3 ± 7.7	86.6 ± 11.4	24.8 ± 2.7	9.5 ± 1.1
May 2015	Wet	212	19.81	76.9 ± 6.2	87.2 ± 8.8	34.3 ± 2.8	13.1 ± 1.1
August 2015	Dry	212	28.77	88.2 ± 3.6	87.0 ± 7.2	36.9 ± 1.6	14.1 ± 0.61
November 2015	Dry	212	30.19	90.7 ± 3.0	79.9 ± 7.3	34.0 ± 1.1	13.0 ± 0.43
February 2016	Wet	212	20.75	73.9 ± 6.3	85.9 ± 8.0	34.2 ± 2.3	13.1 ± 0.88
May 2016	Wet	212	22.17	79.9 ± 5.2	77.9 ± 8.6	35.6 ± 2.0	13.6 ± 0.75
August 2016	Dry	212	37.74	90.3 ± 2,8	91.8 ± 6.0	45.2 ± 1.7	17.3 ± 0.65
November 2016	Dry	212	39.15	93.2 ± 2.4	78.4 ± 7.7	41.8 ± 2.0	16.0 ± 0.79
Mean		**212 ± 0.00**	**24.4 ± 3.5**	**81.6 ± 5.8**	**84.3 ± 8.1**	**35.0 ± 2.0**	**13.4 ± 0.74**

^Note: Fewer trap nights were conducted in February 2015 at Davies Creek and November 2014 at Emu Creek due to traps being stolen during the day and thus unable to be baited for one night.

3.4.1.2 Comparison between seasons

Estimated population density was slightly higher during the dry season ($\bar{x}$ = 10.52 ± 0.92 bettongs/km^2) compared to the wet season ($\bar{x}$ = 8.92 ± 0.83 bettongs/km^2), with this result approaching significance ($F_{1,20}$ = 3.987, p = 0.0596). For each site, >80% of the total rain during my study fell during trapping sessions conducted in the wet seasons (Davies Creek 87.52%; Emu Creek 90.07%; Tinaroo Creek 80.73%), with this difference being significant ($F_{1,21}$ = 117.77, p<0.001). Total rainfall also differed between sites ($F_{1,21}$ = 117.77, p<0.001). Tinaroo Creek was the wettest site (1,382.50 mm) compared with Davies Creek (p = 0.022, 853.95 mm), and Emu Creek (p<0.01, 725 mm). Davies Creek and Emu Creek had similar rainfall (p = 0.76). There was no interaction between site and season ($F_{2,20}$ = 2.655, p = 0.095).

3.4.1.3 Comparison to 20 years prior

Five trapping sessions from my study and from Vernes and Pope (2006) were conducted during the same months. At Davies Creek, 2014-2016 density estimates of 7.43 ± 0.35 ($\bar{x}$ ± SE) bettongs/km^2 were slightly, but not significantly, higher than 1994-1996 estimates of 6.72 ± 0.62 bettongs/km^2 (t = 0.99, df = 6, p = 0.35; Table 3.3). Population abundance and density estimates for each trapping session are provided in Appendix F.

Table 3.3. Comparison of previous (1994-1996) (Vernes & Pope 2006) and current (2014-2016) population density estimates of *Bettongia tropica* at Davies Creek. Current estimates include the mean ± standard error. Only cage-trapping sessions conducted during the same month were compared between studies. Previous estimates only have the mean for each trapping session, as the standard error was not computable based on the data available.

Month	Previous (1994-1996) population density estimates (*B. tropica*/km^2)	Current (2014-2016) population density estimates (*B. tropica*/km^2)
February	6.9	6.9 ± 0.81
May	6.9	6.5 ± 0.02
August	8.6	7.6 ± 0.32
November	6.5	7.7 ± 0.06
February	4.7	8.5 ± 0.62
Mean	**6.7 ± 0.62**	**7.4 ± 0.35**

At Emu Creek, previous estimates of 7 to 10 bettongs/km^2 (Vernes & Pope 2006) are equivalent to current estimates of 8.7 ± 0.29 bettongs/km^2. At Tinaroo Creek, current estimates of 15.1 ± 1.4 bettongs/km^2 were slightly higher than 1994-1996 estimates of between 6.5 and 14.6 bettongs/km^2 (Vernes & Pope 2006).

Rainfall in the two months prior to each cage trapping session was similar between my study ($\bar{x}$ = 106.39 mm at Walkamin; $\bar{x}$ = 153.69 mm at Tinaroo Falls Dam) and the 1994-1996 study ($\bar{x}$ = 121.97 mm at Walkamin; $\bar{x}$ = 165.76 mm at Tinaroo Falls Dam) (Kruskal-Wallis (KW) test, $\chi^2 = 0.107$, df = 1, p = 0.744 at Walkamin; $F_{1,17} = 0.047$, p = 0.831 at Tinaroo Falls Dam).

3.4.2 Differences in survival between sites and between seasons

Survival probability was similar between sites ($F_{2,12} = 0.709$, p = 0.702), averaging >84% at all sites for the duration of the study and between 74% and 100% during each trapping session (Table 3.2). Survival was similar between seasons ($F_{1,12} = 0.0028$, p = 0.958; wet season: 86.39% ± 8.62%; dry season: 86.20% ± 9.03%), with the interaction between site and season also being non-significant ($F_{2,12} = 0.898$, p = 0.638).

3.4.3 Influence of site, season and gender on body condition

Males and females had similar body condition ($F_{1,512} = 1.47$, p = 0.227) (Table 3.4), based on 275 measures of body condition from 88 males and 253 from 77 females across all sites. The body condition index of *B. tropica* was also similar between sites ($F_{2,512} = 1.54$, p = 0.215), season ($F_{1,512} = 0.018$, p = 0.893) (Table 3.4), and there were no significant interactions (site*season: $F_{2,516} = 0.455$, p = 0.634; site*season*gender: $F_{2,516} = 0.615$, p = 0.541).

3.4.4 Influence of site and season on proportion of females with young

Across all sites, 73.46% (119/162) of females had pouch young or dependent young at foot, with no difference between sites ($F_{2,21} = 1.54$, p = 0.464, season ($F_{1,21} = 2.67$, p = 0.102) or the interaction between site and season ($F_{2,21} = 2.202$, p = 0.333) (Table 3.4).

Table 3.4. Comparisons of the body condition index (weight/hind foot length) of *Bettongia tropica* and the percentage of females with young (mean ± standard error) at Davies Creek, Emu Creek and Tinaroo Creek during the wet and dry season. The body condition of males and females is also shown.

	Body condition index (kg weight/hind foot length)	Females with young per trapping sessions (%)
Davies Creek	11.46	77.46 ± 3.89%
Emu Creek	12.14	70.84 ± 4.69%
Tinaroo Creek	11.67	74.94 ± 3.15%
Wet season	11.81	70.39 ± 2.94%
Dry season	11.72	77.63 ± 3.16%
Males (all sites)	11.68	N/A
Females (all sites)	11.86	74.41 ± 2.26 %

3.4.5 Differences in trap success between sites, seasons and to 20 years prior

Trap success was influenced by site ($F_{2,19}$ =24.72, p<0.001), with the average trap success at Tinaroo Creek (24.42%) being higher than at Davies Creek (13.18%) (p<0.0041). Trap success at Emu Creek (19.52%) was intermediate between the other two sites and similar to both Tinaroo Creek (p = 0.218) and Davies Creek (p = 0.159). Trap success varied from 5% to 40% between trapping sessions (Table 3.2). Across all sites, trap success was twice as high during the dry season (24.94%) than the wet season (12.10%) ($F_{1,21}$ = 17.083, p<0.001). There was no significant interaction between site and season ($F_{2,21}$ = 0.002, p = 0.998).

At Davies Creek, current trap success of 13.18% was 5.37% higher than the 1994-1996 average of 7.9% (2.4% to 11.1% per session). However, this difference was not significant (t = -1.80, df = 11, p = 0.10). Trap success at Tinaroo Creek doubled from 1994-1996 estimates of 10.8% to 25.00%, whereas current average trap success at Emu Creek (19.43%) was similar to previous estimates of 20.8%. The results for Tinaroo Creek and Emu Creek could not be statistically compared due to insufficient data.

3.5 Discussion

This is the first study to provide a comprehensive assessment of the population density, life history traits and trap success of *B. tropica* within their three main sub-populations on the Lamb Range. In contrast to what I expected, I found that the population density remained similar to 20 years prior. This information has important conservation implications, as it suggests that management actions for the last 20 years have successfully maintained habitat, enabling population stability, for the species. My study also presents new information on how these estimates differ between sub-populations and between the wet and dry season. As expected, trap success was higher at the wettest site and during the dry season. This study provides baseline information on survival and reproduction rates, which have not previously been determined for sub-populations outside Davies Creek. In contrast to expectations, I found that body condition, survival and reproductive rates were similar between sites and seasons.

3.5.1 Assessing population density

3.5.1.1 Comparison between sites

Density varied from 6.45 to 16.30 bettongs/km^2 across the Lamb Range, and as predicted, higher population density was recorded at Tinaroo Creek (wettest site) than either Davies Creek or Emu Creek. Higher density was most likely due to Tinaroo Creek having higher rainfall, with rainfall increasing truffle (food) abundance (Abell et al. 2006) and resulting in truffles being more evenly distributed (Lehmkuhl et al. 2004). Higher food abundance could increase the carrying capacity of the habitat, which would support higher population densities (Marshall & Leighton 2006). Lower and similar population densities at Davies Creek and Emu Creek suggest fewer but similar food resources available at these sites. Food abundance also influences population density of other bettong species, with Tasmanian bettongs (*Bettongia gaimardi*) attaining higher population densities within habitats where truffle abundance is highest (Taylor 1993a).

3.5.1.2 Comparison between seasons

In contrast to expectations, population density remained similar between seasons, indicating there are sufficient food resources on the Lamb Range to maintain a similar population density throughout the year. Seasonal changes in density of mammal populations usually result from species having a peak breeding season, which is related to the abundance of food resources (de Andreazzi et al. 2011; Pinot et al. 2014). For example, de Andreazzi et al. (2011) studied the population density of small mammals in Brazil and determined that agile gracile opossums (*Gracilianus agilis*) had synchronised, seasonal reproduction during the wet season in response to higher food abundance and this higher recruitment resulted in a higher population density during the dry season. *Bettongia tropica* can breed throughout the year when there are sufficient resources available (Johnson & Delean 2001). I found that both the number of females with young and the survival probability remained similar between seasons and thus sufficient food resources throughout the year likely enabled population stability.

3.5.1.3 Comparison to 20 years prior

Contrary to my predictions, the population density on the Lamb Range remained stable between 1994-1996 and 2014-2016. Rainfall totals at Walkamin and Tinaroo Falls Dam were similar prior to cage trapping between the 1994-1996 and this study. This indicates that food resource abundance has remained similar throughout the Lamb Range. It is possible that other environmental or climatic conditions on the Lamb Range may also have remained similar between studies.

Population density estimates varied between trapping sessions throughout my study. These differences were likely due to the availability of resources or environmental factors (Bantihun & Bekele 2015). For example, moonlight, rainfall and temperature can influence the movement patterns or foraging time of small mammals, which in turn influences trap success (Stokes et al. 2001; Barros et al. 2015; Greenville et al. 2016). At all sites, the first trapping session had substantially lower density estimates than the other trapping sessions. The lower trap success during the initial trapping session can most probably be attributed to individuals being less habituated to cage traps (Davis 1982). Similarly, de Andreazzi et al. (2011) and Rocha et al. (2017) determined that the population density varied between trapping sessions for various Brazilian small mammal species, including the Chacoan mouse opossum (*Cryptonanus chacoensis*) (de Andreazzi et al. 2011), hairy-eared cerrado mouse (*Thalpomys lasiotis*), hairy-tailed bolo mouse (*Necromys lasiurus*) and the delicate vesper mouse (*Calomys tener*) (Rocha et al. 2017). However, the long-term population abundance of these species remained stable and was unaffected by seasonal fluctuations in reproductive success or survival rates (de Andreazzi et al. 2011; Rocha et al. 2017).

3.5.2 *Differences in survival between sites and between seasons*

Survival estimates were high (>80%) across all sites, contrasting to the expectation that the driest site would have the lowest survival rate. Under the relatively stable weather conditions that occurred during my study period (no extreme or extended wet or dry periods between August 2014 and November 2016), season did not influence survival estimates. Survival of small mammals is often, but not always, driven by predation rather than food abundance (Korpimäki et al. 2004). For example, Prevedello et al. (2013) found that higher food abundance had limited impact on the survival rates of their small mammal populations. This suggests predation levels on the Lamb Range were similar between sites and seasons. This conclusion is supported by camera trap capture rates of predators, which were similar between sites (Chapter 5).

3.5.3 Influence of site, season and gender on body condition

Male and female *B. tropica* maintained a similar weight during both seasons across all sites. This was surprising given that *B. tropica* were expected to have lower body condition during the dry season and at the driest site. Body condition of mammals, including bettongs (Johnson 1994; Johnson & McIlwee 1997), is usually driven by food abundance (Murray 2002). For example, Chambers and Bencini 2010 found that resource availability resulted in better body condition for tammar wallabies (*Macropus eugenii*) of Garden Island in Western Australia. For example, Johnson (1994) determined that the body condition and fecundity of the Tasmanian bettong increased during peak availability of truffles, with truffles comprising 90% of their diet during this time. In contrast to my result, Johnson and McIlwee (1997) concluded that body condition of bettongs at Emu Creek (driest habitat) declined during the dry season in 1993 and 1994, although body condition remained similar throughout the year at Davies Creek and Tinaroo Creek. A decline in resources, possibly due to less rain, may have resulted in the lower body condition during the dry season. Rainfall estimates for the driest site could not be compared between this and the Johnson and McIlwee (1997) study as rainfall data is not available from the Mareeba BOM weather station prior to 2000. Rainfall was similar between the BOM weather stations at Walkamin and Tinaroo Falls Dam between the two studies (2014-2016 and 1994-1996). However, in this study I found that rainfall at Tinaroo Falls Dam and Walkamin was higher than at Mareeba and so the potential influence of rainfall on the body condition of *B. tropica* at Emu Creek during the 1994-1996 study cannot be discounted.

During my study there was substantially lower rainfall during the dry season compared to the wet season and thus it is surprising that body condition of *B. tropica* did not decline. This indicates that the weather patterns on the Lamb Range during my study were sufficiently stable to maintain adequate food resources throughout the year.

3.5.4 Influence of site and season on proportion of females with young

The proportion of females with young remained high (>70%) across all sites and during both the wet and dry seasons. *Bettongia tropica* were able to maintain their body condition throughout the year, and this likely enabled the species to breed throughout the year. Breeding throughout the year appears a common strategy amongst all bettong species (rufous bettongs (*Aepyprymnus rufescens*) (Strahan 1998), brush-tailed bettongs (*B. penicillata*) (Christensen 1980), Tasmanian bettongs (*B. gaimardi*) (Rose 1987) and burrowing bettongs (*B. lesueur*)). The ability of bettongs to breed throughout the year is most likely attributable to a continuous supply of food (Short & Turner 1999).

Other studies on small mammals have recorded higher reproduction during the wet season in response to higher food abundance (Bronson 2009; de Andreazzi et al. 2011). For example, Phillips et al. (2017) studied quokkas (*Setonix brachyurus*) on Rottnest Island and determined that weaning rates were lowest in poorly resourced habitats, with body condition also declining during summer when resources were scarce. Willers at al. 2011 studied the population dynamics of the black-flanked rock-wallaby (*Petrogale lateralis lateralis*) in the central wheatbelt of Western Australia and found that rainfall six months prior affected their body condition. Although it seems likely that rainfall influenced the food resources of *B. tropica* on the Lamb Range, there was no seasonal change in the proportion of females with young. This suggests that rainfall was sufficient throughout the year to support *B. tropica* reproductive rates.

Although bettongs may carry pouch young throughout the year, nutritional stress or predation can result in pouch young not surviving to pouch emergence (Short & Turner 2000; Priddel & Wheeler 2004). For example, Priddel and Wheeler (2004) concluded that female brush-tailed bettongs carried pouch young throughout the year, but during periods of nutritional stress, pouch young >5 cm were unable to be retained and no young at foot were present. Thus no recruitment occurred (Priddel & Wheeler 2004). Determining the number of young surviving until maturity, rather than only the number of females with young, would provide a more accurate indication of how breeding rates impact upon the population density of *B. tropica*. To accurately monitor the survival of young, pouch young must be measured as they develop (Vernes & Pope 2002), but in my study those measurements were not recorded in order to minimise stress to mothers and young.

3.5.5 Differences in trap success between sites, seasons and to 20 years prior

As expected, trap success was higher at Tinaroo Creek than Davies Creek. This likely reflects the higher population density at Tinaroo Creek. Trap success of *B. tropica* was similar at Emu Creek and

Tinaroo Creek, despite Tinaroo Creek having a higher population density of *B. tropica* than Emu Creek. A similar trap success between the sites can be attributed to *B. tropica* individuals at Emu Creek being recaptured more frequently than individuals at Tinaroo Creek. Emu Creek has the driest habitat (Johnson & McIlwee 1997) and likely had lower food resources. Individuals at Emu Creek may thus need to travel further to access resources (Rong et al. 2013), which should provide greater opportunity to find extra traps (Larrucea et al. 2007) and increase their capture rates. Additionally, lower food resources may have resulted in individuals more frequently consuming bait to maintain their nutritional levels. Trap success was also stable compared to 1994-1996 estimates, except for Tinaroo Creek, where it was double in my study compared to previous estimates. However, this is most likely due to higher trap effort increasing trap success (Barnett & Dutton 1995).

As predicted, trap success was higher during the dry season than the wet season. These seasonal differences in trap success means that if populations were surveyed only during the wet or the dry season, trap success may not accurately represent the true population density (Roubik 2001). It is therefore important to monitor during both seasons to ensure accurate trends (Anderson et al. 2015).

The differences in trap success may be attributed to seasonal changes in food availability, which potentially altered the trappable behaviour of *B. tropica*. Truffle abundance is lower during the late dry season, which results in *B. tropica* becoming more reliant on less nutritious foods, including cockatoo grass (Johnson & McIlwee 1997; Abell et al. 2006). The reduced availability of high-quality natural food resources (truffles) likely resulted in the baited traps becoming more attractive. Greater bait consumption during the dry season is thus a likely explanation for increased trap success compared to during the wet season (Vieira 1997; Rocha et al. 2017). Similarly, Fitch (1954) observed the behaviours of 14 small mammals and determined that season had an important influence on their trappability, including for the California ground squirrel (*Otospermophilus beecheyi*), Heermann's kangaroo rat (*Dipodomys heermanni*) and the western harvest mouse (*Reithrodontomys megalotis*). Mammals tended to be trapped more frequently when natural food resources were low and animals were hungrier (Fitch 1954). Despite the differences in trap success, population abundance remained similar between seasons.

3.6 Management implications

On the Lamb Range, low-intensity management burns have been undertaken every two to five years between the early 1990s and 2005, with burns conducted every two to three years since around 2005 (R. Miller, pers. comm.). Management burns have the aim of reducing vegetation thickening, particularly on the ecotone where the habitat transitions from wet sclerophyll to *Eucalyptus* woodland (Department of Environment and Heritage Protection (DEHP) 2017). Low-intensity burns can also promote a grassy understorey and cockatoo grass growth (Bateman & Johnson 2011). Thickened vegetation supports lower densities of *B. tropica* than *Eucalyptus* woodlands (Vernes & Pope 2006) so reducing thickening is expected to benefit *B. tropica*.

Although detailed information on the habitat prior to the implementation of fire management is not available, current adequate fire management strategies could explain the stable populations at each study site. The population density at Tinaroo Creek may even have increased under that management, although the data are not sufficient to be certain. Fire management regimes commenced just prior to 1994 (R. Miller, pers. comm.). Habitat alterations since 1996, particularly a reduction in woody thickening (*Allocasuarina* and lantana encroachment), may have assisted in maintaining the populations. *Allocasuarina* is susceptible to fire (DEHP 2017a), with anecdotal evidence indicating that woody thickening and lantana encroachment at Davies Creek has been reduced by up to 10 m from the edge of the *Eucalyptus* woodland and replaced with a grassy understorey since prescribed burnings started (R. Miller, pers. comm.). The stability of populations on the Lamb Range indicates that fire management regimes have not detrimentally impacted upon *B. tropica* populations and possibly may be improving habitat quality for *B. tropica*.

Despite the stable population, consistent and regular monitoring should still continue to assess population trends (Gerber et al. 2012; Pacheco et al. 2013). Monitoring during both seasons was demonstrated to be very important as trap success differed between seasons. Surveys only during the one season may produce estimates that are not an accurate reflection of true population abundance (Roubik 2001). Additionally, regular monitoring enhances the likelihood of detection of small but real changes in populations (Lurz et al. 2008). This is important as small changes often pre-empt larger declines that are harder to reverse and can have major ramifications on important processes, including ecosystem functioning (Gaston & Fuller 2008). Early detection of changes may also enable the implementation of more efficient, long-term management strategies (Antao et al. 2010) designed to prevent, reduce or reverse population declines (Redford et al. 2011). Consistent and regular monitoring is vital for accurate population estimates for *B. tropica*.

Future monitoring and management of *B. tropica* could also be improved by understanding how this species moves and utilises its habitat. This includes an understanding of home range size and movement patterns to ensure that fire management is being undertaken at an appropriate scale, addressed in the next chapter.

Chapter 4: Seasonal home range size and movement patterns of *Bettongia tropica*

4.1 Abstract

Context. The spatial distribution and behaviour of species within the landscape provides important information about habitat requirements that is useful for conservation management.

Aims. I aimed to determine the home range, home range overlap and movement patterns of *Bettongia tropica* within their three main sub-populations on the Lamb Range.

Methods. Between February 2016 and February 2017, 51 bettongs were collared with Global Positioning System (GPS) units and home range size estimated using Kernel Brownian Bridge Movement Models. The GPS fixes of collared *B. tropica* were visually assessed on Google Earth® to ascertain the different types of movement patterns bettongs undertake. These patterns were further assessed by calculating the speed *B. tropica* travelled, creating trajectory plots to assess nightly movement patterns and constructing rose diagrams to demonstrate the angle that *B. tropica* turn when moving.

Key results. Forty-one GPS collars recorded data for between 3 and 42 days, with a total of 1,040 days of movement data. The mean home range size was 20.90 ± 1.55 ha (mean ± SE), with no significant difference in home ranges between sites. Male home ranges were approximately double the size of female ranges and mean home range size for both sexes increased in the dry season. This is most likely due to fewer resources being available during the dry season, resulting in bettongs travelling further for resources and needing larger home ranges. *Bettongia tropica* had relatively large core foraging areas (5.53 ± 0.42 ha, ≈ 26% of home range) and an average of six small core nesting areas (0.67 ± 0.10 ha). Although home ranges overlapped (71.66 ± 4.42%), *B. tropica* maintained almost exclusive core areas. Notable movement patterns were recorded: slow, angular movements corresponding to foraging, and fast, linear movements indicating travel between resources.

Conclusion. The spatial distribution of male *B. tropica* was most likely influenced by female distribution and their search for mating opportunities. In contrast, female movements appeared to be associated with habitat productivity and the distribution of food resources. Overlap between home ranges indicates that defending access to the entire home range was inefficient. Core foraging and nesting areas suggests that certain areas within the landscape are able to support *B. tropica* for proportionally longer than other areas.

Management implications. Management burns on the Lamb Range are currently conducted over a 60 ha scale, based on previous estimates of *B. tropica* home rage size. It is recommended that fire management be conducted at a 20 ha scale to 60 ha scale, with a 30 ha scale favoured during periods that are particularly dry. Females at Tinaroo Creek tended to spend a larger proportion of their time foraging and less time travelling, indicating that resources may occur at higher density at Tinaroo Creek. This indicates that Davies Creek and Emu Creek may be a more marginal habitat for *B.*

tropica. Future monitoring should focus on these two sites, as this may enable trends in *B. tropica* populations to be detected earlier than at Tinaroo Creek.

4.2 Introduction

Examining home range size and movement patterns of animals can provide an insight into how species respond to their environment (Nathan et al. 2008). The home range for an animal is the area needed to acquire mating opportunities and sufficient resources, including food, water, habitat, shelter and nesting areas (Burt 1943). Theoretically, species should utilise the smallest area needed to survive and reproduce (Saïd et al. 2005; Schradin et al. 2010). However, home ranges of the same species can vary between or within populations (Sprent & Nicol 2012; Ofstad et al. 2016) or due to other factors, including environmental conditions (van Beest et al. 2011), predation risk (Fisher 2000; Dussault et al. 2005; Edwards et al. 2013) or the availability, quality and distribution of habitat and food resources. An assessment of the difference in home range size between genders or populations can provide an indication of the factors influencing species occurrence and behaviour (McLoughlin et al. 2000; Powell 2012).

Home ranges often contain core areas that are used disproportionally more than the remainder of the home range (Burt 1943). Core areas generally occur within an area with a high density of important resources (e.g. nesting, foraging or breeding resources) (Asensio et al. 2012; Feldhamer et al. 2015). For example, Rader and Krockenberger (2006) found that the size of core areas used by fawn-footed melomys (*Melomys cervinipes*) was determined by their requirement to achieve a specific level of canopy resources. Determining the location of core areas should assist in identifying aggregations of important resources (Bingham & Noon 1997).

The spatial distribution of home ranges also provides an insight into species' behaviours, including potential social interactions (Frederick & Johnson 1996). To maximise fitness, according to optimal foraging theory (Emlen 1966; MacArthur & Pianka 1966), individuals should defend a territory containing sufficient resources for themselves and their offspring (Frafjord 2016). However, if resources are clumped yet abundant enough to support multiple individuals, excluding competitors may not be cost-effective (Miller et al. 2014). This is because more energy would be used defending the territory than gained from the defended resources (Oldfield et al. 2015; Hinsch & Komdeur 2017). By sharing resources, the amount available for each individual is reduced, resulting in individuals requiring larger home ranges to access a similar abundance of resources (Markham et al. 2015).

The fine-scale movement patterns of animals, including changes in movement speed, distance and angle, can also indicate resource distribution and/or habitat heterogeneity within the animals' home range (Wells et al. 2008). Different movement patterns are associated with various behaviours, including competitive interactions, searching behaviours (for mates or resources), foraging, predator avoidance and dispersal (Patterson et al. 2009; Davies et al. 2013; Laidre et al. 2013; Chimienti et al. 2014). For example, Taylor (1993b) studied the home range, nest use and activity of the Tasmanian bettong (*Bettongia gaimardi*) and found that males occasionally undertook more regular movement patterns than females, which was potentially related to males searching for females. Tasmanian bettongs also commonly moved 500 m to 600 m within half an hour, suggesting they travelled quickly when searching for resources (Taylor, 1993b). Vernes and Haydon (2001) used 750 m spool lines to track the fine-scale movements of *B. tropica* at Davies Creek for relatively short distances, concluding that *B. tropica* undertake area-restricted search patterns (short, angular movements) upon initially detecting or after encountering food patches. An understanding of movement patterns can also indicate the factors that constrain animals (Wells et al. 2008) and indicate populations that are more marginal and likely to be under greater stress (Murgatroyd et al. 2016).

The northern bettong, *Bettongia tropica*, is a small (≈ 1.2 kg) endangered Australian marsupial (Burbidge & Woinarski 2016). The specialised diet of *B. tropica* predominantly dictates the large-scale distribution of the species (Bateman et al. 2012a), with the species favouring *Eucalyptus* woodlands with a grassy understorey (Vernes & Pope 2006) and containing cockatoo grass (Abell et al. 2006; Bateman et al. 2012b). However, little is known about the fine-scale movement patterns of *B. tropica*.

Movement patterns of *B. tropica* have only previously been assessed in one sub-population (Davies Creek), with the variation of space use between *B. tropica* sub-populations unknown. Radio-tracking of 23 individuals every two hours determined that *B. tropica* have large (59 ha) home ranges for their body size (Vernes & Pope 2001). The more recent technology of Global Positioning System (GPS) collars can provide higher resolution tracking data, enabling a broader range of ecological questions to be answered. By obtaining fine-scale movement data over long periods from multiple sub-populations, the factors influencing a species' spatial distribution across the wider landscape can be investigated.

4.2.1 Aims

In this chapter I aimed to:

1) estimate the home range and core areas of *B. tropica* from the three main sub-populations on the Lamb Range,
2) examine differences in the size of seasonal (monthly) home ranges and seasonal core foraging and nesting areas between study sites, genders and sub-populations with different densities,
3) assess the overlap between *B. tropica* seasonal home ranges and between seasonal core areas to indicate potential social interactions, and
4) assess movement trajectories of *B. tropica* to quantify speed and movement directions.

It was expected that *B. tropica* would have larger home ranges at drier sites and during the dry season, when resource abundance is assumed to be lower. Bettongs within higher density populations were also expected to have larger home ranges, as increased competition was assumed to reduce the abundance of resources per individual. Truffles and cockatoo grasses, the main food resources of *B. tropica* (Johnson & McIlwee 1997; Abell et al. 2006), are patchily distributed in clumps throughout landscapes (Claridge 2002; O'Malley 2006). Due to the patchy distribution of these resources, I expected that both the home ranges and core foraging areas of *B. tropica* would overlap, as it would be energetically inefficient to defend access to these areas. *Bettongia tropica* were expected to forage using slow, angular movements, with the proportion of time spent foraging expected to be similar across all sites. Linear movements are the most effective pattern for travelling long distances rapidly (Davies et al. 2013; Bracis et al. 2015; Massa et al. 2015), so I expected *B. tropica* to travel directly and quickly between resources.

4.3 Methods

This study was conducted at Davies Creek, Emu Creek and Tinaroo Creek on the Lamb Range, Queensland, Australia (described in detail in Chapter 3). Tracking collars were deployed on a total of 51 individuals during five cage trapping sessions (February 2015 to February 2016) (Chapter 3). At Davies Creek 10 males and eight females were collared, at Emu Creek nine males and five females were collared and at Tinaroo Creek eight males and 11 females were collared.

Cage-trapped *B. tropica* were selected for tracking if they weighed >960g (collar 4.9% of body weight), were healthy and free from injuries (such as substantial fur loss or cuts) and did not have pouch young >6 cm or young at foot <500 g. Unless the battery failed to record data for more than three days, *B. tropica* were only collared once to maintain independence of data (Pizzuto et al. 2007).

When collars were being fitted around the necks of *B. tropica*, individuals were gently restrained by holding the shoulders, with paws tucked under their body (Plate 4.1). Collars were fitted around the necks of *B. tropica*. The collar was orientated so the battery canister was underneath the bettong's chin, with the GPS chip on the back of the neck (Plate 4.2). An index finger was placed under the collar to ensure the collar was not too tight. Once the equipment was secured, each *B. tropica* was closely monitored until the bettong jumped away normally. The collar was removed if the animal showed signs of distress.

Plate 4.1. Technique for restraining *Bettongia tropica* whilst a GPS collar is attached, with (a) *B. tropica* being restrained around the shoulders, and (b) the paws being under the animal, whilst the collar was fitted around the neck and secured with a zip-tie. (Photographs by Dr. Miriam Goosem).

Plate 4.2. *Bettongia tropica* with collar attached, showing the orientation of the collar from the (a) right hand side, and (b) left hand side. On both collars the antennae has broken off. (Photographs by Dr. Miriam Goosem).

Each collar weighed 47 g and was constructed of an adjustable leatherette (artificial leather) band with a GPS unit, a very high frequency (VHF) radio-tracking unit and a battery (Plate 4.3). The leatherette band was lined with sheepskin to prevent rubbing and was secured with a zip-tie (Plate 4.4). The zip-tie rubbed against the leatherette band, with the band designed to break within two to three months. Band diameter was based on measurements of two captive bettongs at Cairns Tropical Zoo. The GPS receiver (i-GotU GT-120 USB GPS Travel and Sports logger by Mobile Action) recorded a GPS fix every 10 minutes. Each VHF transmitter emitted a unique VHF signal (Pinter-Wollman & Mabry 2010), enabling collared *B. tropica* to be tracked. Collars were dusted with paprika to deter bettongs from chewing them and then sealed with heat-shrink tubing to prevent water damage.

Collars had to be recovered to download the GPS data and to re-deploy the collars in future sessions. To allow this, dedicated follow-up trapping was conducted a month after each round of collar deployment. Collars were retrieved after a month as the collars had an estimated battery life of around one month (based on the manufacturer's advice). One month of data were assumed to be sufficient to estimate seasonal home ranges. Appendix G details the cage trapping methodology for retrieving collars.

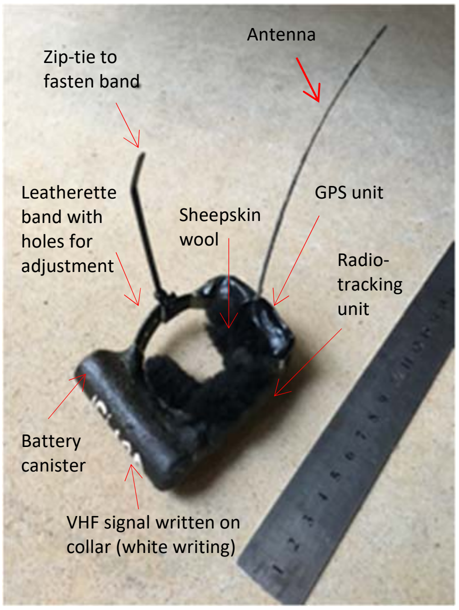

Plate 4.3. GPS collar for *Bettongia tropica*. (The ruler indicates scale in centimeters).

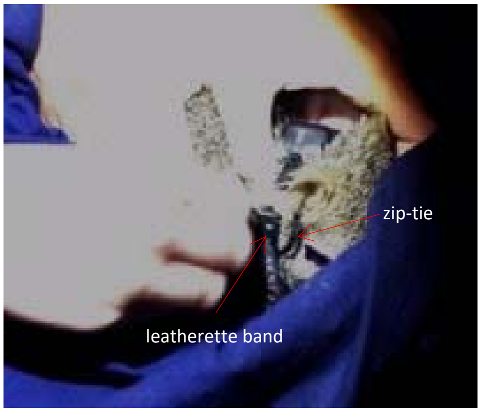

Plate 4.4. Zip-tie being threaded through the leatherette band on a GPS collar that is being attached to a *Bettongia tropica* individual. (Photograph by Maree Baade).

4.3.1 Data cleaning

Once collars were retrieved, data were downloaded using the computer program @trip PC (Mobile Action Technology, 2016). The data comprised GPS fixes approximately every 10 minutes, although occasionally no fix was recorded for 20 minutes. For each GPS fix, the devices recorded the date, time, latitude, longitude, altitude, speed of travel, satellite numbers used to record the fix, and the estimated horizontal precision error (EHPE).

Bettongs with <3 days of GPS data were excluded from analyses, as there was insufficient data to compute home range estimates or movement trajectories. GPS data were then filtered to remove fixes that were recorded before the collar was deployed or when *B. tropica* was within a cage trap. Fixes were filtered by firstly removing the fixes where the EHPE was >25 m. Once these outliers were removed, the mean error was 8.38 m ± 0.088 m, which was considered appropriate (Ellis et al. 2015). Secondly, fixes were removed if the altitude recorded was 100 m higher than the highest altitude or 100 m lower than the lowest altitude for that site. Using altitude as a discriminatory variable removed obviously erroneous fixes and those that appeared to result from satellite drift. Satellite drift was recognised when a line of fixes moved away from a cluster of fixes, but the next fix was back within the original cluster (Nethery et al. 2014). Fixes were lastly excluded if the speed between two fixes was greater than the maximum *B. tropica* can travel. The speed *B. tropica* travelled in the 30 minutes post-release from a cage trap was considered maximal. Fixes for each *B. tropica* were separately plotted on Google Earth® in hourly periods, with a final visual assessment determining that no unrealistic fixes remained.

4.3.2 Data analysis

The data analysis section is presented in four sections to correspond with the main aims of this chapter.

4.3.2.1 Calculating seasonal home range

I used Kernel Brownian Bridge Movement Models (BBMM) (Horne et al. 2007) to estimate the seasonal home range sizes (henceforth referred to as home range size) for each *B. tropica*. BBMM predicts the trajectory an animal is expected to follow between successive points, based on the order of fixes and the time and distance between fixes (Horne et al. 2007; Kranstauber et al. 2012; Fischer et al. 2013). The method also allows for serial autocorrelation between fixes, with fixes only contributing to the home range estimate when consecutive fixes occur at short time intervals (Kie et al. 2010; Fischer et al. 2013). Analysis was computed in RStudio (RStudio Team 2015) using the adehabitatHR package (Calenge 2006).

Home range size for each *B. tropica* was estimated for the 50%, 95% and 99% utilisation distributions (UD). Utilisation distributions are three-dimensional probability densities that calculate the smallest area based on the probability of relocating an animal within that area (Cermeño et al. 2015). These distributions are based on how intensely animals use parts of their home range (Kranstauber et al. 2012). A 50% UD is often used to represent the core area (Clapp & Beck 2015), whilst a 95% UD minimises the importance of rarely used areas, but may result in a disjunct distribution if important but rarely used areas are excluded (Kie et al. 2010). A 99% UD provides the most inclusive home range estimate (Clapp & Beck 2015).

One female at Tinaroo Creek was unintentionally collared twice, once in February 2015 (wet season) and once in November 2015 (dry season). To ensure independence of data (Pizzuto et al. 2007), only the data from February 2015 was included in analyses that compared home range and core areas between sites, genders and seasons.

4.3.2.2 Standardising home range and core areas

Home range size varies depending on the number of fixes recorded (Bengtsson et al. 2014). My collars recorded data for different numbers of days and therefore I standardised the data to enable comparisons between individuals. To do this, I undertook preliminary analysis of home range sizes for individuals at all sites by calculating the 95% and 99% home ranges for six time periods: 12, 15, 20, 25 and 30 days/nights (24 hour period, referred to as a day) and all days of data. I selected 15 days of data as the most suitable time period for comparisons. Home range estimates using 15 days were most similar to those estimated from all the data and also retained a sufficiently large sample size to enable comparisons between sites and genders. I therefore calculated the 95% and 99% UDs for home range for the first 15 days for each *B. tropica*. The methodology and justification for using 15 days of data is detailed in Appendix H. Appendix H also contains the methodology and results of the analysis for the six time periods (for both 95% and 99% home range).

The decision to use 15 days of data meant that at Davies Creek only one female was included in the analysis. This limited the accuracy of analyses that compared female home ranges between study sites. To ensure at least three females from each site were included in the analyses, the home range of females was also calculated using eight days of data. Fifteen days of data were used for all analyses where female data were combined across sites to increase the amount of data and accuracy of results.

4.3.2.3 Calculating core nesting and foraging areas

Some mammals use core areas, with these areas being more intensively used than others (Eccard et al. 2004). Core areas typically include important nesting and foraging locations (Eccard et al. 2004; Goldingay 2015). Core ranges are often calculated using a 50% isopleth, which uses 50% of the data to estimate a smaller range (Goldingay 2015). A limitation of using this method is that it generates a core area regardless of whether the area is biologically relevant or not to the species (Goldingay 2015). Plotting the GPS fixes of each *B. tropica* on Google Earth® showed that all individuals intensively used certain areas within their home range for nesting or foraging. I used the 50% UD to separately calculate the core foraging areas (fixes between 7 pm and 3am) and nesting areas (fixes between 7 am and 6 pm). This was done for all data and a subset of the first 15 days.

4.3.2.4 Comparing home range and core areas

Using separate generalised least squares (GLS) models, with post hoc tests, I examined 1) home range size for 95% and 99% UD, 2) core foraging area, and 3) core nesting area, in response to site, season and gender (nested within site). Separate analyses were conducted for males and females, with data pooled across sites. Cage trapping sessions were separated into wet and dry seasons.

The home ranges of males (using 15 days of data) were compared between sites using a one-way ANOVA with Tukey honest significance difference (HSD) post hoc tests, whilst a Kruskal-Wallis test was undertaken to compare female home ranges between sites (using 8 days of data). One-way ANOVAs were used to compare the core home ranges of females between sites with the core areas of males. The core areas of males were compared between sites using a Kruskal-Wallis test (using 15 days of data). I also calculated the proportion of the home range that was occupied by core nesting and foraging areas. The proportion was then separately compared between sites and seasons using ANOVAs and Kruskal-Wallis. Separate analyses were conducted for nesting and foraging areas.

Analysis of covariance (ANCOVA) assessed whether the number of nesting areas (for the first 15 days) was influenced by site, season, home range or core foraging area. Separate analyses were conducted using 95% and 99% home ranges and for the core foraging area. To determine the number of nesting areas each *B. tropica* used, nesting fixes (7 am to 6 pm) were plotted (for all and the first 15 days of data). Nesting areas for each *B. tropica* were then visually counted, with a nesting area being a discrete cluster of points.

4.3.2.5 Influence of population density on home range and core areas

Linear regressions were performed to assess the relationship between population density and 95% and 99% home range and core areas (Sanchez & Hudgens 2015). Separate regressions were undertaken for males and females, with data from all sites combined. Population density estimates for each trapping session were sourced from Chapter 3. Population estimates were converted to number of *B. tropica* per hectare, so that home range area (ha) and population density were in the same units.

4.3.2.6 Calculating overlap of home ranges and core areas

I plotted the overlap of 95% and 99% home range and core foraging and nesting areas of *B. tropica* at each site, with plots constructed using kernel overlap in RStudio. From each plot, I visually assessed the maximum and minimum number of collared *B. tropica* that had overlapping home ranges and core areas. Overlap was calculated individually for each collared *B. tropica*, with overlap defined as the proportion of a *B. tropica*'s home range that was shared by at least one other collared individual (Fieberg & Kochanny 2005). Overlap was calculated based on all days of GPS data (rather than only 15 days) and the results were descriptively analysed. I aimed to determine the maximum overlap between individuals and, since sites were not being compared, I used all days of data.

I calculated the proportion that the 95% home range of each collared *B. tropica* was overlapped by other collared *B. tropica*. Data were pooled by gender at each site and classified into eight categories. The categories 'male-male', 'male-female', 'male-total' and 'male-unoccupied' signify the amount that the home ranges of males were overlapped by other males, females, any gender (total overlap) and unoccupied respectively. The same four categories were computed but for females ('female-male', 'female-female', 'female-total' and 'female-unoccupied').

Analyses used package adehabitatHR in RStudio (RStudio Team 2015), function kernel overlap (grid size 200), method HR, which calculates the proportion of the home range of one animal that is covered by another (Calenge 2015). It is noted that the use of kernel overlap assumes that the data points are independent (Kie 2013), which is not the case for my data. However, the proportion of overlap between home ranges could not be statistically computed using Brownian Bridge Movement Models. Kernel density overlap has been successfully used to estimate the overlap in home range in other studies where data were also non-independent (Sugishita et al. 2015; Warning & Benedict 2015).

4.3.2.7 Analysing movement patterns of B. tropica

Movement trajectories whilst foraging (7 pm to 3 am), including distance and turning angles, were calculated using package adehabitatLT (Calenge 2011) in RStudio (RStudio Team 2015). GPS fixes were programmed to record 10 minutes apart but the time between consecutive fixes actually varied between 10 and 11 minutes. Removing outliers also resulted in some fixes being non-consecutive. To create a regular trajectory whereby all fixes were constant (10 minutes apart), I followed the procedure outlined in Calenge (2011). The resulting output included distance travelled within the 10 minutes and relative turn angle (definition below in 'Turning angle' section).

4.3.2.7.1 Distance and speed B. tropica travelled

The distance and speed *B. tropica* travelled were calculated for each individual. The calculated distances are the minimum because a straight line is assumed between each GPS fix, which is in general unlikely to be the case. Nevertheless, by applying a standard method to all the data, comparisons can be made between the relative speeds and distances travelled by the collared bettongs. I compared the mean speed male and female *B. tropica* travelled during each hour between 7 pm and 3 am (7-8 pm, 8-9 pm, etc.), with data from all nights pooled. I also compared the average speed per hour *B. tropica* travelled at each site. Analyses were undertaken using ANOVAs and Kruskal-Wallis tests.

4.3.2.7.2 Slow, medium and rapid movements

A visual assessment of GPS fixes on Google Earth® determined that *B. tropica* tended to have three distinctive movements patterns based on speed of travel; travelling at a slow (<3 m/min), medium (3-8m/min) and rapid (>8m/min) pace. The percentage of time that males and females travelled at each speed was compared using one-way ANOVAs with Tukey HSD post hoc tests and Kruskal-Wallis with Dunn's post hoc test (adjusted with Bonferroni correction). I also calculated the percentage of time that males and females travelled at each pace at each site. The percentage was calculated as the number of fixes at each speed, divided by the total fixes. Trajectory plots of nightly movement patterns of *B. tropica* were created using adehabitatLT (Calenge 2011) in RStudio (RStudio Team 2015) to demonstrate movement patterns.

4.3.2.7.3 Turning angle

Movement patterns were investigated by calculating the relative turning angle between three consecutive GPS locations. Relative turning angle is the change in direction between fixes (Calenge 2011) and is referred to as 'turning angle' hereafter.

The turning angle of *B. tropica* was calculated for each speed category and presented as rose diagrams, which were constructed using the program GeoRose (Yong Technology Inc 2015). Separate plots were constructed for males and females at each site. The turning angle represents the direction relative to the previous direction that the bettong was travelling. Turning angle was classified in increments of 15º, with 0° representing a continuation in the same direction (the three points are in a straight line) and 180° representing a complete reversal in direction. Turning angles of less and greater than 180º indicate bettongs deviated to the right and left respectively. For example, 15° represented a divergence of 15° to the right, whilst 345° was a divergence of 15° to the left.

4.4 Results

Overall, collars on 24 males and 16 females recorded data (Davies Creek = 8 males, 3 females; Emu Creek = 9 males, 4 females; Tinaroo Creek = 7 males, 10 females). In total, 30 collars recorded data for ≥15 days. Of the 51 collars deployed, 41 (80%) recorded GPS data for between 3 and 41 days ($\overline{x}$ = 25.43 ± 1.65 days and nights, mean ± SE). The 41 collars were deployed on 40 individual *B. tropica*, as one female was collared twice due to it being mistakenly microchipped and collared twice. Nine individuals did not provide sufficient data for analysis due to battery or programming failure (n = 5) or loss of collars (two fell off within a day and two could not be recovered. Appendix Table J.1, J.2 and J.3 provides information regarding the deployment and retrieval of collars from each individual. In total, 5,760 targeted cage trap nights were undertaken to attach and remove collars. The number of fixes removed as outliers was 6.36% (8,006/125,917 fixes).

4.4.1 Home range and core areas

4.4.1.1 Home range and core foraging and nesting areas (all data)

For simplicity, only the 99% UD home ranges will be reported in the text. Appendix H contains the results for the 95% UD home ranges. In the following sections, unless specified, home ranges were calculated using all valid GPS locations for each individual whose collar recorded >3 days of GPS data.

Mean home range size across all sites was 20.90 ± 1.55 ha (99% UD). Home ranges of males were almost twice the size of female home ranges (Table 4.1). Core foraging (5.53 ± 0.42 ha, 50% UD) and nesting areas (0.67 ± 0.10 ha, 50% UD) comprised 26.45% and 3.21% of the mean home range respectively, with males having substantially larger core foraging areas than females (Table 4.1). Home ranges and core foraging and nesting areas were 14.23%, 24.92% and 16.22% larger during the dry season than the wet season respectively (Table 4.1). Appendix Tables K.1, K.2 and K.3 details the home range size and core foraging and nesting areas of each *B. tropica* at Davies Creek, Emu Creek and Tinaroo Creek.

Table 4.1. Gender and seasonal differences in the home ranges (99% UD) and core foraging and nest areas (50% UD) of *Bettongia tropica*, using all valid GPS fixes for each animal. Values are mean and standard errors.

	Home range (ha)	Core foraging area (ha)	Core nesting area (ha)
Males	25.76 ± 1.56	6.77 ± 0.52	0.63 ± 0.12
Females	13.69 ± 2.03	3.67 ± 0.36	0.73 ± 0.18
Dry season	21.78 ± 2.00	6.02 ± 0.58	0.62 ± 0.12
Wet season	18.67 ± 2.34	4.52 ± 0.43	0.74 ± 0.18

4.4.1.2 Home range area (standardised by days)

Home range sizes of females were similar between sites (Kruskal-Wallis (KW) test, $\chi^2 = 2.2833$, df = 2, p-value = 0.3193 (eight days); Table 4.2), as were male home ranges ($F_{2,11} = 0.21$, p = 0.813 (15 days); Table 4.2). Males had substantially larger home ranges than females ($F_{3,22} = 6.71$, p = 0.0021 (15 days); Table 4.2). At Davies Creek and Tinaroo Creek, the home ranges of males were over twice the size of female home ranges, however ranges were similar at Emu Creek (Table 4.2). Home ranges during the dry season were around one-third larger than home ranges recorded during the wet season ($F_{1,22} = 8.74$, p = 0.0073; Table 4.2) when data were combined from males and females.

Table 4.2. Average size of home range and core nesting and foraging areas after 15 days of GPS tracking male *Bettongia tropica* and after 15 and 8 days of tracking females. Areas were estimated at Davies Creek, Emu Creek and Tinaroo Creek and during the wet and dry seasons. Estimates include standard errors.

	Core (50%) UD nesting area (ha)	Core (50%) UD foraging area (ha)	Home range 95% UD (ha)	Home Range 99% UD (ha)
All males	1.35 ± 0.25	6.66 ± 0.81	13.72 ± 2.35	22.15 ± 1.54
All females	0.48 ± 0.09	2.30 ± 0.45	7.70 ± 1.61 (15 days) 5.12 ± 2.08 (8 days)	11.35 ± 1.77 (15 days) 8.66 ± 2.71 (8 days)
Davies Creek males	1.39 ± 0.42	7.61 ± 1.98	13.49 ± 3.27	22.95 ± 3.67
Davies Creek females	0.60	1.06	5.26 (15 days) 5.12 ± 2.08 (8 days)	7.03 (15 days) 8.66 ± 2.71 (8 days)
Emu Creek males	1.38 ± 0.53	5.12 ± 0.83	12.41 ± 2.28	20.78 ± 2.39
Emu Creek females	0.44 ± 0.19	3.18 ± 0.86	10.57 ± 1.09 (15 days) 7.74 ± 2.33 (8 days)	18.31 ± 1.87 (15 days) 12.45 ± 2.33 (8 days)
Tinaroo Creek males	1.28 ± 0.36	7.52 ± 1.32	15.25 ± 1.51	22.94 ± 2.21
Tinaroo Creek females	0.49 ± 0.13	2.06 ± 0.56	7.28 ± 2.13 (15 days) 6.48 ± 1.62 (8 days)	12.18 ± 3.43 (15 days) 10.48 ± 2.62 (8 days)
Dry season (all individuals)	1.24 ± 0.26	6.28 ± 0.90	13.54 ± 1.42	20.92 ± 1.88
Wet season (all individuals)	0.69 ± 0.16	3.03 ± 0.51	6.28 ± 0.90	13.68 ± 1.86

4.4.1.3 Core foraging areas after 15 days

Core foraging areas averaged 5.16 ± 0.67 ha (mean ± SE), with males having significantly larger core foraging areas than females ($F_{3,22} = 4.29$, $p = 0.0158$; Table 4.2). Core foraging areas of males were similar between sites (KW test, $\chi^2 = 0.711$, df = 2, $p = 0.701$), as were those of females ($F_{2,7} = 1.06$, $p = 0.396$) and both genders combined ($F_{2,22} = 1.33$, $p = 0.28$; Table 4.2).

Across all sites, the core area comprised 28.44% of *B. tropica* home range area, with the proportion being similar between sites ($F_{1,23} = 1.88$, $p = 0.175$; Davies Creek: 28.88 ± 3.52%; Emu Creek: 22.09 ± 2.02%; Tinaroo Creek: 27.04 ± 2.54%). *Bettongia tropica* used larger core foraging areas during the dry season (6.28 ± 0.90 ha) compared to the wet season (3.03 ± 0.51 ha) ($F_{1,22} = 8.19$, $p<0.001$), but in each season core foraging areas comprised a similar proportion of the home range (dry season: 27.60 ± 2.03%; wet season: 22.32 ± 2.02%; $F_{1,23} = 2.86$, $p = 0.104$).

4.4.1.4 Core nesting areas after 15 days

Core nesting areas were similar between males and females ($F_{3,22} = 1.22$, $p = 0.33$), between sites ($F_{2,22} = 0.38$, $p = 0.687$) and between seasons ($F_{1,22} = 1.81$, $p = 0.192$; Table 4.2). On average, core areas comprised only 5.70% of *B. tropica* home ranges, with a similar proportion during both seasons (dry season: 5.68 ± 0.09%; wet season: 5.18 ± 0.78%; KW test, $\chi^2 = 2.43$, df = 1, $p = 0.119$). There was no difference in the proportion of area covered between sites ($F_{2.26} = 0.625$, $p = 0.543$; Davies Creek: 6.56 ± 1.42%; Emu Creek: 4.63 ± 1.32%; Tinaroo Creek: 5.63 ± 0.79%).

4.4.2 Number of nesting areas (all days and 15 days of data)

When including all days of data, *B. tropica* utilised on average six nesting areas (5.73 ± 0.35) (mean ± SE) during both the wet (5.53 ± 0.40) and dry seasons (5.85 ± 0.50). From the first 15 days of data, *B. tropica* used a mean of four (3.96 ± 0.11) nesting areas, with the number of nesting areas being similar across sites ($F_{2,25} = 0.00$, $p = 1.00$) and seasons ($F_{1,25} = 0.00$, $p = 1.00$). There was no interaction between the number of nesting areas and season ($F_{2,25} = 0.029$, $p = 0.971$), core foraging area ($F_{1,25} = 0.036$, $p = 0.851$), or home range area ($F_{1,25} = 0.447$, $p = 0.510$).

A day-by-day visual assessment of the GPS fixes on Google Earth® showed there were multiple nests within a nesting area, with multiple nests observed to be only a few metres apart in the field (pers. obs.). There was no apparent trend in the number of days *B. tropica* used each nesting area. Nests were often used for a few consecutive days and were often returned to later even when not used for multiple days. The number of nests within each nesting area could not be accurately determined due to the small errors associated with the GPS fixes.

4.4.3 Influence of population density on home range and core areas

There was no relationship between population density and home range sizes and core foraging and nesting areas of males or females (Table 4.3).

Table 4.3. Results of linear regression assessing the relationship between population density, and the home range and core foraging and nesting areas of male and female *Bettongia tropica*.

Gender	Area	t value	p-value (<0.05 being important)	R^2
Male	Home range 99% UD	0.672	0.51	0.0259
	Home range 95% UD	0.106	0.246	0.0784
	Core foraging area	0.976	0.343	0.0530
	Core nesting area	0.269	0.791	0.00425
Female	Home range 99% UD	-1.057	0.32	0.123
	Home range 95% UD	-1.093	0.36	0.13
	Core foraging area	0.582	0.58	0.0406
	Core nesting area	-0.034	0.97	0.00014

4.4.4 Overlap of home ranges and core areas (all days of data)

On average, there was high (≈ 73.45 ± %) overlap between *B. tropica* home ranges. Between 77% and 96% (x̅ = 87.55 ± 4.56%) of female and 57% to 79% (x̅ = 65 86 ± 5.37%) of male home ranges were occupied by at least one other collared individual (Table 4.4).

More *B. tropica* were collared at Tinaroo Creek (n = 17) and thus the results from Tinaroo Creek are more likely to be accurate in terms of overlap than at the other sites. At Tinaroo Creek, around 80% of male and 90% of female home ranges were overlapped by another collared *B. tropica*. Over 79% of female home ranges were overlapped by at least one collared male (female-male overlap), which equated to less than 50% male-female overlap (Table 4.4).

Table 4.4. Average percentage of overlap between 99% UD home ranges of collared *Bettongia tropica* at Davies Creek, Emu Creek or Tinaroo Creek. 'Total' indicates that the home ranges of both collared male and female bettongs overlapped with that of another collared individual. 'M' and 'F' represents the number of males and females collared within each site. Standard errors are shown

Site	Male-Male	Male-Female	Male-Total	Male-Nil	Female-Male	Female-Female	Female-Total	Female-Nil
Davies Creek (M = 8, F = 3)	52.97 ± 10.01	18.40 ± 3.98	57.19 ± 8.07	42.81 ± 8.07	96.01 ± 2.62	0.00	96.07 ± 2.62	3.93 ± 2.62
Emu Creek (M = 9, F = 4)	49.86 ± 7.79	29.75 ± 5.08	61.67 ± 9.06	38.33 ± 9.06	77.42 ± 14.67	7.25 ± 0.00	77.44 ± 12.76	22.56 ± 21.36
Tinaroo Creek (M = 7, F = 10)	69.21 ± 12.97	44.60 ± 3.58	79.76 ± 9.80	20.24 ± 9.80	71.46 ± 11.36	62.98 ± 10.48	88.15 ± 6.33	11.85 ± 6.33

Note: Male-female denotes overlap of male home ranges by females, whilst female-male denotes the overlap of female home ranges by males.

At all sites, home ranges of multiple collared *B. tropica* partially overlapped. Some males completely overlapped the home range of one female and partially overlapped with other females (Figure 4.1, 4.2 and 4.3). The home range of each individual overlapped (either partially or completely) with up to seven others (Table 4.5).

Across all sites, up to four collared bettongs had partially overlapping core foraging areas (Table 4.5). Most individuals maintained separate or only partially shared foraging areas, although a few *B. tropica* had largely overlapping areas (Figure 4.1, 4.2 and 4.3). Most collared *B. tropica* had separate core nesting areas (Figure 4.1, 4.2 and 4.3). For the few *B. tropica* that did overlap, overlap tended to occur at the periphery of the area (Figure 4.1, 4.2 and 4.3).

Table 4.5. The minimum and maximum number of collared *Bettongia tropica* that occurred within another collared individual's home range (99% UD and 95% UD) and core foraging and nesting areas at Davies Creek, Emu Creek and Tinaroo Creek.

	Bettongs within 99% UD home ranges	Bettongs within 95% UD home ranges	Bettongs within core foraging areas	Bettongs within core nesting areas
Davies Creek	2 – 6	1 – 5	0 – 3	0 – 1
Emu Creek	1 – 5	0 – 4	0 – 3	0 – 1
Tinaroo Creek	0 – 7	0 – 5	0 – 4	0 – 1

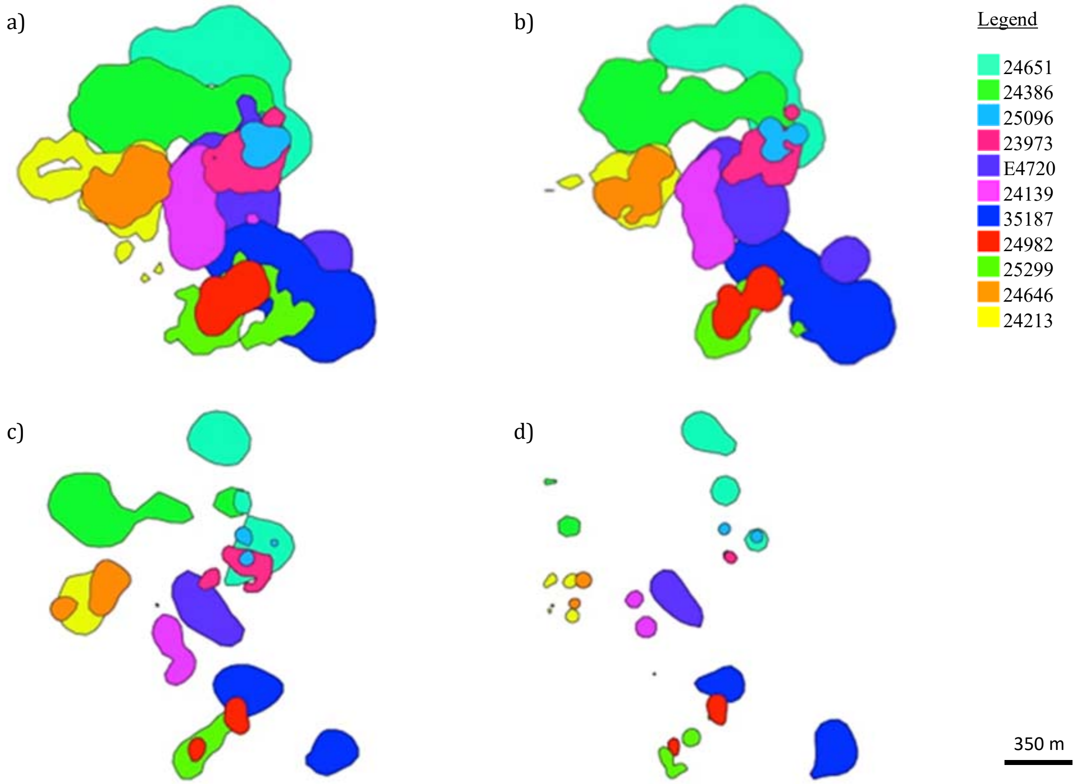

Figure 4.1. Overlap of *Bettongia tropica* (a) 99% and (b) 95% home ranges, and (c) core foraging and (d) nesting areas at Davies Creek. The microchip numbers of collared *B. tropica* are shown in the legend.

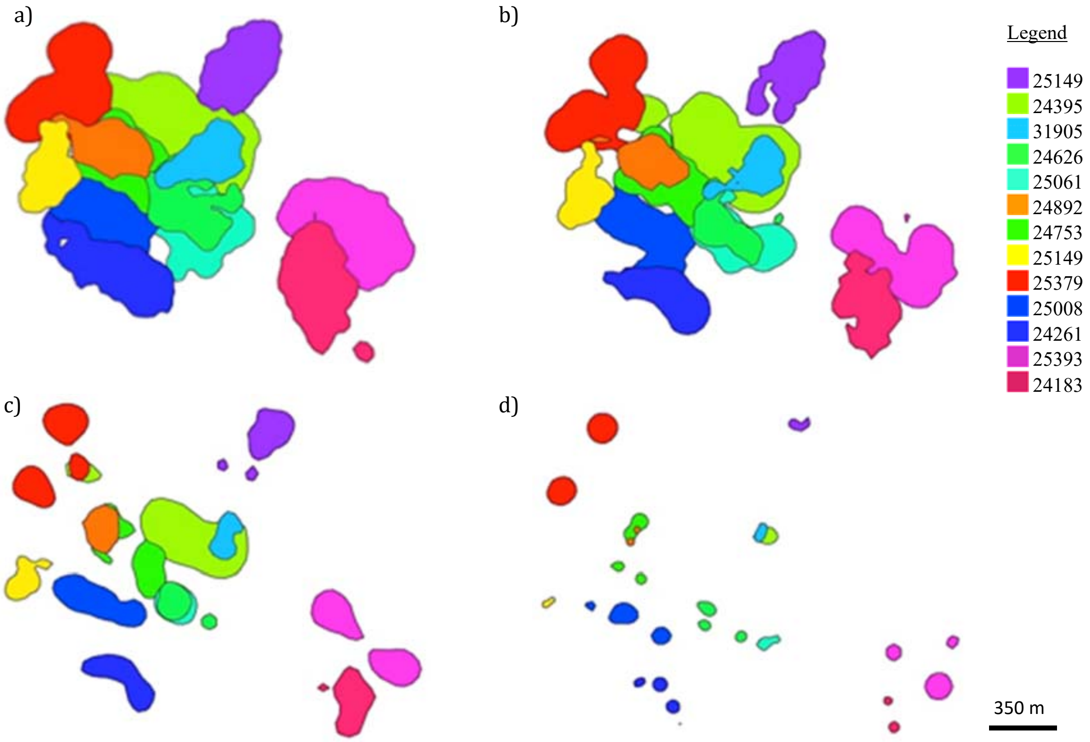

Figure 4.2. Overlap of *Bettongia tropica* (a) 99% and (b) 95% home ranges, and (c) core foraging and (d) nesting areas at Emu Creek. The microchip numbers of collared *B. tropica* are shown in the legend.

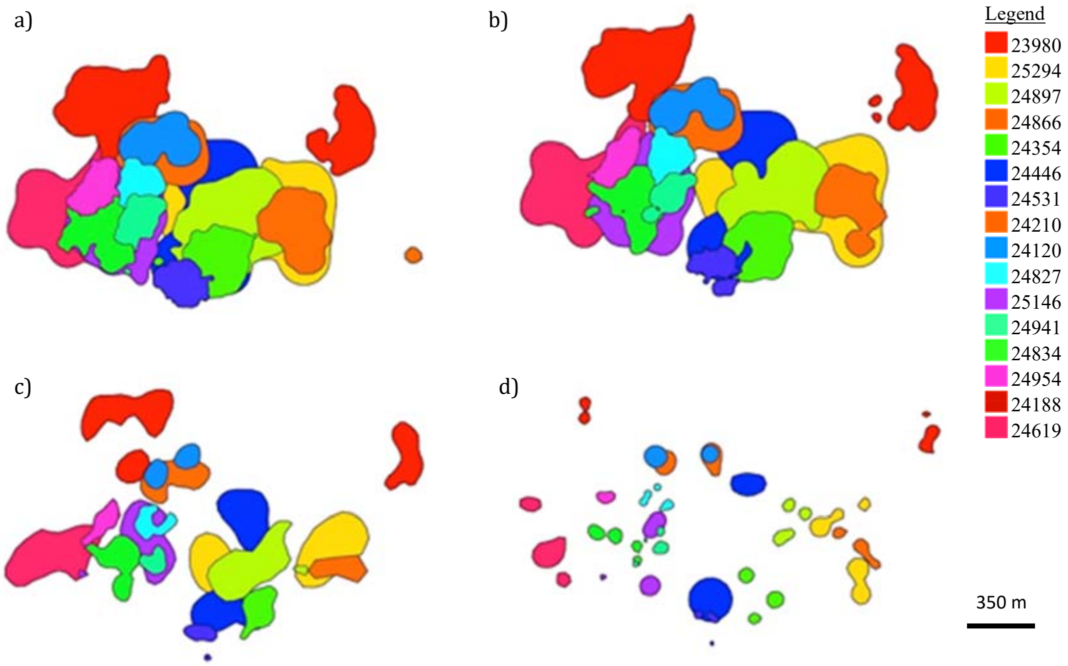

Figure 4.3. Overlap of *Bettongia tropica* (a) 99% and (b) 95% home ranges, and (c) core foraging and (d) nesting areas at Tinaroo Creek. The microchip numbers of collared *B. tropica* are shown in the legend.

4.4.5 Movement patterns

4.4.5.1 Distance and speed B. tropica travelled

Across the whole night, males travelled at similar speeds at each site, travelling around 190 ± 16.3 m/hr (KW test, $\chi^2 = 5.47$, df = 2, p = 0.0648). The mean distance male *B. tropica* travelled at Davies Creek was 1,840 ± 167 m/night, 1,873 ± 166 m/night at Emu Creek and 1,938 ± 154 m/night at Tinaroo Creek (Figure 4.4a).

Throughout the night, females at Tinaroo Creek travelled significantly slower (109 ± 7.6 m/hr) (KW test, $\chi^2 = 38.46$, df = 2, p<0.001) and shorter distances ($\bar{x}$ = 1,176 ± 76.7 m/night) than females at Davies Creek (136 ± 15.5 m/hr, $\bar{x}$ = 1,344 ± 155 m/night) (p<0.01) and at Emu Creek (162 ± 23.0 m/hr, $\bar{x}$ = 1,659 ± 230 m/night) (p<0.001) (Figure 4.4b). Interestingly, at Tinaroo Creek females appeared to return to their nest around 1am, rather than 3 am. This is evident by the movement rate between 1 and 2 am and 2 and 3 am being similar to the rate between 3 and 4 am when individuals were assumed to be nesting (Figure 4.5b).

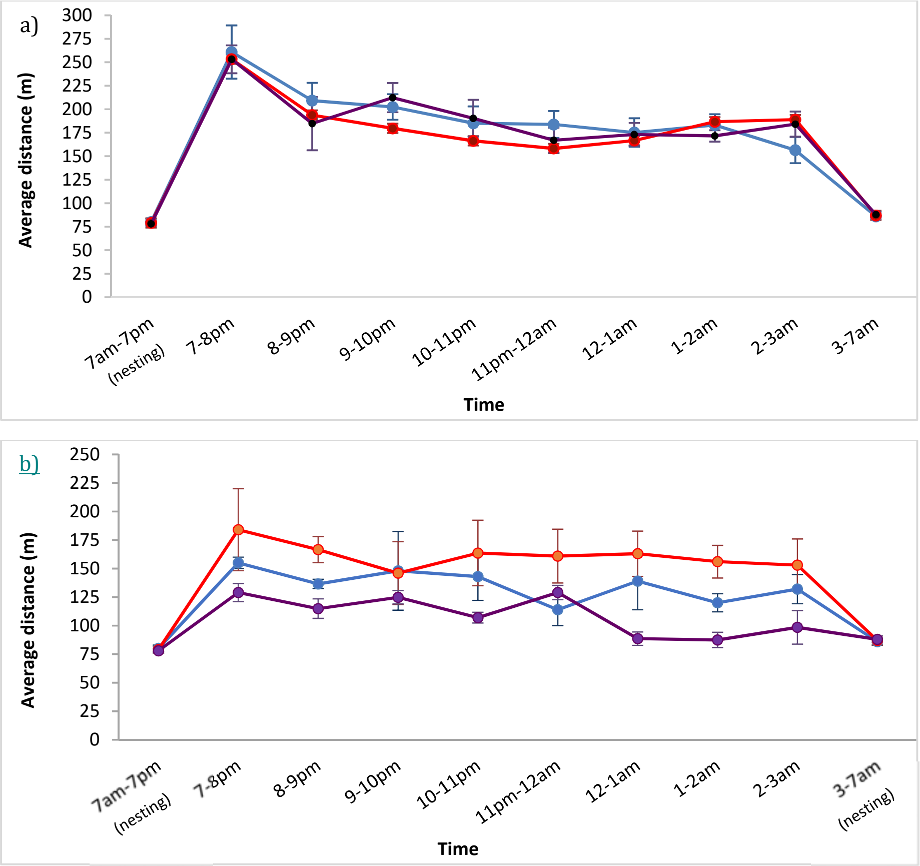

Figure 4.4. Mean speed travelled by (a) male and (b) female *Bettongia tropica* each hour between 7 pm and 3 am at Davies Creek (blue), Emu Creek (red) and Tinaroo Creek (purple). The movement rate recorded when *B. tropica* were nesting (and stationary) is caused by variations in the accuracy of GPS fixes.

Across all sites, males travelled 199.7 m/hr and 1,884 m/night. This was significantly (24 m/hr to 90 m/hr) faster (KW test, $\chi^2 = 1110.3$, df = 1, $p<0.001$) and 493 m/night further than females (Figure 4.5). Females travelled on average 126.8 m/hr and 1,391 m/night. Males travelled faster (235 m/hr) in the first hour of foraging (7-8pm) compared to any other hourly time period (KW test, $\chi^2 = 873.41$, df = 7, $p<0.001$; Figure 4.5). In contrast, female *B. tropica* travelled at a similar speed throughout the night (KW test, $\chi^2 = 4.69$, df = 7, p = 0.0957; Figure 4.5). Seasonally, both males and females travelled significantly further (roughly 300 m/night) during dry seasons (males: 2,030 m/night, females: 1,544 m/night) than during wet seasons (males: 1,704 m/night, females: 1,227 m/night) (males: KW test, χ^2 = 4.98, df = 1, p = 0.026; females: KW test, χ^2 = 3.93, df = 1, p = 0.047).

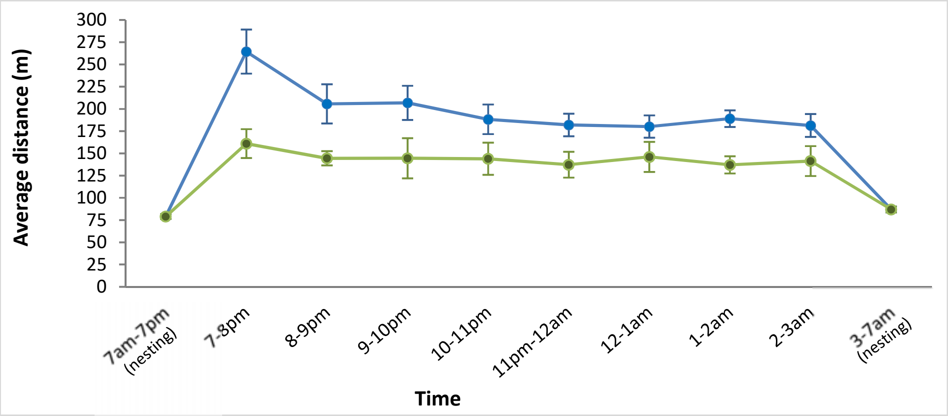

Figure 4.5. Mean speed travelled by male (blue) and female (green) *Bettongia tropica* each hour between 7 pm and 3 am, with data pooled for all study sites (Davies Creek, Emu Creek and Tinaroo Creek). Standard errors are shown. The movement rate recorded when *B. tropica* were nesting (and stationary) is caused by variations in the accuracy of GPS fixes.

4.4.5.2 Slow, medium and rapid movements

Across all sites, both males and females spent most (>60%) of the time travelling slowly, with around 20% to 30% of their time travelling at a medium pace and minimum time (<10%) travelling rapidly (Table 4.6). Males travelled at a medium and rapid pace significantly more than females (Figure 4.5; medium: $F_{1,39} = 20.77$, $p<0.001$; rapid: KW test, $\chi^2 = 22.69$, df = 1, $p<0.001$). Females spent a greater proportion of time travelling at a slow pace compared to males (Table 4.6; slow: $F_{1,39} = 28.81$, $p<0.001$).

Table 4.6. Percentage of time male and female *Bettongia tropica* spent travelling at a slow (<3 m/min), medium (3-8 m/min) and rapid (>8 m/m) pace across all sites and at Davies Creek (DC), Emu Creek (EC) and Tinaroo Creek (TC).

	All *B. tropica*	Males	Females	Males at DC	Males at EC	Males at TC	Females at DC	Females at EC	Females at TC
< 3m/min	68	62	77	60	66	62	75	64	82
3-8 m/min	26	29	20	31	26	30	22	30	17
> 8 m/min	6	9	3	9	8	8	3	6	1

4.4.5.3 Turning angle

When travelling slowly, both male and female bettongs used each 15º turning angle increment relatively evenly (Figure 4.6). This indicates *B. tropica* undertake relatively random movements when travelling slowly. There was a slight tendency for bettongs to reverse their direction of travel (with angles around 180º preferred), especially for females (Figure 4.6). At a medium pace, males tended to continue travelling straight or with a low turning angle (turning up to 30º to the left or right) (Figure 4.6). In contrast, females tended to reverse their direction of travel (turned 180º) (Figure 4.6). When travelling quickly, males tended to maintain a similar direction of travel, with females generally either continuing straight ahead or reversing their direction (Figure 4.6).

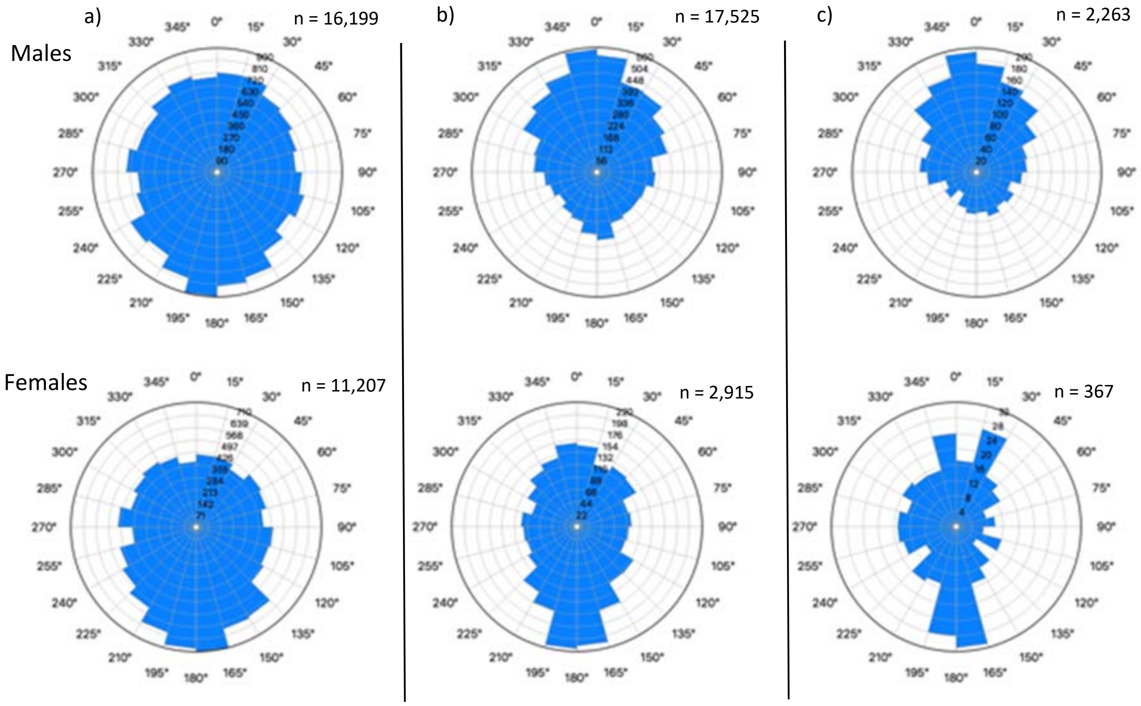

Figure 4.6. Turning angle of male and female *Bettongia tropica*, when travelling at (a) slow (<3 m/min), (b) medium (3-8 m/min) and (c) rapid (>8 m/min) pace. The frequency for each radius (rings within the rose diagram) is shown, whilst n indicates the total number of fixes recorded for each speed category.

Analysis of *B. tropica* movement trajectories from one night showed bettongs travelled slowly and moved back and forth (i.e. high angle of deviation) within a small area. These are considered to be foraging movements (Figure 4.7). *Bettongia tropica* undertook medium pace movements when travelling to a foraging area to and from their nest and between nearby foraging patches (Figure 4.7). When moving rapidly, *B. tropica* usually travelled from their nest to a foraging area or, less commonly, between two foraging areas that were far apart (Figure 4.7).

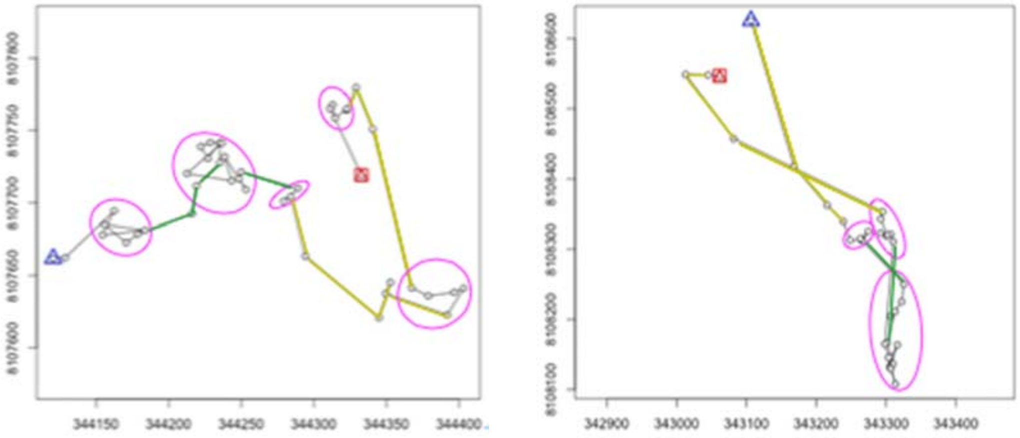

Figure 4.7. Movement patterns of two different *Bettongia tropica* travelling at slow, medium and rapid paces throughout a night (7 pm to 3 am) during the February 2016 trapping sessions. Slow movements patterns with fixes close together are thought to indicate foraging and are circled in pink. Medium and rapid movements are highlighted in green and yellow respectively. The blue triangle represents the starting point of travel (after *B. tropica* emerge from their nest), whilst the red square indicates the nesting area when *B. tropica* finish foraging for the night. The numbers along the x- and y-axes are spatial co-ordinates for plotting the GPS fixes.

4.5 Discussion

This study is the first to use Global Position System (GPS) technology to track *B. tropica* and to assess their home range and movement ecology across the three main sub-populations within the Lamb Range. This study provides baseline and detailed information on the movement patterns of *B. tropica*.

Home range estimates from this study are around a third of the size of the previous estimate of 59 ha obtained using radio-telemetry collars (Vernes & Pope 2001). This difference is likely due to Vernes and Pope (2001) radio-tracking *B. tropica* over 3 to 17 months, with their data therefore accounting for seasonality. Tracking animals for longer time periods generally increases home range estimates (Conner et al. 1999). Seasonal changes in habitat use also have an important influence on home range size (Girard et al. 2002). For example, Conner et al. (1999) determined that as the duration of monitoring increased, the annual home range size of bobcats (*Lynx rufus*) increased, whilst the home range size of females decreased from the previous year. My home range estimates are seasonal estimates only and likely underestimate the home range size an individual would require for an entire year. Additionally, Vernes and Pope (2001) determined that nest area of *B. tropica* increased with each new fix until an asymptote was reached. It is likely that my home range estimates would have been larger if more fixes were recorded.

4.5.1 Home range area

Bettongia tropica had similar home ranges across sites. This was in contrast to expectations, as I had expected that *B. tropica* at Emu Creek would have larger home ranges due to Emu Creek being on the drier, western margin of *B. tropica*'s distribution (Bateman et al. 2011) and having the driest habitat of the three sites (Chapter 3; Vernes & Pope 2006). The diversity and/or abundance of truffles are typically lower and more affected by seasonality within drier habitats (Abell et al. 2006; Danks et al. 2013). Similar home range size of *B. tropica* and similar body condition between sites (Chapter 3) suggests the sites had equally productive habitats, including similar food and nesting resources, for the duration of my study. This is also reflected in similar population density between the three sites (Chapter 3).

It is possible that habitat productivity, in terms of sufficient food resources and safe nesting sites for raising young, were the drivers of female home range size. The use of space by females is usually focussed on maximising offspring survival (Bond & Wolff 1999) and the high cost of reproduction often results in females primarily competing with other females for food and space (Bond & Wolff 1999). The distribution of resources is thus an important factor influencing female home range size (Maher & Burger 2011; Schoepf et al. 2015). Finlayson and Moseby (2004) studied the home range of female burrowing bettongs (*Bettongia lesueur*) within two enclosures in the Arid Recovery Reserve. The researchers found that in areas with more food, bettongs had slightly small home ranges and higher reproductive rates (Finlayson and Moseby 2004). Fisher and Owens (2000) reviewed the home range size and social organisation in 28 species of Australian or Papua New Guinean macropod marsupials, including bettongs, musky rat-kangaroos, potoroos, kangaroos, wallabies, wallaroos, tree kangaroos, pademelons and hare-wallabies. Habitat productivity had the greatest influence on marsupial home range size and females had smaller home ranges in productive habitats compared to less productive habitats (Fisher and Owens 2000).

Males had larger home ranges than females, despite both genders having similar body condition (Chapter 3). For mammal species with polygynous mating systems, such as *B. tropica* (Pope et al. 2012), the size or location of male home ranges is often influenced by access to mates (Loe et al. 2009) and female movements, as well as food resources (Bond & Wolff 1999; Hanski et al. 2000). It is likely that males required larger home ranges as they searched for and defended access to receptive females, with these behaviours also increasing their energy expenditure. Similarly, Fisher and Owens (2000) found that in high rainfall areas where habitats are productive, there is a large sex difference in the home range size of macropod marsupials. Males competed with each other for females by searching widely and in productive habitats increased their home range size to overlap with more females (Fisher and Owens 2000). In contrast, in less productive habitats, males were unable to increase their already large home range and females also required larger home ranges (Fisher and Owens 2000). Resultantly, in less productive habitats, males and females had similar sized home ranges (Fisher and Owens 2000). Larger home ranges of male *B. tropica* suggests that the Lamb Range supports highly productive habitat for *B. tropica*.

Bettongia tropica that were collared during the wet season had smaller home ranges than those collared during the dry season. Higher rainfall increases the abundance of highly nutritious truffles (Abell et al. 2006) reducing the need for individuals to travel long distances to access food. This would allow for smaller home ranges at that time. Similarly, Cook (2010) radio-tracked the movements of northern quolls (*Dasyurus hallucatus*) in Mitchell Plateau on the Kimberly (Australia) during the wet and dry seasons and also determined that home ranges were smaller during the wet season when there was a higher abundance of food resources (invertebrates). In contrast, Taylor (1993b) radio-tracked Tasmania bettongs (*Bettongia gaimardi*) for three weeks in August and November 1986 and February and May 1987 and determined that there was no major shift in the size or location of individuals' home ranges between seasons.

4.5.2 Core foraging areas

Bettongia tropica had relatively large core foraging areas (≈ 26% of the home range). Core areas often contain a high density of resources (Asensio et al. 2012; Feldhamer et al. 2015). The presence of core areas indicates that resources used by *B. tropica* occur within higher density patches in parts of the landscape. For *B. tropica*, males had larger core foraging areas than females, likely reflecting their larger home ranges and higher nutritional requirements. In contrast, Vernes and Pope (2001) concluded that *B. tropica* at Davies Creek did not have core areas. The difference between results is likely due to difference in analysis methods and my study having more fixes at a fine-scale, which enables intensely used areas to be determined.

Core foraging areas were substantially smaller (around half the area) during the wet season than the dry season, corresponding with smaller home ranges in the wet season. Interestingly, the core foraging area comprised a similar proportion of the home range during both wet and dry seasons (20 to 30%). This suggests that there may be a relationship between the size of home ranges and foraging areas, with the habitat being sufficiently productive that *B. tropica* are supported by 20 to 30% of their range for most, but not all, of the time.

The core foraging areas of *B. tropica* are relatively large for an Australian marsupial. For example, the core foraging areas of brush-tailed rock-wallabies (*Petrogale penicillata*) (≈ 5 to 10 kg (Eldridge & Close 1998)) were only 2.5 ha ± 0.24 (mean ± S.E) and comprised 9.62% of their 26 ha ±1.69 (mean ± S.E) home range (Molyneux et al. 2010). This indicates that the resources that *B. tropica* rely upon are sparsely distributed, even when at higher density within core areas, compared to resources used by other mammals. This accords with the recognised sparse distribution of truffles (Claridge 2002; O'Malley 2006), one of the major food resources of *B. tropica*.

4.5.3 Core nesting areas

Nesting areas were similar across all sites and between genders. Field observations identified multiple nests within a nesting area. Constructing multiple nests within a relatively small area may reduce predation risk when *B. tropica* are nesting. Constructing more nests may provide greater camouflage from predators (Wallis et al. 1989; Vernes & Pope 2001) and using multiple nests may also decrease the chance of predators learning the movement patterns of prey species (Ji et al. 2003) and then returning to hunt prey within their nest (Weidinger 2010). Predator abundance influences nesting behaviours of other species (Sherry et al. 2015), with common brushtail possums (*Trichosurus vulpecula*) usually favouring one den tree but having multiple dens to minimise predation risk, assist in territorial defence and/or decrease ectoparasite infestations (Statham & Statham 1997; Ji et al. 2003; Harper 2005; Carthew et al. 2015).

My result contrasts with Pope et al. (2012), who radio-tracked *B. tropica* and found that male nesting areas were double the size of females. Pope et al (2012) calculated nesting area based on triangulating radio-tracking signals. The difference in the size of nesting areas between studies is most likely due to the difference in methodologies and the spatial scale at which data were recorded.

4.5.4 Number of nesting areas

Bettongia tropica used multiple nesting areas throughout their home range. This result differs from previous studies, which found that *B. tropica* have a central nest range (Seebeck et al. 1989; Pope et al. 2012). The difference between studies may be due to the difference in number of fixes used. Vernes and Pope (2001) used between 3 and 32 fixes throughout the year to estimate nesting area, whereas my study used an average of 1,419 fixes per individual during a season to calculate nesting area. The distance between nesting and foraging areas usually depends on food availability (Catry et al. 2013), as nesting far from foraging areas is generally inefficient (Kerbiriou et al. 2006). The location of *B. tropica* nests appears to have minimised travel between nesting and foraging areas, with these areas tending to be either in the centre or at the two peripheral ends of home ranges (Figures 4.4, 4.5 and 4.6). For example, Taylor 1993b found that Tasmanian bettongs used different sets of nests in different months, despite the home range size and location not shifting substantially between seasons.

Other bettong species, including the Tasmanian bettong (*Bettongia gaimardi*) and rufous bettongs, also tend to have a clumped distribution of nesting areas, with nests of Tasmanian bettongs usually, but not always, being near the periphery of their range (Mooney & Johnson 1979; Wallis et al. 1989; Taylor 1993b).

Both male and female *Bettongia tropica* used a similar number of nesting areas across all sites and during both seasons. This was surprising considering home range size varied between genders and seasons and it was expected that an increase in home range size would correspond with an increase in the number of nesting areas. It is possible that *B. tropica* can only maintain a certain number of nests, after which the cost of constructing nests is greater than the energy that would be saved by having additional nests. Alternatively, there may have been insufficient resources for *B. tropica* to create more nesting areas. However, this seems unlikely given that some individuals had up to 10 nesting areas and *B. tropica* utilise a variety of commonly available materials for nesting (Chapter 5; Vernes & Pope 2001).

4.5.5 Influence of population density on home range, core foraging and core nesting areas

Interestingly, the home ranges and core areas of both males and females were unrelated to population density. This is surprising considering an increase in population density usually increases overlap of individual home ranges (Schoepf et al. 2015), which then reduces the availability of productive habitat and/or resources available per individual (Nummi et al. 2015). Tinaroo Creek had the highest population density and a wetter habitat and thus should support more productive habitat and/or food resources than other sites (Chapter 3). It was expected that female home ranges at Tinaroo Creek would be smaller than at other sites, as individuals would not need to travel as far to access resources, whilst male home range size was expected to be larger or smaller depending on their proximity to females. For example, both male gray-tailed voles (*Microtus canicaudus*) and brushtail possums (*Trichosurus vulpecula*) expanded their home range sizes in response to population density to maintain contact with females (Bond & Wolff 1999; Ramsey et al. 2002). For *B. tropica*, competition for resources may balance resource density, resulting in a lack of relationship between population density and home range size or core areas. Although the habitat at Tinaroo Creek should provide more food resources, the higher population density means those resources are likely shared between more individuals. This results in home ranges being larger than would be required without the influence of competition (if only food resources were considered). In contrast, the drier habitat and fewer food resources at Davies Creek and Emu Creek, where population density is lower (Chapter 3), means that fewer resources are shared amongst fewer individuals. This results in the home ranges being similar in size to the home ranges of *B. tropica* at Tinaroo Creek. This indicates that overall competition per resource may be similar between populations and result in home ranges being similar sizes. Since home ranges are similar, this means that core areas are also similar (as the core area is proportional to the home range size). Alternatively, there might have been insufficient variation in population density between trapping sessions and sites to detect a relationship between home range size and population density.

4.5.6 Overlap

4.5.6.1 Overlap between home range areas

As expected, there was large overlap between *B. tropica* home ranges. Mammals often have overlapping home ranges in order to access sufficient food resources (Di Pierro et al. 2008). When resources are patchily distributed, it is inefficient for animals to defend access to their entire home range (Oldfield et al. 2015; Hinsch & Komdeur 2017). For *B. tropica*, the sparse distribution of resources, especially their main food resources (truffles and cockatoo grasses), means it is likely to be more energy efficient for home ranges to overlap.

Home ranges of male *B. tropica* tended to overlap with multiple females, with some males completely overlapping with one female and partially overlapping with other female ranges. Due to their smaller size, female home ranges usually only overlapped with small areas of male *B. tropica* home ranges. Male home ranges did not completely overlap with that of another male, suggesting that the location of male home ranges is likely influenced by the distribution of females. Females had no consistent trend in use of nesting areas meaning male *B. tropica* need to cover large areas to find females. By locating their home range so it overlaps with multiple females, males would increase their chance of encountering a female. This suggestion is supported by genetic studies by Pope et al. (2012), which found that mating primarily occurred between individuals that had home ranges close to one another. Previous studies on other small mammals, including rufous bettongs, found that when females were sparsely or uniformly distributed, male home ranges overlapped with female ranges and females were shared amongst males (Ostfeld 1990; Frederick & Johnson 1996; Hanski et al. 2000; Kjellander et al. 2004; Aronsson et al. 2016). Frederick and Johnson (1996) found that male rufous bettongs maintained transitory contact with multiple females likely to maximise their mating opportunities. For management, it is important to understand the degree of overlap between individuals to ensure the habitat is managed to support multiple individuals (Porolak et al. 2014).

Some collared *B. tropica* did not overlap with any other collared individuals. However, this was most likely due to those individuals being collared near the edge of the trapping grid and the majority of their home range being outside of the grid. It is probable that these *B. tropica* overlapped with other bettongs outside of the trapping area. Only the overlap of collared *B. tropica* was analysed. Non-collared bettongs were cage trapped within the home ranges of collared bettongs and it is likely that more *B. tropica* have overlapping ranges than suggested by my data.

4.5.6.2 Overlap between core foraging areas

At all sites, there was little or no overlap of core foraging areas of most collared *B. tropica*. This was surprising considering the high overlap between home ranges. This suggests *B. tropica* may be territorial in defending foraging areas. Fighting was also occasionally observed on camera trap photos (Whitehead, 2017 unpublished data). The energy gained from sole access to the resources must outweigh the associated cost of their defence (Frafjord 2016). Similarly, Sharpe and Goldingay (2007) concluded that the Australian squirrel glider (*Petaurus norfolcensis*) had 50% overlap of home ranges with gliders from different social groups, but only a 12% overlap of core areas. Alternatively, if individuals depleted the resources within their core area, there would be no attraction for others to use it.

4.5.6.3 Overlap between core nesting areas

Collared *B. tropica* also tended to have no or minimal overlap between core nesting areas. Defending these resources may also have a net benefit. *Bettongia tropica* may also avoid sharing nesting areas to minimise predation risk. Increased prey density can enhance the ability of predators to detect prey, which increases predation risk (Ioannou et al. 2009). Christensen and Leftwich (1980) determined that brush-tailed bettongs typically had territorial nesting areas, with overlap occasionally occurring between males and females. In contrast, Pope et al. (2012) determined that the nesting areas of radio-tracked *B. tropica* overlapped, although there was minimal female-female overlap. Mooney and Johnson (1979) and Taylor (1993b) also used radio-tracking and determined that the nesting areas of multiple female Tasmanian bettongs overlapped, whilst male Tasmanian bettongs had partially overlapping nesting areas. Differences in predation pressure between study sites may cause differences in nesting behaviours between bettongs.

4.5.7 Movement patterns

4.5.7.1 Distance and speed B. tropica travelled

Bettongia tropica travelled substantially faster in the hour following nest emergence. Travelling quickly through areas indicates either that the habitat is high risk or of low quality and individuals are trying to minimise time within these areas (Calcagno et al. 2014; Mäkeläinen et al. 2016). Individuals often undertook fast, relatively linear and direct movements to foraging areas. Similarly, Thompson (1982) determined that the desert woodrat (*Neotoma lepida lepida*) moved rapidly from their den to foraging areas and between foraging areas, with few exploratory movements undertaken.

Travelling quickly after nest emergence possibly reduces the chance of predators learning the location of nesting areas (Borgo 2008). Whilst radio-tracking *B. tropica* to their nest, all individuals rapidly exited their nests when approached to within 5 to 10 m and travelled quickly away from the nest for at least 50 m (pers. obs.). Based on the GPS tracks, these collared *B. tropica* fled to another known nesting area. Only on one occasion did an individual flee to a previously non-tracked nesting area.

Fleeing behaviour has also been observed for rufous bettongs, and is thought to be a response to predators (Jarman 1991).

Upon emerging from the nest, *B. tropica* often travelled rapidly and directly to a previously used foraging area. In contrast, when returning to the nest, individuals often moved slower, with their last foraging area often close to the nesting area. This pattern was evident even when a bettong returned to the same nesting area. Similarly, Hanski et al. (2000) found that 49% of nesting areas of Siberian flying squirrels (*Pteromys volans*) were situated near foraging areas, whilst José-Domínguez et al. (2015) concluded that 77% of the time, northern pigtailed macaques (*Macaca leonina*) nested close to their last feeding area or the first used the next morning. For *B. tropica*, this strategy should minimise energy spent in travel. It also indicates that individuals might plan their foraging routes so that they travel towards a nesting area at the end of the night. Interestingly, in the 20 minutes prior to reaching their nest, some *B. tropica* occasionally travelled faster and relatively directly (linear movements) to the nest. This behaviour is thought to assist in avoiding detection by predators at the nest site.

Interestingly, female *B. tropica* at Tinaroo Creek appeared to return to their nest at around 1 am rather than 3 am. Undertaking fewer medium- and rapid-paced movements indicates Tinaroo Creek females spent less time travelling between resources. Travelling slower and foraging for a shorter time (until 1 am) indicates that resources at Tinaroo Creek occur at much higher density than at the other sites. Thus *B. tropica* can spend more time foraging (indicated by slower movements) and can acquire sufficient resources within a shorter time period. Similarly, studies on birds show that longer foraging trips and greater distances from nest to foraging areas indicate fewer or less preferred resources within the habitat (Catry et al. 2013; Heldbjerg et al. 2017).

4.5.7.2 Slow, medium and rapid movements

Bettongia tropica commonly undertook three different speeds of travel. Both male and female *B. tropica* spent the majority of their time travelling slowly, indicative of foraging. Vernes and Pope (2001) previously found that slow, highly angular movements were indicative of *B. tropica* foraging, although it is acknowledged that it might indicate moving through dense vegetation. Medium and rapid movements were assumed to indicate travelling between resources, searching for mating opportunities or possibly fleeing from predators. Females spent more time (77%) moving slowly, and assumed to be foraging, than males (62%). This is likely due to males also spending time searching for mating opportunities, a result also found for short-beaked echidnas (Sprent & Nicol 2012).

4.5.7.3 Turning angle

When travelling slowly, both males and females appeared to move at random, with all angle increments being used in similar proportions. Vernes and Haydon (2001) previously used spool-and-line tracking and determined *B. tropica* at Davies Creek undertook area-restricted searching patterns (slow, angular movements) when food resources were detected. Area-restricted searching improves the efficiency of locating resources, as animals move slower and turn at greater angles to increase their use of high-density resources (Vernes & Haydon 2001; de Knegta et al. 2007). My results suggest that *B. tropica* display this movement pattern across all study sites.

When moving at a medium and rapid pace, both male and female *B. tropica* tended to travel in a linear direction (either continuing straight or turning at 180º). This indicates *B. tropica* might use linear features for orientation, and either follow ridges or valleys or maintain a constant elevation along the side of a ridge when travelling between resources or nesting and foraging areas (Davies et al. 2013; Bracis et al. 2015; Massa et al. 2015). Vernes (2003) found that *B. tropica* were more frequently cage trapped when cages were placed along ridgelines compared with cages placed on mid-slopes or gullies. It is likely that *B. tropica* utilise ridgelines when travelling quickly to or between resources. Interestingly, males tended to continue travelling straight (or with minimal deviation), whilst females tended to reverse their direction of travel and travel back and forth along a ridgeline within a night. This may indicate males who are seeking females continue on a linear search path to find females when initially unsuccessful. Based on the movement trajectory plots (Figure 4.7), *B. tropica* alternated between slower (foraging) and faster (travelling) movements throughout the night. Switching between movement patterns provides an efficient way for species to forage and cover large distances when resources are limited or patchily distributed (Davies et al. 2013; Bracis et al. 2015; Massa et al. 2015).

4.6 Management implications

Bettongia tropica populations within the Lamb Range are currently managed at a 60 ha scale (R. Miller, pers. comm.), based on the previous home range estimate of 59 ha (Vernes & Pope 2001). My study determined that *B. tropica* had a seasonal mean home range size of 20.90 ± 1.55 ha. Management actions tend to be undertaken at a seasonal scale (e.g. management burns are conducted during one season) and therefore a 20 ha scale is a more appropriate measure for management. It is noted that fire management conducted at a 60 ha scale was being applied regularly across the Lamb Range since 2005 and the population density of *B. tropica* remained stable during this time. This suggests that management burns of between 20 ha and 60 ha are suitable for *B. tropica*. During dry years when resources are likely to already be scarce, it is recommended that management burns be applied at a 20 ha scale to ensure there are sufficient nesting and foraging resources for *B. tropica* post-burn. The fine-scale nesting and foraging requirements of *B. tropica* are discussed in the following chapter.

Chapter 5: Fine-scale habitat use by *Bettongia tropica*

5.1 Abstract

Context. Information regarding microhabitat selection is crucial for the conservation of endangered species, as it enables managers to promote and protect the resources that are important to species.

Aims. For three sub-populations on the Lamb Range, Queensland, I aimed to determine the microhabitats that the northern bettong (*Bettongia tropica*) selected whilst nesting and foraging. I also assessed the nesting materials *B. tropica* used and the presence of predators and competitors in each sub-population.

Methods. *Bettongia tropica* were radio-tracked to their nest and the nesting material they used was recorded. Vegetation surveys were conducted at 90 nesting and foraging areas of 18 GPS-collared *B. tropica* and compared with the microhabitat at 90 areas not known to be used for nesting or foraging (random areas). Additionally, camera trapping was undertaken for 12 nights targeting bettongs and 12 nights for predators and competitors every two to three months, with 4,320 camera trap nights conducted at each site (12,960 in total).

Key results. *Bettongia tropica* predominantly constructed nests from grass (*Poaceae* spp.) or nested underneath grass trees (*Xanthorrhoea johnsonii*). Nesting areas had higher grass cover, more grass trees, and were situated on steeper slopes than random areas. In contrast foraging habitats of *B. tropica* had more cockatoo grass (*Alloteropsis semialata*) (food resource) and diggings (indicating consumed food resources) and were situated on steeper slopes than non-foraging areas. At all sites, mammalian predators included dingoes/wild dogs (*Canis lupus*), with a cat also detected at Tinaroo Creek. Feral pig competitors (*Sus scrofa*) occurred throughout the landscape, whilst rufous bettongs (*Aepyprymnus rufescens*) and cattle (*Bos taurus*) were also present at Emu Creek. There was a ratio of around one predator image per 60-70 *B. tropica* images and an average of one competitor to 92 *B. tropica* images across all three sites.

Conclusions. Microhabitats selected for nesting appeared influenced by variables that increased camouflage from predators, whilst microhabitats chosen for foraging had a higher abundance of food resources and offered cover from predators.

Management implications. Predation risk appeared to influence both nesting and foraging microhabitat selection in *B. tropica* and further research into predation pressures would benefit the conservation of this species. The microhabitat variables important for nesting and foraging should guide the focus of future conservation management. *Bettongia tropica* populations require maintenance of high levels of grass cover, grass trees and cockatoo grass on steeper slopes. By concentrating in areas with those attributes, the efficiency of future bettong surveys can also be improved.

5.2 Introduction

An understanding of where species occur should provide an insight into their habitat requirements (Beerens et al. 2015) and other factors that influence habitat use and distribution (Stirnemann et al. 2015). Biotic factors, such as species interactions, habitat variables and food availability, usually drive species occurrence on a local scale, whilst abiotic factors are important on a large scale (Anson & Dickman 2012; Anson et al. 2013; Allen et al. 2015). Small mammals are often associated with specific broad or fine-scale habitat features (Tulloch & Dickman 2006; Pizzuto et al. 2007) or topography (Claridge et al. 1993). Claridge et al. 1993 studied the foraging patterns of the long-nosed potoroo (*Potorous tridactylus*) in mixed-species and regrowth eucalypt forests in southeastern Australia by examining the occurrence and abundance of diggings as a measure of foraging effort. They found that in multi-aged forests, long-nosed potoroos preferred foraging in midslope-shelter aspects and in gullies compared to other habitats, such as midslope-exposed aspects (Claridge et al. 1993). In southern Brazil, Melo et al. (2013) studied microhabitat selection by six small mammal species in deciduous forest and determined that rodents favoured ferns, tree trunks or lianas, whilst opossums selected fallen or standing trunks, *Piper* spp. shrubs and/or lianas. Subtle habitat changes may substantially impact upon the population size or survival of a species (Entwistle & Stephenson 2000). It is thus important that managers know which microhabitats are important for species and tailor their management practices to promote them (Entwistle & Stephenson 2000).

Mammals may use different habitats for foraging and nesting (Killeen et al. 2014). Some mammals use nests to rest, shelter from harsh environmental conditions, avoid predators and/or raise young (Korb 2008; Cudworth & Koprowski 2011; Minias 2014). These species typically nest in natural cavities (e.g. logs or tree hollows), under vegetation, within burrows or dens (Lesmeister et al. 2008) or construct nests from vegetation (Naughton 2012; Juškaitis et al. 2013). Optimal foraging theory (Emlen 1966; MacArthur & Pianka 1966) suggests that animals should select habitats that maximise fitness, whilst reducing the costs associated with acquiring resources (Morellet et al. 2013; Favreau 2014; Stirnemann et al. 2015). These costs can include predation risk, competitive interactions (Morellet et al. 2013; Favreau 2014; Stirnemann et al. 2015) and distance required to travel to resources (Fanson et al. 2008). Ideally species would nest and forage either within the same area or nearby to minimise travel between areas (Chapman et al. 1989). However the different purposes of nesting areas (to provide safety whilst resting (Korb 2008; Minias 2014)) and foraging areas (to maximise food intake (Pyke et al. 1977)), often results in different habitat requirements for nesting and foraging (Lee et al. 2010).

Species interactions can also influence habitat use (Young et al. 2017). Predation is often the main factor influencing survival at nesting areas (Ricklefs 1969) and theoretically habitat features at nesting areas should be selected to minimise predation risk (Chiavacci et al. 2014). Predation risk is usually a large cost associated with foraging, with habitat selected for foraging being a balance between maximising food intake and minimising predation risk (Brown & Kotler 2004; Stone et al. 2017). A typical response to predation risk is that individuals will select denser vegetation when predation pressure is high and more open vegetation when predation risk is low (Matessi & Bogliani 1999). Alternatively, animals may avoid habitats used by predators (Santin 2016). For example, Santin (2016) determined that in the Pilbara region in Western Australia, northern quolls (*Dasyurus hallucatus*) avoided habitats favoured by feral cats, including open habitats, spinifex grasslands and recently burnt areas. Instead, quolls utilised rocky outcrops, which appeared to act as refugia for the species (Santin 2016). Predation can also influence nest design or nesting materials (Beyer & Goldingay 2006; Le Roux et al. 2016). Competition between and within species can also affect habitat use, with high inter- or intra-specific competition potentially limiting the availability of high-quality nesting or foraging areas for non-dominant individuals or species (Young et al. 2017). Determining the presence of predator species and the level of competition within habitats is vital to understand the extent that predators and competitors influence habitat selection (Luttbeg & Sih 2004).

Interestingly, where species nest may influence where they forage and vice versa (Bjørneraas et al. 2012). For example, regardless of forage availability, animals may choose open habitats that only provide reasonable, rather than ideal forage, due to a preference for well protected resting habitats nearby (Bjørneraas et al. 2012). An understanding of both nesting and foraging habitat requirements is thus crucial for a comprehensive assessment of habitat use and to allow management that maintains or improves habitat quality (Beerens et al. 2015; Stirnemann et al. 2015). Maintaining habitat quality is important, as small changes in habitat or microhabitat features can result in substantial changes in predation risk, food availability or cover from inclement temperatures (Arthur et al. 2004; Brown & Kotler 2004). This may influence fitness and ultimately population abundance (Arthur et al. 2004).

The northern bettong (*Bettongia tropica*) is an example of a cryptic species with little known about its usage of nesting or foraging microhabitat. *Bettongia tropica* rest during the day in a nest they construct in locations designated as nesting areas (Vernes & Pope 2001). Between 1994 and 1996, Vernes and Pope (2001) studied the nesting material of *B. tropica* within one sub-population (Davies Creek) and determined that *B. tropica* constructed dome nests on the ground typically from grass, as well as building nests near logs or under grass trees. Microhabitat requirements were also assessed by relating cage-trapping capture rates with the habitat variables at each trap location (Vernes 2003). *Bettongia tropica* was trapped more frequently along open ridgelines than within more densely vegetated mid-slopes and gullies (Vernes 2003). However, in the Vernes (2003) study, the microhabitat surveyed was dependent on the placement of cages. Prior to my study, areas where bettongs naturally prefer to forage had not been assessed without the bias of baited traps. Additionally, microhabitat requirements for *B. tropica* were previously assessed at only one sub-population (Vernes

2003). Microhabitat requirements may differ between populations (Bjørneraas et al. 2012) and thus, a more comprehensive assessment of the microhabitat requirements of *B. tropica* was necessary.

5.2.1 Aims

This chapter aimed to determine the materials used for nesting and the microhabitat variables that were selected for nesting and foraging by *B. tropica* across the three main study sites on the Lamb Range (Davies Creek, Emu Creek and Tinaroo Creek). It was expected that at nesting areas, *B. tropica* would select locations that provided camouflage to increase protection from potential predators, including areas with high grass cover. *Bettongia tropica* was expected to forage within areas containing a higher abundance of food resources, including cockatoo grass. I also aimed to assess predator and competitor pressure at each site.

5.3 Methods

Tracking collars were deployed on *B. tropica* at the three study sites during cage trapping sessions, as detailed in Chapter 3.

5.3.1 Nesting materials

Most collared *B. tropica* were radio-tracked to a nest between one and four times during trapping to remove collars. Each individual had multiple nesting areas (Chapter 4). By surveying the multiple nesting areas, I obtained a clear indication of the habitat requirements for nesting. *Bettongia tropica* would flee when approached whilst radio-tracking, allowing the nest to be detected and the nest shape and construction materials to be recorded. Nesting materials were classified into five groups; grass trees, grass, logs, rocks and teepee nests constructed from sticks and grass (Plate 5.1). Very occasionally a nest was constructed from *Allocasuarina* branchlets and grass, with this nest type also classified as a grass nest (Plate 5.1). A nest was classified as a 'grass tree' when *B. tropica* built a grass nest under the 'skirts' of the grass tree (*Xanthorrhoea johnsonii*). Other features of nests were noted, including the plant species used for constructing nests and the grass within the nesting area. Plant species were identified based on expert knowledge (wildlife rangers) and personal knowledge.

Plate 5.1. Nests of *B. tropica* constructed from (a) and (b) grass, with (b) showing the top view outlined in red, (c) grass and *Allocasuarina* needles, (d) and (e) under the skirts of grass trees, and (f) teepee structure.

5.3.2 Habitat requirements at nesting, foraging and random areas

To determine whether *B. tropica* selected particular microhabitats for foraging or nesting, habitat surveys were conducted at foraging and nesting areas, as well as non-foraging and non-nesting areas (henceforth referred to as random areas). The locations of nesting and foraging areas were determined by plotting the fine-scale movement patterns (obtained from GPS data) on Google Earth® (Chapter 4). Nesting areas were identified as described in Chapter 4 (cluster of fixes between 7am and 6 pm). *Bettongia tropica* foraged between 7 pm and 3 am regardless of time of year (Chapter 4), with a high concentration of GPS fixes between these times indicating areas where individuals frequently foraged. The centre of each nesting and foraging cluster was selected for microhabitat sampling.

To select random areas, I plotted all GPS fixes and home ranges of collared *B. tropica* on Google Earth® (Chapter 4). I chose random areas (ones without any GPS fixes) based on random numbers that were generated to correspond with the latitude and longitude of the animal's home range. Areas selected were 25 m x 25 m to account for potential errors in GPS fixes. Although the random areas were not used for nesting or foraging by collared *B. tropica,* non-collared individuals may have used them.

Habitat surveys were conducted for three males and three females at each site. Individuals that had the most data recorded by their GPS collar were selected. At Davies Creek, only three GPS that were deployed on females recorded data (Chapter 4). Surveying the habitats of three individuals of each gender at each site provided an equal sample size across gender and sites. For each of the 18 selected *B. tropica*, habitat surveys were undertaken at five foraging, five nesting and five random (non-nesting and non-foraging) areas (15 areas per individual). A total of 270 areas were surveyed across the three study sites. Females used an average of five nesting areas (Chapter 4) and sampling at five areas (for each category) was deemed appropriate to accurately estimate habitat requirements.

At each foraging, nesting and random area, 15 habitat variables were measured. Habitat variables were sampled within a 20 m^2 area (2.5 m radius from each sampling location). Grass trees (*Xanthorrhoea johnsonii*) were counted and the diameter at breast height (dbh) for all trees ≥10 cm dbh was measured to calculate tree basal area (Plate 5.2). At the centre of the 20 m^2 area, tree canopy cover was measured in each cardinal direction using a densitometer (Paletto & Tosi 2009) (Plate 5.2). Cover for each of the four directions was averaged to ascertain overall canopy cover (Paletto & Tosi 2009). Soil volumetric water content (soil moisture) was measured at the central location within each 20 m^2 area using a HydroSense II to an accuracy of ± 3% (Campbell Scientific 2011). Soil resistance (R) was measured to 15 cm depth at six random points using a soil penetrometer. This depth was chosen as field observations indicated bettongs dig to a depth of up to 15 cm for truffles and around 5 cm for the shoot base of cockatoo grass (pers. obs.). Soil resistance was calculated using the equation $R = 2.439 \times$ mean number of blows (simplified from Alameda and Villard (2012)). Tree height (of a tree that was flush with the canopy) was calculated using trigonometry, with the angle measured using an inclinometer (Plate 5.2) and the distance to the base of the tree measured with a tape. Slope was measured as the angle of inclination from two points 10 m apart.

Every cockatoo grass (*Alloteropsis semialata*) stem (from the shoot base) and bettong digging was counted along a 5 m x 1 m transect through the centre of the 20 m^2 area (Plate 5.3). Diggings indicated consumed food resources. Leaf litter depth and grass height were averaged from 10 randomly sampled points along the 5 m transect (Plate 5.2). Three 1 m^2 quadrats were randomly placed within the 20 m^2 area and the percent cover of coarse woody debris (≥2.5 cm), leaf litter, rock, grass and bare soil estimated and averaged (Plate 5.4).

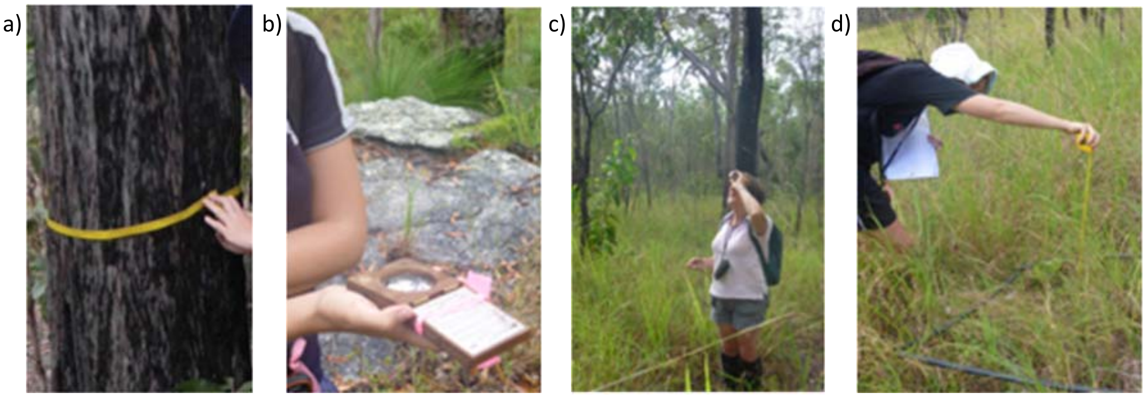

Plate 5.2. Measuring (a) tree diameter, (b) canopy cover using a densitometer, (c) angle of inclination to the tree canopy and (d) grass height. Photographs: (a) Peter Whitehead and (b) and (d) Elaine Whitehead.

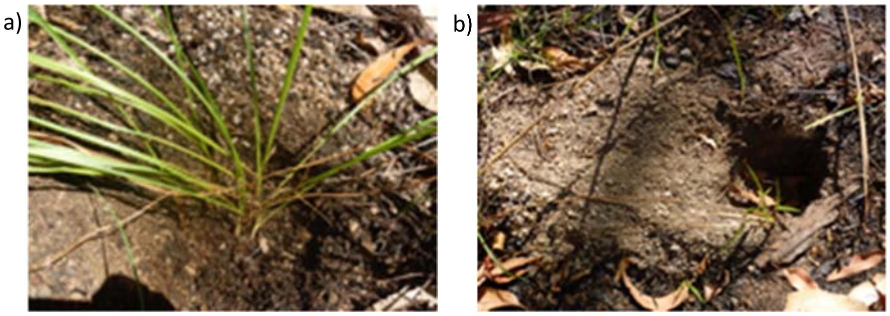

Plate 5.3. (a) Cockatoo grass (*Alloteropsis semialata*) and (b) digging of *Bettongia tropica*.

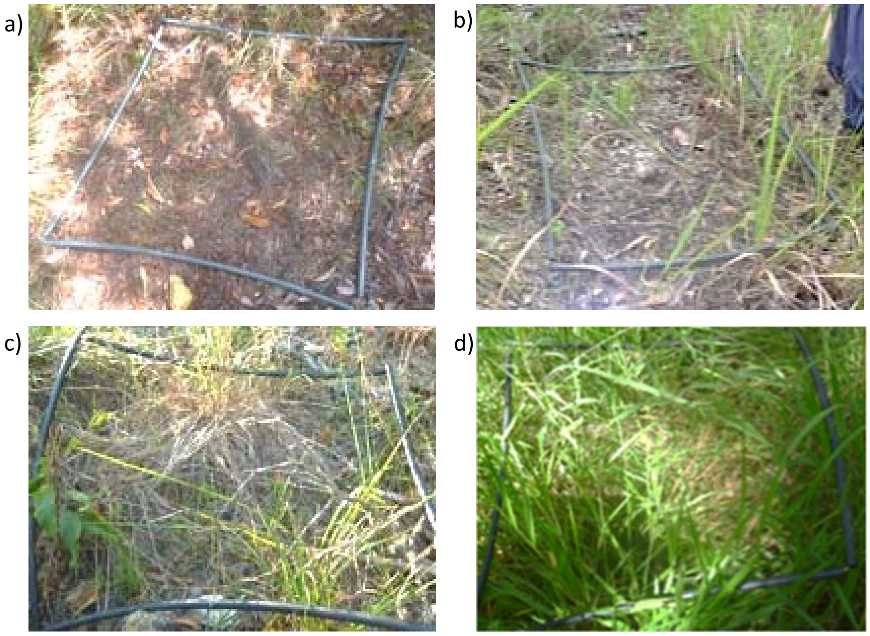

Plate 5.4. Examples of 1 m^2 quadrats at (a) and (b) foraging areas and (c) and (d) nesting areas.

5.3.3 Camera trapping

Camera trapping was conducted at Davies Creek, Emu Creek and Tinaroo Creek, with 30 cameras (Recoynx white-flash, heat-and-motion sensor camera traps) deployed at each site. Cameras operated between 5 pm and 7 am, with no lag time programmed between animal detection and photographs. Each time a camera was triggered, three consecutive photographs were taken a minimum of one second apart, with no delay between each set of photographs.

Cameras were deployed for six trapping sessions at each site between September 2014 and March 2016. Each session commenced several days after the cage trapping session and comprised 12 consecutive nights targeting *B. tropica*, with another 12 consecutive nights targeting potential mammalian predators (dingoes/dogs (*Canis lupus dingo*/*familiaris*) and cats (*Felis catus*)) and competitor species (rufous bettong (*Aepyprymnus rufescens*), pigs (*Sus scrofa*) and cattle (*Bos taurus*)). The second 12 nights occurred between 0 and 24 days after the first set. Dingoes/dogs (MacKenzie et al. 2002; McDonald et al. 2015) and feral cats are known predators of bettongs (Fancourt 2014; Priddel & Wheeler 2004). Rufous bettongs overlap in diet (Vernes 2000; Brook & Kutt 2011), cattle compete for grass, as well as alter vegetation cover and compact soil structure (Yates et al. 2000; Oldfield & Evans 2016; Wang 2017) and feral pigs potentially consume cockatoo grass and truffles, as well as uproot vegetation (Laurance 1997; Laurance & Harrington 1997; Crowley et al. 2004). Pigs may also predate juvenile bettongs. However, no study has verified this and therefore pigs will only be classified as known competitors.

A pilot study conducted in April 2014 determined that baiting the camera traps doubled trap success and increased the clarity of photographs. Camera traps were therefore baited for the main study. Type of bait can alter species capture rates (Astúa et al. 2006), so when targeting bettongs, camera traps were baited with a 2.5 cm diameter ball of peanut butter, rolled oats, vanilla essence, honey and sardines. The ball of bait was placed in a bait container, made from PVC pipe and wire mesh, which was attached to a wooden plank (60 cm x 5 cm x 3 cm) and pegged into the ground. The camera trap set up is shown in Plate 5.2. At each camera location, three smaller (1 cm diameter) balls were placed outside of the bait container and buried to a depth of around 3 cm to 5 cm to provide a food reward for attracted individuals.

Cameras targeting predators and competitors had 2 cm pieces of minced beef, tuna and chicken placed inside each bait container and three 1 cm pieces of each of these meats were placed under rocks, buried or placed in tree branches or in *Xanthorrhoea* (grass trees) within 2 m of the bait container. New bait was used for each camera trapping session.

Plate 5.5. Camera trap set up, comprising a camera secured to a tree trunk and facing downwards towards a bait container.

Cameras were positioned 1.5 m up a tree trunk. The bait container was positioned 1.5 m from the base on the tree and the camera was angled downwards towards the container using pre-cut wooden chocks. Cameras were housed in metal security cases and secured to a tree with a python cable and bungee cord. When setting up the camera, it was programmed to flash red when the bait board was in the centre of the field of view. This assisted in ensuring cameras were directed towards the bait container and meant that if an animal approached the bait board, it was likely to be detected. Grass in the camera field of view was trimmed to around 5 cm to 10 cm to minimise camera detections due to grass movement.

The trapping grid used for camera trapping was similar to that used for cage trapping (Chapter 3), except the transect lines for camera trapping were extended by 100 m or 200 m (depending on the transect) (Figure 5.1). Cameras were also offset 25 m alternating to the right and the left from the cage trapping transects to minimise the chance of theft. The first camera trap was positioned 50 m after the first cage trap. At Davies Creek, four cameras were spaced 200 m along the 800 m transect, whilst five cameras were placed 200 m apart along the 1 km transects. At Emu Creek and Tinaroo Creek, four cameras were placed along the 800 m transects and two along the 400 m transects. On the longer transects, the first three cameras were positioned 200 m apart, with the last camera being only 100 m further on. This was to avoid placing the camera within *Allocasuarina* forest, a habitat where *B. tropica* occurs in lower density (Vernes & Pope 2006). The effective trapping area of camera traps was calculated for each site using the methodology described in Chapter 3, except that 431 m was added to the camera trap locations rather than the cage locations. The effective trapping area for camera trapping was 323 ha at Davies Creek, 359 ha at Emu Creek and 240 ha at Tinaroo Creek.

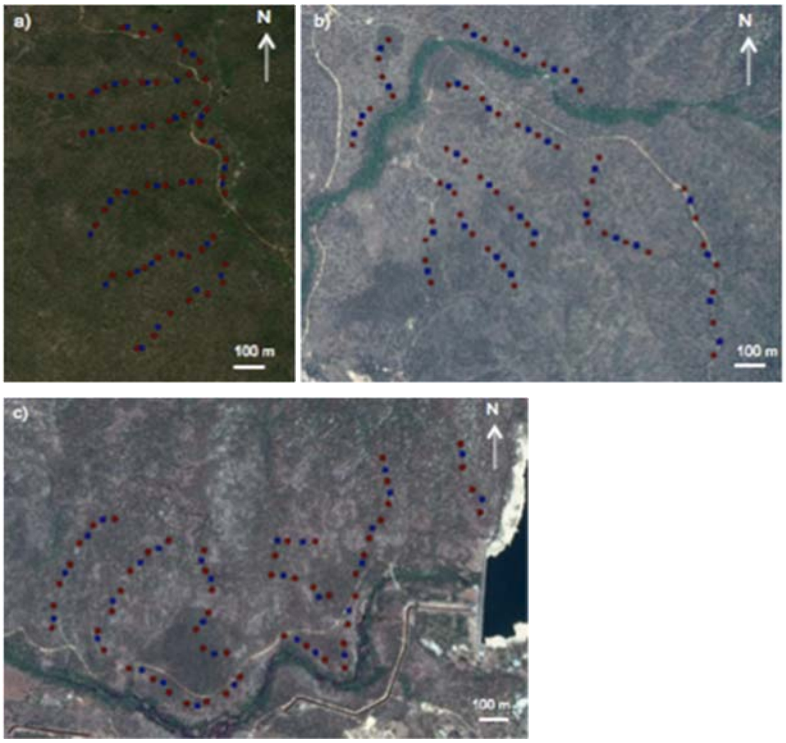

Figure 5.1. Camera trapping grid at (a) Davies Creek, (b) Emu Creek and (c) Tinaroo Creek, comprising 30 camera traps along eight transect lines. Camera trap locations are shown by blue squares and were located between and slightly offset from cage traps (indicated by the red circles). (Source: Google Earth®, 2014).

5.3.4 Data analysis

5.3.4.1 Nesting materials

The proportion of use for each of the five groups of nesting material was calculated for each site. These data were compared using a Chi-square test of independence (package MASS) (Venables & Ripley 2002), with post-hoc tests (adjusted with Bonferroni correction) (package fifer) (Fife 2017).

5.3.4.2 Habitat requirements at nesting, foraging and random areas

I assessed whether *B. tropica* selected different microhabitat variables between nesting and random areas, and foraging and random areas. I performed non-metric multi-dimensional scaling (NMDS) ordinations comparing:

1) nesting or foraging and random areas, with habitat variables combined from all sites to provide an insight into the habitat variables that were important for *B. tropica* across the Lamb Range (i.e. nesting/foraging vs. random),

2) nesting or foraging and random areas between sites to indicate similarities in important habitat variables between the three sites (i.e. nesting/foraging vs. random at Davies Creek, Emu Creek and Tinaroo Creek), and

3) nesting or foraging and random areas separately at each site (i.e. nesting/foraging vs. random at Davies Creek/Emu Creek/Tinaroo Creek).

Habitat variables were standardised using the mean and standard deviation and correlated at the 0.05 significance level in package hmisc (Harrell & Dupont 2015) in R Studio (RStudio Team 2015). For each pair of correlated variables, I retained the variable that was likely to be more ecologically important based on previous knowledge of the species ecology (Melles et al. 2003; Vernes 2003). If a variable was highly correlated with many other variables, it was removed so there were fewer habitat variables overall, with the exception of retaining highly correlated variables that were ecologically important (Clark et al. 2014).

Using PCOrd 6.08, each habitat variable and each nesting, foraging and random area were investigated for outliers (≥2 standard deviations), which were removed. Ordinations computing highly orthogonal principal axes used a Sorensen distance matrix and Monte Carlo $p<0.05$ for stress of 1000 runs of habitat data compared with 10,000 random runs. Axes were correlated with each habitat variable using Bonferroni corrections for multiple tests. I used a permanova test, with function adonis (package vegan) (Oksanen et al. 2017) and pairwise permanovas (with Bonferroni correction) (package RVAideMemoire) (Hervé 2017) to determine whether habitat at nesting or foraging areas differed from that of random areas. I also compared whether habitat differed between study sites, with post-hoc Kruskal-Dunn tests (package PMCMR) (Pohlert 2014)) used to examine which sites differed. Ordination plots were produced comparing nesting or foraging and random areas for the combined analysis and also for each of the three sites separately. Kruskal-Wallis tests with Bonferroni correction were used to examine which habitat variables differed between nesting or foraging and random areas for each site. As a conservative measure, I used a p value of 0.01 with Bonferroni corrected values of 0.0083 (0.1/14 habitat variables) at Davies Creek and Tinaroo Creek and 0.0071 (0.1/12 habitat variables) at Emu Creek.

5.3.4.3 Camera trapping

Photographs were visually examined to identify captures of *B. tropica*, potential predators (dingoes/dogs and cats) and competitors (rufous bettong, pigs and cattle) for each night cameras were deployed at each camera location. For each photograph, the species, study site, trapping session, date, camera trap location, bait type, time of first and last images and the number of images were recorded. Species captures, rather than individuals, were recorded, as bettongs and feral pigs could not be individually distinguished. Consecutive images at the same camera location taken more than 30 minutes apart were classified as a new capture (Symonds & Moussalli 2011). Predators (cats and dingoes/dogs) were individually identifiable based on their fur colour and the number of individuals for these species was recorded. Trap success for each species was also calculated at each site (number photographs/total photographs). Other potential predators, such as snakes and birds of prey, that may \ predate bettongs were observed at each field site but were not detected on camera traps and not included in the analysis.

The area captured by the camera varied based on the angle of the camera lens, with differences in area influencing the probability of detecting animals (Glen et al. 2013). However, by baiting camera traps animals were attracted to the bait container, increasing the likelihood that animals would be photographed (Fleming et al. 2014b). This minimised differences in the probability of detecting *B. tropica*. Bait boards were sometimes moved away from camera traps by animals (usually dingoes/wild dogs, pigs or giant-white tailed rats (*Uromys caudimaculatus*)) or the camera angle was altered due to animals climbing or cows rubbing against the camera. To standardise for this, I removed images that had noticeably different sampling areas from the majority of photographs. For each trapping session, between 3 ± 0.7 % and 26 ± 3% (average of 12.7 ± 1.2%) of camera trap photos were misaligned and not pointing at the bait container and were removed from analyses.

5.4 Results

5.4.1 Nesting materials

Nesting material was recorded for 121 nests across the three study sites. The amount that *B. tropica* used each nesting material differed (Chi-squared test, $\chi^2 = 27.589$, df = 8, $p<0.001$), with nesting material significantly differing between Emu Creek and both Davies Creek ($p<0.001$) and Tinaroo Creek ($p = 0.0255$) and approaching significance between Davies Creek and Tinaroo Creek ($p = 0.057$).

Bettongia tropica predominantly constructed nests from grass (*Poaceae* spp.) or nested under the ‘skirts’ of grass trees (*Xanthorrhoea johnsonii*), with rocks, logs or teepee structures utilised less often than grass and grass trees (Table 5.1). *Bettongia tropica* at Davies Creek favoured nesting under grass trees (65.38%), whilst at Emu Creek and Tinaroo Creek grass nests were most commonly utilised (75.56% and 50% of nests respectively) (Table 5.1). Grass nests were generally ovoid in shape and well camouflaged. Most grass nests were constructed of grass species from the immediate area, with kangaroo grass (*Themeda australis*) primarily used. Blady grass (*Imperata cylindrica*) was also used, typically for nests positioned within stands of blady grass near creeks. Some grass nests and nests under grass trees were situated within a shallow depression, which appeared to have been excavated, with this most commonly observed at Davies Creek (Plate 5.6). Nests constructed under grass trees were usually more difficult to detect in the field compared to the other nest types. Tinaroo Creek was the only site where individuals constructed teepee nests from sticks and grass. These nests were often constructed around a narrow (<10cm diameter) tree trunk and situated in small (an estimated 1.5 m^2)

open areas surrounded by dense patches of lantana and/or *Allocasuarina* seedlings, with sparse grass cover.

Plate 5.6. Front view of a *Bettongia tropica* nest, showing a small area where vegetation has been flattened and removed.

Table 5.1. Nesting material of *B. tropica* at Davies Creek, Emu Creek and Tinaroo Creek. 'Nests' and '*B. tropica*' refers to the number of nests and individual *B. tropica*. The numbers of *B. tropica* in each column does not equal the total as multiple nesting areas of the same individuals were surveyed.

Nesting microhabitat	Davies Creek			Emu Creek			Tinaroo Creek		
	Nests	% total	*B. tropica*	Nests	% total	*B. tropica*	Nests	% total	*B. tropica*
Grass trees (*Xanthorrhoea johnsonii*)	17	65.38	16	8	17.78	6	16	32	12
Grass (*Poaceae* spp.)	8	30.77	5	34	75.56	15	25	50	16
Logs	1	3.85	1	0	0	0	3	6	3
Rocks	0	0	0	3	6.66	2	2	4	2
Teepee (sticks and grass)	0	0	0	0	0	0	4	8	3
Total	26	100	16	45	100	16	50	100	18

5.4.2 Habitat requirements at nesting and foraging areas

The results are presented in two sections below, comparing the habitat variables at 1) nesting areas to random areas and 2) foraging areas to random areas. Each of these two sections are further divided into three sections, as listed below:

1) comparing nesting or foraging and random areas, with habitat variables combined from all sites,
2) comparing nesting or foraging and random areas between sites, and
3) comparing nesting or foraging and random areas separately at each site.

5.4.2.1 Comparing nesting and random areas

5.4.2.1.1 Habitat variables combined from all sites

The three-dimensional solution of the NMDS ordination comparing habitat variables at nesting and random areas of all three sites, explained 77.9% of variation in 11 uncorrelated habitat variables, 88 nesting areas and 85 random areas (after removal of outliers) (Table 5.2). Permanova demonstrated significant differences in microhabitat between nesting and random areas ($F_{1,168} = 17.93$, $p<0.001$; Table 5.2). Overall, *B. tropica* selected nesting areas that were situated on steeper slopes with more grass trees, grass cover and less bare soil cover than random areas (Figure 5.2; Table 5.2). At all sites, values of grass trees, grass cover, cockatoo grass, grass height, slope and coarse woody debris cover were significantly higher in nesting areas than random areas (Table 5.2). Tree basal area was significantly lower in nesting areas than random areas, except at Emu Creek, where basal area was lower throughout the landscape than at Davies Creek and Tinaroo Creek (Table 5.3). However, only grass cover, slope, grass trees and bare soil cover, which approached significance, separated nesting and random areas (Figure 5.2).

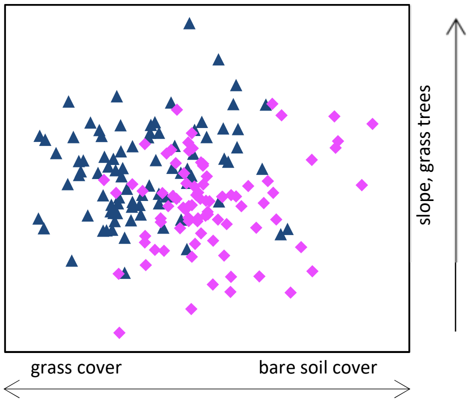

Figure 5.2. Microhabitat variables (more grass cover, more grass tress, less bare soil cover and steeper slopes) at *Bettongia tropica* nesting areas (blue) than at random areas (pink). Nesting and random areas are plotted in habitat space of a three-dimensional NMDS ordination of 11 habitat variables.

Table 5.2. Microhabitat variables significantly correlated with axis 1, 2 and 3 of an NMDS ordination of nesting and random areas at Davies Creek, Emu Creek and Tinaroo Creek and at all sites. The final stress value and the percentage of the total variance explained by the ordination are also shown. A dash (-) indicates the variable was correlated with other variables and excluded from analyses.

	Davies Creek			Emu Creek			Tinaroo Creek			All three sites		
Stress value	0.151			0.164			0.164			0.181		
No. variables	12			14			12			11		
No. of sampling areas	58			58			57			173		
Bonferroni-corrected p value	0.00028			0.00024			0.00028			0.0000001		
	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3
Variance explained	44.1%	30.4%	12.9%	39.9%	23.3%	16.9%	31.8%	31.2%	16.9%	40.2%	22.5%	15.2%
Variables												
Grass trees					-0.468			0.718			0.525	
Grass cover (%)	-0.705			0.669			-0.749			-0.719		
Cockatoo grass		0.465		0.480								
Grass height (cm)	-	-	-	0.746			-0.477			-	-	-
Rock cover (%)		-0.750										
Tree height (m)									-0.529			
Slope (º)	-0.585		0.529	0.683					-0.662		0.583	
Coarse woody debris cover (%)												
Soil resistance (mPa)	0.778											
Tree basal area ($m^2/20\ m^2$)	0.496											
Bare soil cover (%)	0.481						-	-	-			
Soil moisture (%)			-0.472			-0.772		-0.472		0.662		-0.708
Diggings	-	-	-				-	-	-			
Leaf litter cover (%)	-	-	-	-	-	-	0.738	-0.491		-	-	-
Canopy cover (%)	0.655				0.766		0.569			-	-	-

[a] Conservative significance levels of Bonferroni-corrected <0.01 (r>0.460) for single sites, and <0.000005 (r>0.390) for all three sites combined were used to focus interpretation on most important variables.

Table 5.3. Microhabitat variables at nesting and random areas at Davies Creek, Emu Creek and Tinaroo Creek, with mean value (x̄) and standard error (SE) for each habitat variable. The Kruskal-Wallis test statistic (χ^2) and Bonferroni corrected significant values are shown in bold. An asterisk (*) indicates that the habitat variable was correlated with another habitat variable and excluded from the ordination.

	Davies Creek				Emu Creek				Tinaroo Creek				All sites			
Habitat variables	Nesting x̄ ± SE	Random x̄ ± SE	χ^2	p-value	Nesting x̄ ± SE	Random x̄ ± SE	χ^2	p-value	Nesting x̄ ± SE	Random x̄ ± SE	χ^2	p-value	Nesting x̄ ± SE	Random x̄ ± SE	χ^2	p-value
Grass trees (/20 m^2)	3.93 ± 0.86	0.23 ± 0.079	1.28	0.259	2.00 ± 0.84	1.29 ± 0.35	1.06	0.302	22.30 ± 4.01	9.24 ± 2.89	10.37	**0.0013**	8.17 ± 1.72	3.52 ± 1.05	8.56	**0.0034**
Grass cover (%)	64.94 ± 3.98	30.63 ± 4.73	21.40	**<0.001**	53.40 ± 5.05	31.97 ± 4.30	9.17	**0.0025**	32.01 ± 4.88	12.38 ± 2.92	12.66	**<0.001**	50.14 ± 3.03	24.99 ± 2.50	34.07	**<0.0001**
Cockatoo grass (/m^2)	3.83 ± 0.76	2.37 ± 0.41	0.42	0.519	3.67 ± 0.78	1.27 ± 0.39	4.74	0.0294	7.17 ± 1.38*	2.53 ± 0.51*	8.99*	**0.0027***	4.89 ± 0.60	2.06 ± 0.26	12.46	**<0.001**
Grass height (cm)	50.66 ± 2.69*	42.32 ± 2.97*	4.39*	0.036*	52.50 ± 4.10	31.98 ± 3.55	11.98	**<0.001**	34.31 ± 2.72	21.57 ± 2.05	12.10	**<0.001**	45.82 ± 2.04	31.94 ± 1.90	22.77	**<0.0001**
Rock cover (%)	1.57 ± 0.63	7.03 ± 2.78	0.33	0.57	3.57 ± 2.05	2.43 ± 1.49	0.83	0.36	3.51 ± 1.27	4.32 ± 1.70	0.379	0.54	2.88 ± 0.83	4.60 ± 1.20	0.27	0.61
Tree height (m)	18.85 ± 1.29	15.91 ± 0.89	2.78	0.096	15.63 ± 0.70	15.23 ± 1.26	1.35	0.25	16.24 ± 0.90	14.23 ± 0.86	1.28	0.26	16.91 ± 0.59	15.12 ± 0.59	4.61	0.032
Slope (º)	12.87 ± 1.76	2.82 ± 0.58	26.25	**<0.001**	12.73 ± 1.57	9.20 ± 1.66	3.74	0.053	12.11 ± 1.26	8.60 ± 1.32	4.25	0.039	12.57 ± 0.88	6.89 ± 0.78	29.37	**<0.0001**
Coarse woody debris cover (%)	2.19 ± 0.96	4.13 ± 2.68	0.228	0.63	2.52 ± 0.71	0.67 ± 0.32	7.52	**0.0061**	1.64 ± 0.53	0.12 ± 0.07	11.00	**<0.001**	2.13 ± 0.43	1.64 ± 0.91	13.40	**<0.001**
Soil resistance (mPa)	4.69 ± 0.38	10.78 ± 1.27	26.02	**<0.001**	8.75 ± 0.74	10.45 ± 0.78	2.17	0.14	7.24 ± 0.53	5.63 ± 0.43	5.43	0.020	6.89 ± 0.37	8.95 ± 0.57	6.45	0.011
Tree basal area (m^2/20 m^2)	0.13 ± 0.035	0.61 ± 0.091	25.35	**<0.001**	0.46 ± 0.14	0.16 ± 0.20	0.0014	0.97	0.15 ± 0.021	1.05 ± 0.41	17.14	**<0.0001**	0.24 ± 0.055	0.61 ± 0.23	25.22	**<0.0001**
Bare soil cover (%)	4.63 ± 1.38	16.53 ± 4.25	3.40	0.065	3.59 ± 1.07	8.97 ± 2.71	0.38	0.54	3.84 ± 1.61	31.04 ± 6.94	4.63	0.031	4.03 ± 0.79	18.85 ± 2.99	7.34	0.0067
Soil moisture (%)	4.26 ± 0.45	4.31 ± 0.40	0.11	0.74	6.97 ± 0.57	5.11 ± 0.46	7.28	0.0069	6.25 ± 0.35	6.59 ± 0.68	0.0035	0.95	5.82 ± 0.29	5.34 ± 0.32	2.04	0.15
Diggings (/m^2)	0.47 ± 0.16*	0.67 ± 0.16*	1.29*	0.26*	0.27 ± 0.12	0.067 ± 0.046	1.62	0.20	1.33 ± 0.25	0.60 ± 0.18	2.43	0.12	0.62 ± 0.11	0.44 ± 0.085	0.72	0.40
Leaf litter cover (%)	24.49 ± 2.93*	46.37 ± 4.85*	10.07*	0.0015 *	36.93 ± 4.92*	58.90 ± 6.04*	7.17*	0.0074*	57.93 ± 5.11	50.87 ± 8.00	0.0035	0.95	39.78 ± 2.92*	52.05 ± 3.71*	5.22*	0.022*
Canopy cover (%)	27.40 ± 1.15	37.98 ± 3.23	14.22	<0.001	29.88 ± 1.88	31.51 ± 2.28	1.23	0.27	42.39 ± 1.75	44.86 ± 1.87	0.43	0.50	33.22 ± 1.16*	38.12 ± 1.55*	12.01 *	<0.001*

5.4.2.1.2 Comparing nesting and random areas between sites

The overall nesting and random habitat differed significantly between the three study sites ($F_{2,168}$ = 9.71, p<0.001), with post-hoc tests concluding that the overall habitat at Davies Creek differed from Emu Creek (p = 0.012) and Tinaroo Creek (p = 0.003). Habitat also differed between Emu Creek and Tinaroo Creek (p = 0.003). There was also a significant interaction between study sites with nesting and random areas ($F_{2,168}$ = 4.33, p<0.001; Appendix Table L.1). Appendix L contains the results from the permanova post-hoc tests comparing habitat at nesting and foraging areas with habitat at random areas.

The importance of habitat variables also differed at nesting and random areas between study sites, with grass cover, slope and grass trees influencing where *B. tropica* nested (Table 5.3). Grass cover was higher at nesting areas than random areas across all study sites (Figure 5.3a and 5.3b; Table 5.3), with the percentage grass cover in nesting areas greater at Davies Creek than Tinaroo Creek (p<0.001; Appendix Table L.1). Bettongs at Davies Creek favoured nesting areas with steeper slopes than randomly sampled (Table 5.3). At Tinaroo Creek, nesting areas had significantly more grass trees than random areas and also more than nesting areas at Davies Creek and Emu Creek (p<0.001; Table 5.3; Appendix Table L.1). Surprisingly, selection of nesting habitat by bettongs did not appear to be guided by the presence of grass trees at Davies Creek or Emu Creek, even though grass trees were commonly used for nesting at Davies Creek (Table 5.1). *Bettongia tropica* appeared to avoid nesting in areas with higher cover of bare soil (Axis 1, Figure 5.3a and 5.3b), despite there being no difference in bare soil cover between nesting and random areas (Table 5.3). Soil moisture was lower at nesting areas at Davies Creek than nesting areas at other sites (Table 5.3; Appendix Table L.1).

5.4.2.1.3 Comparing nesting and random areas separately at each site

At Davies Creek, nesting areas comprised significantly different habitat from random areas ($F_{1,57}$ = 15.37, p<0.001). Nesting areas were well separated from random areas (axis 1), due to the occurrence of greater grass cover and steeper slopes than random areas (Figure 5.3a; Tables 5.2 and 5.3). Random areas had significantly steeper slopes, harder soils, greater canopy cover and greater tree basal area than nesting areas (Table 5.3), but other than slope, these variables did not significantly separate nesting from random areas (Figure 5.3a).

For Emu Creek, separation between habitat at nesting and random areas was also well defined ($F_{1,58}$ = 4.61, p<0.001), especially along the horizontal axis 1 (Figure 5.3b). *Bettongia tropica* more often nested at areas with significantly more grass cover and taller grass (Axis 1, Figure 5.3b), and moister soils (vertical axis 2, Figure 5.3b; Table 5.3).

At Tinaroo Creek, habitats at nesting and random areas were significantly different ($F_{1,53} = 6.87$, $p<0.001$), with nesting habitats divided into two types. One type of nesting habitat occurred where bettongs favoured taller grasses, greater grass cover and fewer grass tress and appeared to avoid high levels of leaf litter and canopy cover (Figure 5.3c; Table 5.3). The second type of nesting habitat comprised more grass trees and possibly steeper slopes and/or taller trees (Figure 5.3d; Table 5.3). Due to the division into two nesting habitats, habitat variables that were significant in the ordination did not significantly differ between nesting and random areas, except for grass cover and grass trees (Table 5.3). Although the vertical axis was positively correlated with coarse woody debris and canopy cover and negatively related to grass height (Figure 5.4, Table 5.4), only coarse woody debris differed significantly between foraging and random areas (Table 5.5).

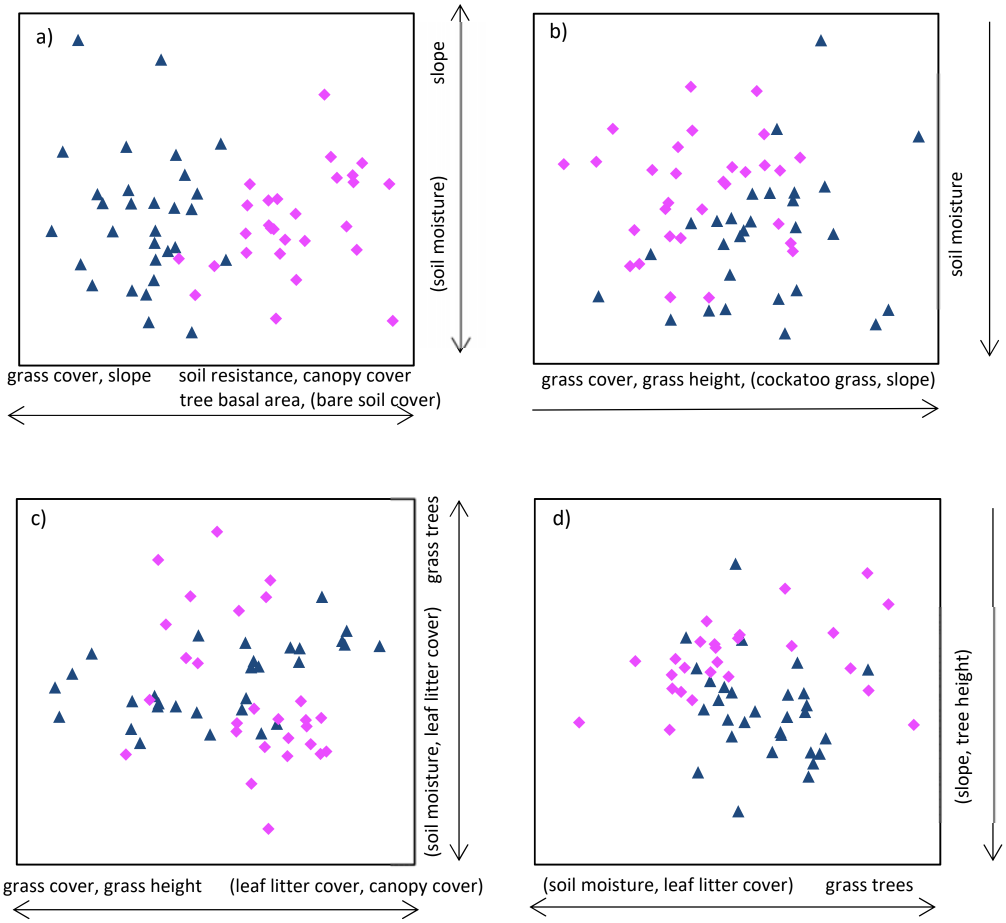

Figure 5.3. Microhabitat variables at *Bettongia tropica* nesting areas (blue) and at randomly sampled areas (pink) at (a) Davies Creek, (b) Emu Creek and (c) and (d) Tinaroo Creek. The plotted variables separated nesting and random areas. Differences were significant except for variables with brackets.

5.4.2.2 Comparing foraging and random areas

5.4.2.2.1 Habitat variables combined from all sites

The three-dimensional NMDS ordination comparing foraging and random areas over all three sites explained 76.9% of the variation in 13 uncorrelated habitat variables associated with 84 foraging and 88 random areas (Table 5.4). Foraging habitat differed from random areas (Permanova $F_{1,166} = 20.07$, $p<0.001$), containing a higher abundance of food resources, including cockatoo grass and diggings (indicating consumed food resources), as well as steeper slopes, more grass trees, taller trees and more coarse woody debris cover (Table 5.5). These variables were the main variables separating foraging and random habitats (Figure 5.4). Bare soil cover was a driver of the horizontal axis 1 (Figure 5.4), but did not differ significantly between random and foraging areas (Table 5.5). The vertical axis 3 was positively correlated with coarse woody debris and canopy cover and negatively related to grass height (Figure 5.4; Table 5.4). However, none of these variables significantly differed between foraging and random areas when all sites were considered (Table 5.5).

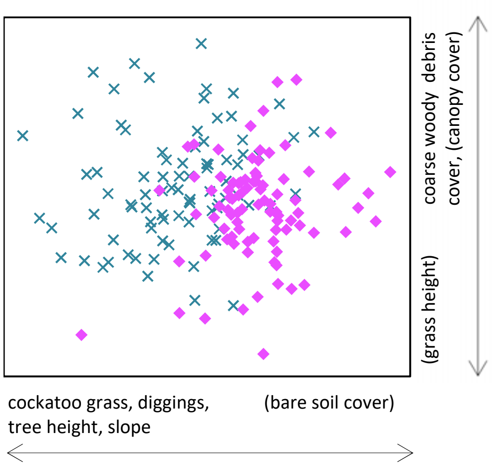

Figure 5.4. Microhabitat variables at *Bettongia tropica* foraging areas (blue) and at randomly sampled areas (pink) for all three sites. Foraging areas were situated on steeper slopes with more cockatoo grass and *B. tropica* diggings, taller trees and more coarse woody debris than randomly sampled areas. Foraging and random areas are plotted in habitat space of a three-dimensional NMDS ordination of 13 habitat variables. The plotted variables separated foraging and random areas. Differences were significant except for variables with brackets.

Table 5.4. Microhabitat variables that are significantly correlated (at the 0.01 level, after Bonferroni correction) with axis 1, 2 and 3 of a three-dimensional ordination of foraging and random areas at Davies Creek, Emu Creek, Tinaroo Creek and all sites. The final stress value, number of variables and sampling areas and the variance explained by each ordination are shown. A dash (-) indicates the variable was excluded from analyses as it was correlated with at least one other variable.

	Davies Creek			Emu Creek			Tinaroo Creek			All three sites		
Stress value	0.1588			0.1515			0.1456			0.1937		
No. variables	12			13			12			13		
Number of sampling areas	58			58			56			172		
Bonferroni p value	0.0028			0.0026			0.0028			0.0000001		
	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3
Variance explained	33.9%	31.6%	17.1%	41.4%	25.8%	17.2%	48.2%	29.6%	10.8%	36.7%	19.5%	20.7%
Variables												
Grass trees (/m^2)						-0.464						
Grass cover (%)				-	-	-	-	-	-	-	-	-
Cockatoo grass (/20 m^2)	-0.501	-0.487		0.688			-0.720			-0.669		
Grass height (cm)				0.684			0.702					-0.618
Rock cover (%)												
Tree height (m)				0.576			-0.739			-0.614		
Slope (°)	-0.828									-0.554		
Coarse woody debris cover (%)		0.503			-0.804							0.445
Soil resistance (mPa)		-0.573			-0.501	0.535						
Tree basal area (m^2/20 m^2)			0.596					0.738	-0.485		-0.414	
Bare soil cover (%)		0.503		-0.501						0.400	0.437	
Soil moisture (%)								0.664				
Diggings (/m^2)	-	-	-							-0.588		
Leaf litter cover (%)	-	-	-	-	-	-	-	-	-	-	-	-
Canopy cover (%)							-	-	-		-0.589	0.455

[a] Conservative significance levels of Bonferroni-corrected <0.01 (r>0.460) for single sites, and <0.000005 (r>0.390) for all three sites combined were used to focus interpretation on most important variable

Table 5.5. Microhabitat variables at foraging and random areas at Davies Creek, Emu Creek and Tinaroo Creek, with mean value ($\bar{x}$) and standard error (SE) for each habitat variable. The Kruskal-Wallis test statistic (χ^2) and Bonferroni-corrected significant values are shown in bold. An asterisk (*) indicates that the habitat variable was correlated with at least one other variable and excluded from the ordination. Grass cover and leaf litter cover are excluded as they were correlated in all analyses.

	Davies Creek				Emu Creek				Tinaroo Creek				All sites			
Habitat variables	Foraging $\bar{x}$ ± SE	Random $\bar{x}$ ± SE	χ^2	p-value	Foraging $\bar{x}$ ± SE	Random $\bar{x}$ ± SE	χ^2	p-value	Foraging $\bar{x}$ ± SE	Random $\bar{x}$ ± SE	χ^2	p-value	Foraging $\bar{x}$ ± SE	Random $\bar{x}$ ± SE	χ^2	p-value
Grass trees (/20 m^2)	3.07 ±	0.23 ± 0.079	19.81	**<0.001**	1.94 ± 0.58	1.29 ± 0.35	0.693	0.405	1.77 ± 0.66	9.24 ± 2.89	0.94	0.33	1.29 ± 0.0.30	0.51 ±	18.39	**<0.0001**
Grass cover (%)	20.29 ± 2.71*	30.63 ± 4.73*	2.46*	**0.12***	34.92 ± 2.69*	31.97 ± 4.30*	0.80*	0.37*	12.62 ± 2.63*	12.38 ± 2.92*	3.49 *	0.062*	22.61 ± 2.68*	24.99 ± 2.50*	14.55 *	**<0.001***
Cockatoo grass (/m^2)	5.80 ± 1.07	2.37 ± 0.41	3.36	0.067	8.38 ± 1.31	1.27 ± 0.39	26.62	**<0.001**	7.00 ± 1.65	2.53 ± 0.51	2.52	0.11	7.06 ± 0.79	1.08 ± 0.22	50.89	**<0.0001**
Grass height (cm)	45.57 ± 2.91	42.32 ± 2.97	0.603	0.44	45.84 ± 2.20	31.98 ± 3.55	9.79	**0.0018**	30.37 ± 2.93	21.57 ± 2.05	5.81	0.016	40.56 ± 1.72	44.26 ± 2.15	2.39	0.12
Rock cover (%)	1.75 ± 0.59	7.03 ± 2.78	0.542	0.46	4.07 ± 1.56	2.43 ± 1.49	2.80	0.095	0.46 ± 0.29	4.32 ± 1.70	5.96	0.15	2.09 ± 0.58	4.38 ± 1.30	0.36	0.55
Tree height (m)	17.02 ± 0.59	15.91 ± 0.89	0.126	0.72	17.57 ± 1.19	15.23 ± 1.26	3.90	0.048	19.04 ± 1.67	14.23 ± 0.86	5.64	0.018	17.87 ± 0.79	13.24 ± 0.47	25.87	**<0.0001**
Slope (°)	15.59 ± 1.46	2.82 ± 0.58	37.03	**<0.001**	11.13 ± 1.12	9.20 ± 1.66	4.13	0.042	9.13 ± 1.15	8.60 ± 1.32	0.31	0.58	11.95 ± 0.77	5.21 ± 0.76	55.70	**<0.0001**
CWD^ cover (%)	1.35 ± 0.43	4.13 ± 2.68	0.401	0.53	2.66 ± 0.51	0.67 ± 0.32	15.12	**<0.001**	1.44 ± 0.61	0.12 ± 0.07	2.39	0.12	1.82 ± 0.30	0.81 ± 0.20	8.70	**0.0032**
Soil resistance (mPa)	5.51 ± 0.45	10.78 ± 1.27	14.66	**<0.001**	11.39 ± 1.01	10.45 ± 0.78	0.30	0.58	6.64 ± 0.69	5.63 ± 0.43	0.64	0.43	7.85 ± 0.51	8.95 ± 0.57	2.30	0.13
Tree basal area (m^2/20 m^2)	0.23 ± 0.055	0.61 ± 0.091	15.06	**<0.001**	0.11 ± 0.029	0.16 ± 0.020	8.97	**0.0028**	0.34 ± 0.70	1.05 ± 0.41	6.89	0.0087	0.22 ± 0.26	0.61 ± 0.18	9.23	**0.0024**

Bare soil cover (%)	14.45 ± 2.46	16.53 ± 4.25	0.922	0.34	14.39 ± 2.41	8.97 ± 2.71	7.24	**0.0071**	16.32 ± 3.89	31.04 ± 6.94	0.76	0.38	15.05 ± 1.71	20.77 ± 3.28	0.24	0.62
Soil moisture (%)	4.03 ± 0.48	4.31 ± 0.40	0.686	0.41	5.95 ± 0.44	5.11 ± 0.46	2.21	0.14	5.46 ± 0.44	6.59 ± 0.68	1.54	0.21	5.15 ± 0.27	5.34 ± 0.32	0.11	0.74
Diggings (/m^2)	2.16 ± 0.49*	0.67 ± 0.16*	9.50*	**0.0021***	0.98 ± 0.39	0.067 ± 0.046	9.72	**0.018**	1.00 ± 0.31	0.60 ± 0.18	0.40	0.53	1.38 ± 0.24	0.23 ± 0.07	30.77	**<0.0001**
Leaf litter cover (%)	62.05 ± 4.17*	46.37 ± 4.85*	5.57*	**0.018***	43.68 ± 2.86*	58.90 ± 6.04*	5.46*	**0.019***	65.22 ± 4.73*	50.87 ± 8.00*	0.36*	0.55*	56.98 ± 3.92*	52.05 ± 3.71*	26.72*	**<0.0001***
Canopy cover (%)	26.16 ± 0.89	37.98 ± 3.23	15.47	**<0.001**	27.35 ± 1.43	31.51 ± 2.28	3.56	0.059	39.25 ± 1.93*	44.86 ± 1.87*	3.70*	0.055*	30.92 ± 1.05	28.77 ± 1.36	0.87	0.35

CWD^ = Coarse woody debris

5.4.2.2.2 Comparing foraging and random areas between sites

Foraging habitat also differed between study sites ($F_{2,166}$ = 10.04, p<0.001), with all comparisons between sites significant (p = 0.03). There was also an interaction between study sites and foraging and random habitat ($F_{2,171}$ = 4.79, p<0.001). Post-hoc tests showed all site-habitat comparisons differed (p = 0.015 all interactions, except p = 0.045 comparing foraging habitat at Emu Creek and Tinaroo Creek), other than between foraging areas at Davies and Emu Creeks, which were similar (p = 1.00).

When all sites were considered, *Bettongia tropica* foraged within areas with more cockatoo grass, more diggings, taller trees, steeper slopes and less tree basal area than randomly sampled areas (Table 5.5). There were some differences in the important habitat variables between sites (Table 5.5; Appendix Table L.2). Cockatoo grass, diggings and soil resistance separated foraging from random areas at Davies Creek, whereas only cockatoo grass was important at Emu Creek (Table 5.5; Appendix Table L.2). This was despite the abundance of cockatoo grass being statistically similar at foraging and random areas at Davies Creek (Table 5.5). Taller grass was important at Tinaroo Creek, but not at the other two sites (Table 5.5; Appendix Table L.2).

5.4.2.2.3 Comparing foraging and random areas separately at each site

At Davies Creek, microhabitat in foraging areas was significantly different from that in random areas ($F_{1,56}$ = 9.99, p<0.001). Foraging areas had steeper slopes, more cockatoo grass and softer soils (Figure 5.5a and 5.5b). However, the difference in cockatoo grass between areas was not significant (Table 5.5) and the preference for softer soil appeared influenced by a few locations (Figure 5.5a and 5.5b). Random areas had greater tree basal area (Figure 5.5a and 5.5b; Table 5.5). Although all the aforementioned variables separated foraging and random areas, slope, soil resistance and tree basal area are thought to be most important, with these variables being significantly different between foraging and random areas (Table 5.5).

At Emu Creek foraging and random habitats differed ($F_{1,56}$ = 10.65, p<0.001). *Bettongia tropica* selected habitats with significantly more cockatoo grass, more coarse woody debris cover and taller grasses for foraging, whilst areas with high bare soil cover were not prime foraging habitat (Figure 5.5c; Table 5.4 and 5.5). Foraging areas also tended to have taller trees (Figure 5.5c; Table 5.4), although there was no significant difference in this habitat variable between foraging and random areas (Table 5.5).

At Tinaroo Creek, the habitat appeared to be more uniform in terms of foraging and random areas, despite foraging and random areas having significantly different habitats ($F_{1,54}$ = 7.14, p<0.001). Foraging areas appeared to be separated from random areas by taller trees, more cockatoo grass, moister soils, shorter grass and lower tree basal area, although no comparisons were significant (Figure 5.5d; Table 5.5).

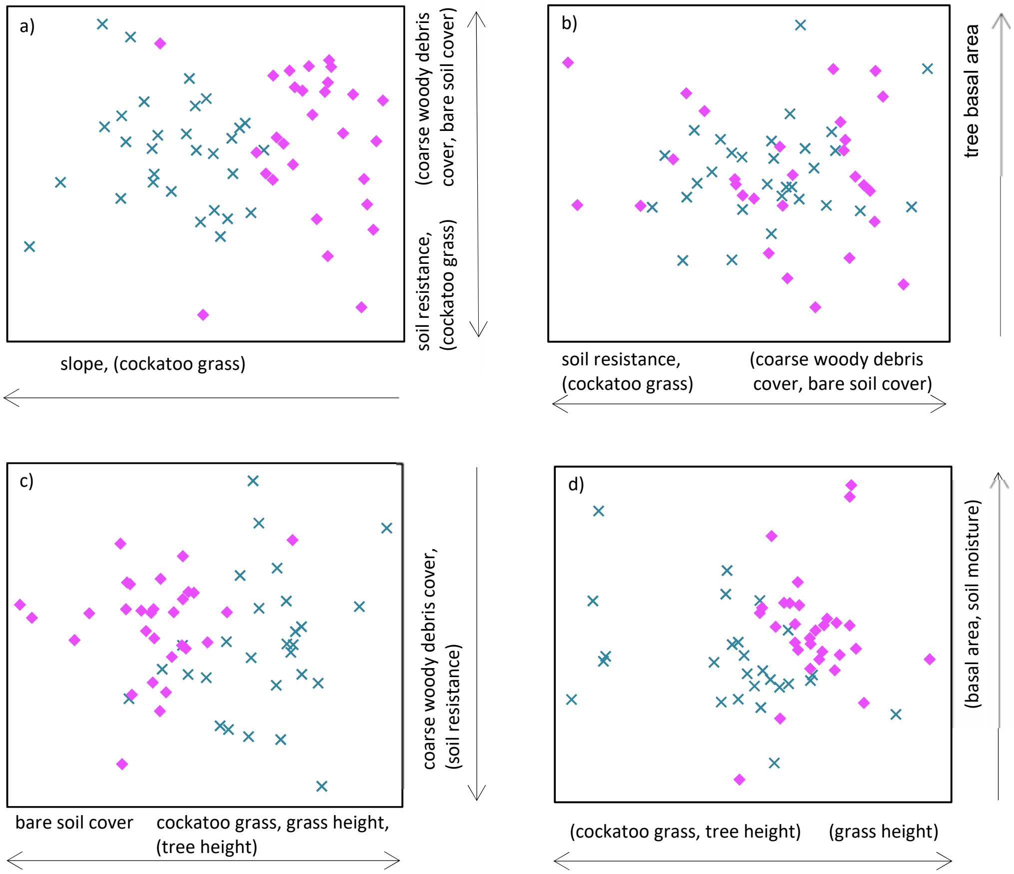

Figure 5.5. Microhabitat variables at *Bettongia tropica* foraging areas (blue) and at randomly sampled areas (pink) at (a) and (b) Davies Creek, (c) Emu Creek and (d) Tinaroo Creek. The plotted variables separated foraging and random areas. Differences were significant except for variables with brackets.

5.4.3 Camera captures

In total, 4,320 camera trap nights occurred at each study site resulting in a total of 154,047 camera images with animal detections. *Bettongia tropica* comprised 18.10% (8,152/45,061), 16.99% (8,408/49,497) and 31.24% (18,584/59,489) of all photographs of animals at Davies Creek, Emu Creek and Tinaroo Creek respectively. At Davies Creek, each camera location had an average trap success for *B. tropica* of 22.64%, whilst at Emu Creek and Tinaroo Creek trap success per camera averaged 23.36% and 51.62% respectively per trap night. In contrast, predator and competitor species only constituted 3.89% (1,751/45,061), 2.64% (1,307/49,497) and 2.36% (1,405/59,489) of the images captured at Davies Creek, Emu Creek and Tinaroo Creek. Based on the number of camera captures and the effective trapping areas, there were 2.35, 2.00 and 4.31 *B. tropica* camera captures per ha at Davies Creek, Emu Creek and Tinaroo Creek respectively.

There was over three times the number of camera captures of feral pigs at Davies Creek than at the other sites (Table 5.6). However, only two dingoes/dogs were photographed at Davies Creek compared to four dingoes/dogs present at both Emu Creek and Tinaroo Creek (Table 5.6). Emu Creek was the only site where rufous bettongs and cattle were recorded (Table 5.6). Cattle were only observed on camera traps located on the lower slopes. Areas where cattle were assumed to graze (cropped grass) were very distinctive in the field (pers. obs.). Tinaroo Creek was the only site where a cat was detected (Table 5.6).

Table 5.6. Camera captures of *B. tropica* and its potential predators, dingoes/dogs and feral cats, and competitors, rufous bettong, feral pigs and cattle, at Davies Creek, Emu Creek and Tinaroo Creek. The number of individuals of dingoes/dogs, feral cats and cattle are also shown in brackets. The number of individual bettongs and feral pigs could not be identified.

	Bettongia tropica	Dingoes/dogs	Feral cat	Rufous bettongs	Feral pigs	Cattle
Davies Creek	760	10 (2)	0	0	121	
Emu Creek	720	13 (4)	0	99	13	25 (8)
Tinaroo Creek	1,035	16 (4)	1 (1)	0	44	

Many other small mammal species were recorded on camera traps, including the northern brown bandicoot (*Isoodon macrourus*), giant white-tailed rat, common brushtail possum (*Trichosurus vulpecula*), northern quoll (*Dasyurus hallucatus*), black-footed tree-rat (*Mesembriomys gouldii*), common ringtail possum (*Pseudocheirus peregrinus*), fawn-footed melomys (*Melomys cervinipes*) and grassland melomys (*Melomys burtoni*). Larger mammals including agile (*Macropus agilis*) and whiptail wallabies (*Macropus parryi*) were also recorded. Time constraints meant the number of captures of other small mammal species has not yet been evaluated.

5.5 Discussion

At all study sites, there were subtle differences in the nesting and foraging microhabitat requirements of *B. tropica*. Overall, *B. tropica* predominantly favoured nesting within habitats with high grass cover, an abundance of grass trees and steep slopes. Steeply sloping areas with an abundance of cockatoo grass were generally favoured by *B. tropica* when foraging.

5.5.1 Nesting materials

Bettongia tropica mainly constructed nests from grass and grass trees, with 82% of nests constructed from these materials, whilst logs, rocks and sticks were rarely used. Field observations indicated *B. tropica* utilised commonly available resources. This strategy probably increased camouflage with the surrounding area (Taylor 1993b; Lovell et al. 2013) and/or reduced energy expended when collecting nesting materials (Cantarero et al. 2015) in their semi-prehensile tails (Rose 1986; pers. obs.).

Bettongia tropica had multiple nests and nesting areas, with the same *B. tropica* individual using both grass trees and grass for nesting materials (Chapter 4). It seems likely that choice between these materials may be related to availability within the particular area.

Grass trees were the favoured nesting resource at Davies Creek, whilst grass was the main nesting resource at Emu Creek and Tinaroo Creek. This was surprising since there were more grass trees recorded at Tinaroo Creek than Davies Creek, more grass cover at Davies Creek than Tinaroo Creek and a similar amount of grass cover at Davies Creek and Emu Creek. However, at Tinaroo Creek grass trees were often distributed in clumps, with either many or few grass trees within the surveyed 20 m^2 area (high standard error compared to the other sites). At Emu Creek, there were fewer grass trees than at the other study sites. This explains why microhabitats with grass trees were not favoured by *B. tropica* at Emu Creek, despite grass trees still being used as a nesting material when available. In contrast, at Davies Creek grass trees were at a slightly higher density and scattered evenly throughout the habitat (low standard error). This indicates grass trees would be available for *B. tropica* throughout the habitat, explaining why they were preferred there. Additionally, grass trees were small ($< \approx 0.7$ m) and *B. tropica* often nested at the base of multiple grass trees (pers. obs.). This suggests that if small grass trees were used for nesting, their proximity to other grass trees may be a limiting factor.

Building grass nests under the 'skirts' of grass trees may increase camouflage compared to nesting in simple grass nests. Nests under grass trees were harder to find in the field (pers. obs.) and appeared easier and thus more energy efficient to construct (as nests are constructed from less grass). Grass trees may be an especially important resource when grass cover is low and insufficient to camouflage grass nests. Additionally, animals often shelter under vegetation during heavy rainfall (Kingdon et al. 2013), with grass trees likely to provide additional cover during high rainfall events. Nesting under grass trees may also reduce the chance of trampling on nests by other animals (Bowman & Panton 1991), such as wallabies, pigs or cattle, with these species observed on camera traps and in the field.

Grass nests were favoured in areas with few grass trees or high grass cover. These variables would assist in camouflaging nests against their background (Vernes & Pope 2001). Constructing nests from grass provides *B. tropica* with greater flexibility in selecting where to nest. This can benefit a species' fitness (Pearson & Knapp 2016), as nests constructed closer to foraging areas would minimise energy expended travelling between nesting and foraging areas (Chapter 4; Lutermann et al. 2010; De Vere et al. 2011). Building grass nests may be especially advantageous where foraging areas are sparsely distributed or where grass trees only occur far from foraging areas. Maintaining sufficient density of both grass and grass trees for nesting materials is essential within bettong habitat.

At Tinaroo Creek, *B. tropica* occasionally constructed teepee-shaped nests from sticks and small amounts of grass. This nest design has not previously been reported for bettongs. Teepee nests were generally poorly camouflaged and located within lantana thickets or areas dominated by *Allocasuarina* with a sparse understorey and no grass trees (pers. obs.). *Allocasuarina* thickening and rainforest expansion into *Eucalyptus* woodlands has occurred over the last 50 years across north Queensland and may be impacting the viability of *B. tropica* populations (Harrington & Sanderson 1994; Tng et al. 2012). *Allocasuarina* and lantana thickets shade out grasses (Harrington & Sanderson 1994), support lower food resources (truffles and cockatoo grass) for *B. tropica* and are considered sub-optimal habitat compared to *Eucalyptus* woodland (Abell et al. 2006; Vernes & Pope 2006). Constructing teepee nests within lantana thickets and *Allocasuarina* at Tinaroo Creek indicates the habitat was sub-optimal for *B. tropica*. This indicates at Tinaroo Creek there is competition between individuals and limited availability of better quality nesting habitat.

Poorly camouflaged nests can increase the risk of predation compared with well-camouflaged nests (Matessi & Bogliani 1999; Albrecht & Klvana 2004; Stevens et al. 2017) and this could ultimately impact upon the survival of individuals and even populations (Vögeli et al. 2011). For *B. tropica*, managers should ensure the habitat contains sufficient nesting resources. An assessment of whether nesting materials and nest design (especially of teepee nests) influence *B. tropica* survival rates is a future research avenue.

Interestingly, at Davies Creek more nests were built underneath grass trees (65.38%) or constructed from grass (but not under grass trees) (30.77%) than previously reported by Vernes and Pope (2001). Vernes and Pope (2001) studied nesting materials at Davies Creek before and after fire and concluded that pre-fire, 46.4% of nests were situated under grass trees, 28.6% near or in logs, whilst only 10.7% were constructed from grass. I found only 3.85% of nests were situated within or next to logs. Differences in nesting material between studies may be due to individual requirements or could signify habitat changes. Low intensity management burns have been conducted every two to three years on the Lamb Range since around 2000 (R. Miller, pers. comm.), with regular fires potentially reducing the availability of suitable logs (Collins 2012). After a large low to medium intensity fire occurred at Davies Creek, Vernes and Pope (2001) found that only 7.9% of individuals utilised logs (compared to 28.6% pre-fire), with boulders being the most used resource (44.7%) post-fire. This indicates that *B. tropica* are flexible in their choice of nesting materials and adjust their choice based on resources available at the time (Vernes & Pope 2001). However, both studies suggested that *B. tropica* prefer grass trees for nesting and in this study *B. tropica* also favoured grass.

5.5.2 Habitat requirements at nesting areas

When all sites were considered, *B. tropica* selected nesting areas situated on steeper slopes within habitats comprising more grass cover and grass trees than random areas. Nesting areas with high grass cover and an abundance of grass trees would assist in camouflaging grass and grass tree nests from predators (Vernes & Pope 2001). Selection of these variables were consistent with my expectations, as minimising predation risk is often crucial for survival (Lawes et al. 2015a). Many small mammals in relatively open (non-rainforest) or sparsely vegetated habitats in northern and southern Australia have suffered population declines primarily due to predation by feral cats, with declines exacerbated by reduced ground cover at shelter, nesting and foraging areas (Woinarski et al. 2010; Fisher et al. 2013; Lawes et al. 2015a). Grass cover and grass trees may also help to regulate environmental conditions within nests by providing shade for animals during the day and cover from rain and wind (Fisher 2000). Choosing habitats with sufficient ground cover may be crucial for the survival of *B. tropica* whilst nesting.

Nesting on steeper slopes may also reduce the chance of predators detecting nests, as steeper slopes are often less utilised by predators (Buckmaster 2011; McGregor et al. 2015). Cats and dingoes/dogs occur on the Lamb Range (see camera trapping section below), with these species being major predators of bettongs (Vernes 2000; Brook & Kutt 2011; Fancourt 2014). Cats and dingoes/dogs both usually forage on flatter, more open ridgelines (Buckmaster 2011; McGregor et al. 2015) and by foraging on steeper slopes *B. tropica* may reduce their risk of predation. Additionally, steeper slopes may facilitate better drainage during periods of heavy rains (Holtmeier 2014). These results have important management implications, as when fire management burns occur throughout the Lamb Range there are patches of habitat where all grass cover is temporarily lost (pers. obs.). *Bettongia tropica* remain within their home range during and after fire (Vernes & Pope 2001) and ensuring that sufficient grass cover is maintained post-fire is important, especially at Davies Creek and Emu Creek.

When nesting areas were analysed separately at each study site, grass height was not selected at Davies Creek. Grass was generally taller throughout the landscape at Davies Creek, meaning *B. tropica* would not need to select for grass height. At Emu Creek, which was the driest site, nesting locations had significantly wetter soils than random areas. Interestingly, Tinaroo Creek was the only site where two distinctive types of nesting habitats were favoured, with taller grasses and more grass cover as one habitat and more grass trees as the second habitat. This indicates Tinaroo Creek is the only site with sufficient grass cover and grass trees for *B. tropica* to regularly utilise both resources.

5.5.3 Habitat requirements at foraging areas

Bettongia tropica selected foraging habitats that had a higher abundance of food resources, facilitated ease of travel and offered cover from predators. Similar environmental variables were generally preferred for foraging across all sites. Under similar climatic conditions, it is thus likely that *B. tropica* would select the same habitat variables for foraging throughout their distribution (Pietersen et al. 2014). As expected, when all sites were considered, *B. tropica* foraged within habitat with more cockatoo grasses (dry season resource) and more bettong diggings (representing either truffles or cockatoo grass) than random areas.

Foraging areas also had significantly lower (or approaching significance) tree basal area than randomly available. *Bettongia tropica* selected more open habitats (more bare soil cover at Emu Creek and Davies Creek and lower tree basal area at Davies Creek and Tinaroo Creek). This is expected to increase the ease of travel for *B. tropica* when escape from predators is required. Other mammal species also select habitats that increase ease of travel (Lawhead 1984; Reid & Jinchu 1991; Vynne et al. 2011). For example, Killeen et al. (2014) studied the fine- and broad-scale habitat selection of GPS tracked elk (*Cervus elaphus*) and determined that at a fine scale, elk avoided the most rugged terrain that was difficult to traverse, whilst at a broader scale habitat selection was driven by forage availability and the terrain being slightly less rugged.

Bettongia tropica at Emu Creek and Davies Creek selected foraging areas with a higher abundance of coarse woody debris cover, with debris cover being significantly higher at Emu Creek. Coarse woody debris may help to provide camouflage from predators (Doherty et al. 2015). Increased ground cover, including taller grass and more coarse woody debris, can increase shelter and refuge for small mammals (Doherty et al. 2015) and reduce the hunting success and habitat quality of introduced predators, such as feral cats (McGregor et al. 2014). Woody debris has the advantage of not substantially hindering the movement of *B. tropica*, with bettongs observed easily hopping over logs and fallen branches (pers. obs.). At Davies Creek, *B. tropica* foraged on steeper slopes than random, which may reduce the chance of predators detecting bettongs (Buckmaster 2011; McGregor et al. 2015).

Predation pressure can drive habitat selection by small mammals and bettongs may choose to forage within more open areas to increase their ability to escape predators. For example, Spencer et al. (2014) found that spinifex hopping-mouse (*Notomys alexis*), an Australian desert rodent, foraged primarily in open areas and most likely used avoidance behaviours when foraging to manage predation risk, with their bipedal movement allowing them to move efficiently across open environments. Similarly, *B. tropica* use bipedal hopping to travel for long distances at high speed (Claridge et al. 2007) and rapidly flee when approached by predators (Chapter 4).

Surprisingly soil moisture did not significantly affect foraging habitat selection. This contrasts with other studies on bettongs, with Yeatman and Wayne (2015) determining that brush-tailed bettongs

(*Bettongia penicillata*) favoured low-lying valleys and slopes with greater water holding capacity, as these regions potentially had greater truffle (food) abundance. Soil moisture may not have varied sufficiently between foraging and random areas for a significant trend to be detected. This is likely given that most foraging areas were sampled during the late dry season/early wet season when soil moisture is likely to be low. Truffle abundance was unable to be sampled in this study due to sampling difficulty and time constraints. The direct association between habitat selection and truffle presence is unknown. Considering truffles comprise around 30% to 90% of *B. tropica* diet throughout the year (Johnson & McIlwee 1997; McIlwee & Johnson 1998; Nuske 2017), truffle abundance is assumed to strongly influence where *B. tropica* forage.

5.5.4 Camera trapping

Camera trapping data suggests that *B. tropica* need to select habitat that reduces their exposure to predation risk. There was a ratio of 1:76 (predator to *B. tropica* sightings) at Davies Creek, 1:55 at Emu Creek and 1:60 at Tinaroo Creek. The cat detected at Tinaroo Creek is of concern, as only a few cats have the potential to cause substantial population declines in bettong populations (Short & Turner 2000; Fancourt 2014). Additionally, the population viability analysis indicates *B. tropica* populations on the Lamb Range would rapidly (<50 years) decline to extinction if a cat population established within the area (Chapter 2). The feral cat was recorded during the camera trapping session conducted in November 2015. However, no decline was detected in the population density of *B. tropica* in the following cage trapping sessions (November 2015 to 2016) (Chapter 3). If the cat had only recently intruded into the area, a decline might occur in future, with any decline currently too minor to be detected. It is also possible that the cat may not regularly forage within the habitat, although this is not known. It is recommended that monitoring of predator populations within the Lamb Range continues. Predators are often difficult to detect, with different species and individuals either being deterred or attracted to camera traps (Meek et al. 2016). Consequently, it is possible that predator numbers were much higher than detected. Additionally, habitat surveys were undertaken within a relatively small proportion of the landscape (600 m^2 or 0.06 ha compared to an average effective camera trapping area of 307.33 ha for the three sites). The presence of other predators, such as snakes and owls, was not assessed, with further study into predator density required on the Lamb Range.

Davies Creek and Emu Creek had similar camera capture rates of competitors, with a ratio of approximately 1:6 (potential competitor to *B. tropica*), whilst Tinaroo Creek had a lower ratio of 1:24. Pigs were present at each site, although uprooted vegetation, consistent with pig foraging (Laurance 1997), was only observed at Davies Creek in two small locations (<3 m^2) (pers. obs.), with no habitat damage observed at Emu Creek or Tinaroo Creek. Cattle were only detected at Emu Creek. Feral pigs and cattle can alter habitats by reducing grass cover, changing plant community composition to favour invasive plant species and altering soil fertility and structure (Yates et al. 2000; Oldfield & Evans

2016; Wang 2017). Feral pigs may also selectively graze and uproot cockatoo grass (Crowley et al. 2004) and may also forage for truffles (Laurance 1997; Laurance & Harrington 1997). When management burns are undertaken in far north Queensland, cattle often congregate in areas of new growth (A. Hedges, pers. comm.). This may result in fire-adapted grass species that re-shoot quickly after fire, such as cockatoo grass (Bateman & Johnson 2011), being targeted by cattle. The detrimental impacts of predation and fire on small mammals can be exacerbated by habitat alteration caused by competitors and grazing (Fisher et al. 2013; McGregor et al. 2014). It is recommended that the extent of competition (and possibly predation) between *B. tropica* and feral pigs as well as competition by cattle be assessed in future.

Rufous bettongs were detected on camera traps at Emu Creek, with all captures in the lower section (300 m) of four transects. In this region the vegetation was drier with a sparse understorey of shrubs and less grass cover (pers. obs.). Rufous bettongs utilise very similar nesting materials to *B. tropica* (Wallis et al. 1989) and have a similar diet, although grass constitutes a greater proportion of their diet (around 80%) (McIlwee & Johnson 1998). *Bettongia tropica* are likely to be under stronger competitive pressure from rufous bettongs where truffle abundance is lower and *B. tropica* relies more on grasses for food, such as during the dry season and within drier habitats (such as Emu Creek) (Bateman et al. 2011). A more comprehensive study is required to determine both predator and competitor densities on the Lamb Range and to assess their influence on *B. tropica*.

5.6 Management implications

Overall, *B. tropica* foraged within relatively open habitats, with these habitats potentially making it easier to travel throughout the landscape and to flee from predators. In contrast, habitats that provided cover from predators were selected at nesting areas. This suggests predation pressure is a major factor governing habitat use by *B. tropica*. Competitor pressure may also influence habitat use, especially at Emu Creek. At Emu Creek managers need to consider the competitive interactions between rufous bettongs and *B. tropica* to ensure there are sufficient resources to support both bettong species, particularly during the dry season.

Poorly camouflaged nests may increase the predation risk of *B. tropica*, highlighting the importance of ensuring the habitat contains high grass cover and an abundance of grass trees. Vegetation thickening (lantana infestation and *Allocasuarina* thickening) may be reducing the abundance of nesting resources at Tinaroo Creek, resulting in the construction of less well-camouflaged teepee nests. Fire can reduce the rate of woody thickening or rainforest encroachment and may enable the weedy and/or thickened habitat to transition back to *Eucalyptus* woodland (Scott et al. 2012; Department of Environment and Heritage Protection 2017). When undertaking management burns throughout the

Lamb Range, managers should focus on burning the patches of thickened vegetation, especially lantana and *Allocasuarina* stands (DEHP 2017a).

The presence of *B. tropica* outside of the Lamb Range is poorly known, with current distribution maps largely based on modelling of the distribution of truffles and cockatoo grass (two main food resources of *B. tropica*) (Bateman et al. 2011). Modelling the occupancy of *B. tropica* based on the fine-scale habitat requirements of the species would enable the presence/absence outside of the Lamb Range to be predicted. On-ground surveys should focus on surveying within areas with a grassy understorey with an abundance of grass trees and cockatoo grass, steep slopes and low tree basal area, as these variables were important to *B. tropica*. Such a focused survey would increase the chance of detecting *B. tropica* in the field (McDonald et al. 2015). Monitoring programs are often time and labour intensive (Garden et al. 2007) and improving the efficiency of monitoring will enable greater coverage during surveys. Once presence within an area is confirmed, managers can focus on protecting *B. tropica* at all locations where the species is present, rather than mainly within the core population on the Lamb Range. This new knowledge of habitat requirements for nesting and foraging can assist in preserving or improving habitat quality throughout the range of the species (Beerens et al. 2015; Stirnemann et al. 2015) and ultimately benefit the species' conservation (Griffen & Drake 2008).

Chapter 6: Synthesis and management recommendations

6.1 Thesis summary and implications

The overall aim of my research was to determine the population trends and habitat requirements of *B. tropica* to understand more about their ecology and improve the conservation management of the species. This is the first study on *B. tropica* that used the combination of cage and camera trapping and GPS collars to assess multiple aspects of the species ecology, including movement patterns, habitat requirements at nesting and foraging areas, the presence of predator and competitor species and the population density of *B. tropica*. This chapter highlights the major findings and significance of the research and makes recommendations for implementing management actions to improve the conservation of the species.

6.1.1 Population viability of B. tropica (Chapter 2)

Population viability modelling indicated that within all sub-populations (Bridle Creek, Davies Creek, Emu Creek and Tinaroo Creek) on the Lamb Range, *B. tropica* were highly vulnerable to increases in predation by feral cats. More frequent or intense droughts and fires, as expected with climate change, were not expected to substantially impact the viability of *B. tropica* populations. However, the interaction between fire and predation can influence the viability of *B. tropica*, as fire reduces the vegetation cover that conceals prey species, thereby increasing the hunting success of predators (Cherry et al. 2017). Viability analyses also determined that under current conditions, *B. tropica* sub-populations were resilient to fluctuations in population abundance. The most important finding from Chapter 2 was that mortality in juvenile and sub-adults rather than adults, has the largest impact on the viability of *B. tropica* populations.

Increasing the survival rate of juveniles and sub-adults may increase the population size of *B. tropica*. This would benefit the species viability as larger populations have greater resilience to change (Spradling et al. 2010). However, *B. tropica* populations may already exist at their optimal carrying capacity, given that the population has remained stable but not increased despite 10 years of changed fire management. When populations are at carrying capacity, increasing the survival rates of particular age classes can result in the habitat becoming heavily oversaturated and consequently cause over-compensatory mortality of the age class (Ayllón et al. 2012). This then prevents the population from reaching carrying capacity in the following years (Ayllón et al. 2012). Habitat area, as well as quality, would need to be increased to allow *B. tropica* populations to expand.

6.1.2 Population trends of B. tropica (Chapter 3)

The population density on the Lamb Range has remained stable for the last 20 years. This is the first study to provide evidence indicating that low-intensity mosaic burns have not detrimentally impacted upon *B. tropica* populations. Tinaroo Creek had the highest population density, potentially due to the site having a more productive habitat. Seasonality or site did not influence body condition or the number of females with pouch young, indicating that under the stable weather conditions experienced during and prior to my study, the Lamb Range provided sufficient resources to sustain *B. tropica* populations throughout the year.

Although the population on the Lamb Range appears stable, consistent and regular monitoring needs to continue in order to detect potential changes in the species' population density and/or distribution. Trap success fluctuated seasonally, meaning population density estimates are likely to be inaccurate if the population is inconsistently monitored or monitored only during one season. It is recommended that camera trapping be conducted twice a year for one month in February (wet season) and August (dry season). This would minimise the influence of seasonality and time of year on camera capture rates. If camera trapping twice a year is not feasible, it is recommended that camera trapping be conducted once a year for two to three months from November (late dry season) to December (transition from late dry to early wet season), or preferably, to January (early wet season). Cage trapping each year would be preferable, as it would enable *B. tropica* to be individually identified and the population density to be accurately ascertained. However, cage trapping is much more time and labour intensive than camera trapping and would not be logistically possible for long-term monitoring. Cage trapping should be conducted every five to 10 years to reassess the population density, with camera trapping undertaken once or twice a year to monitor population trends. If camera trapping indicates a continual population decline, cage trapping should be conducted to verify the decline before extensive management strategies are undertaken.

Future monitoring should be undertaken along the same sampling transects, with cages placed in the same locations for each survey and preferably in the locations used in this study to allow comparisons of density estimates over time. Regular monitoring ensures long-term trends can be accurately assessed and maximises the chance of early detection of changes in population density (Lurz et al. 2008). More frequent monitoring also increases the likelihood of detecting trends and correctly interpreting their direction (Nuno et al. 2014). Systematic information regarding population trends can provide insights concerning the causes of decline (Bonebrake et al. 2010), which is crucial for mitigating declines (Holsinger 2000).

6.1.3 Home range and movement patterns of B. tropica (Chapter 4)

The assessment of the home range and movement patterns of *B. tropica* provided information regarding the habitat quality and broad-scale distribution of resources at each of the study sites. The home ranges of *B. tropica* were similar across all sites, indicating similar resource distributions. However, females at Tinaroo Creek spent more time foraging, compared to travelling, indicating resources occurred at higher density.

Some collared *B. tropica* at Tinaroo Creek constructed teepee nests within sub-optimal nesting areas. Increasing the area and quality of habitat may increase the carrying capacity of the habitat and potentially enable non-dominant individuals to have higher breeding success (Griffen & Drake 2008). This may increase the population size and improve the population viability of *B. tropica*.

Fire management is currently conducted at a 60 ha scale based on the previous estimate of home range (Vernes & Pope 2001). It seems likely that current fire regimes are suitable for maintaining the population density of *B. tropica* given that the population density is stable from estimates 20 years ago. However, as seen in the population viability analysis, if fire intensity or the abundance of predators increased on the Lamb Range, *B. tropica* may be more reliant on sufficient grass cover to provide camouflage from predators. It is therefore recommended that management burns be conducted at a 20 to 60 ha scale, with a 20 ha scale highly recommended during particularly dry periods.

6.1.4 Microhabitat requirements of B. tropica (Chapter 5)

The habitat requirements of *B. tropica* on the Lamb Range differed between the three study sites. Habitat selection whilst nesting appeared to be influenced by predation pressure and nests were often well camouflaged and difficult to detect in the field. For nesting, *B. tropica* selected habitats with steep slopes, high grass cover and an abundance of grass trees. Foraging areas were selected for their abundance of food resources (cockatoo grass), to minimise predation risk (by using steep slopes) and to increase ease of travel throughout the landscape including areas with low tree basal area. Variables that are selected across all sites are expected to be important throughout the rest of the species distribution. Based on these results, management can be tailored to increase the microhabitat suitability for *B. tropica*.

This study provides an insight into the predator (dingoes and cats) and competitor species (feral pigs, cattle and native rufous bettongs) that are present on the Lamb Range. The results from this study provide an approximate baseline of the number of predator individuals and camera capture rates of competitor species and predator species. The stability of *B. tropica* populations on the Lamb Range, together with the camera capture rates, indicate that cats and dingoes rarely occur within the study sites. However, *B. tropica* selected nesting habitats that increased camouflage and foraging habitats that were open enough to allow them to flee from predators. This indicates that predation pressure strongly impacts on the habitat use and movements of *B. tropica*, even if the population density is currently not adversely affected.

Bettongia tropica at Emu Creek are likely to be under greater predation risk than at other sites, as there was a higher ratio of predators to *B. tropica* individuals. In addition, *B. tropica* competed with rufous bettongs and cattle, neither of which were detected at the other sites. Monitoring at Emu Creek may thus provide the earliest indication of changes in competitor and/or predator pressure.

It is recommended that the competitive interaction between *B. tropica* and non-native species be comprehensively assessed, with competitor and predator populations to regularly monitored. To assess the competition between species, the area uprooted by feral pigs could be measured as a proportion of the total habitat. Measuring the area where there is very short, cropped grass (indicative of grazing) (Kuiper & Parker 2013) could assess the influence of cattle. At Emu Creek, cattle are able to intrude into the area due to a downed fence from the nearby cattle property (pers. obs.). It is recommended that the fence is repaired and maintained to stop cattle grazing within the area. If competition between feral pigs or cattle and *B. tropica* is high, it is recommended that pigs are controlled, cattle excluded from the area and grazing leases not be renewed within habitats where bettongs occur.

6.2 Future research

6.2.1 Using habitat requirements to determine the distribution and population abundance of B. tropica

The total population abundance of *B. tropica* has not yet been accurately estimated, as my study only ascertained the population density within a specified area. It is not logistically possible to cage trap throughout the entirety of the Lamb Range to ascertain the species population density across the whole landscape. Instead, future studies should focus on using cameras traps to estimate population abundance and occupancy.

Areas of potentially suitable habitat for *B. tropica* have been modelled (Bateman et al. 2011; Bateman et al. 2012) and camera trapping commenced in late 2017 to assess for the presence of *B. tropica* within potentially suitable habitat elsewhere in the Wet Tropics bioregion (outside of the Lamb Range). Cameras were spaced one camera/km^2 (Todd et al. 2017, unpublished) based on the mean home range diameter of a male *B. tropica* being 862 m (Chapter 3). *Bettongia tropica* individuals cannot be identified visually and it is unknown how many individuals are represented by multiple camera captures at the same location. However, since *B. tropica* seasonal home ranges are less than 1 km^2 (or 100 ha) (Chapter 4), it can be assumed that a *B. tropica* individual recorded at one camera trap would be unlikely to travel to another camera trap if trapping was conducted within the same season.

This allows a surrogate of population abundance to be calculated using occupancy modeling (Burton et al. 2015) and also provides crucial information on the species detectability and presence/absence.

The accuracy of population estimates, calculated using occupancy modelling, should be verified by comparing them to my estimates calculated from camera and cage trapping. Verification is important as occupancy does not necessarily reflect population abundance, especially on a small-scale or when the maximum distance for detecting animals on cameras is unknown or variable between cameras due to various factors, such as vegetation density, weather or background noise (Matthews et al. 2011; Efford & Dawson 2012). I found across the three study sites, there was an average camera trapping density of approximately 289 *B. tropica* captures per km^2 (converted from density estimates per ha from Chapter 5). This equated to a population density of approximately 10 per km^2 across the three study sites based on cage trapping (Chapter 3). This equates to a ratio of one *B. tropica* individual to 28.9 *B. tropica* camera captures. Future studies could also calculate a ratio of camera captures to population density calculated using occupancy modelling. Although the ratio may vary throughout the landscape, comparing the ratios between studies may provide an indication of whether the occupancy estimates are likely to be accurate.

Trap placement can influence trap success rate, as mammals are more likely to be trapped within habitats or areas they favour (Astúa et al. 2006). To detect for the presence/absence of species in order to ascertain the species' distribution, I recommend camera traps be placed on steep slopes within areas with a high abundance of cockatoo grass. Surveying within favoured habitats can increase the efficiency of detecting animals, provide a more accurate assessment of a species distribution (Gibson et al. 2004; McDonald et al. 2015) and improve population density estimates (Plumptre 2000). To estimate population densities, it is recommended that future studies be conducted within both favoured and non-favoured habitats (Plumptre 2000). Sampling within only favoured habitat should be avoided for detecting population trends, as populations may concentrate within these habitats when the species is declining elsewhere (Plumptre 2000).

6.2.2 Tracking the fate of juveniles

There is minimal information on juvenile *B. tropica* and no study has studied juvenile survival rates. Future studies should track the long-term survival rates of juveniles from within the pouch until adulthood. If the current stable population density of *B. tropica* on the Lamb Range was to decline, my models suggest that juvenile mortality would be the likely driver. Research should therefore also determine the factors that contribute to juvenile mortality including verifying the assumption that predation is the major cause. Management would then be able to focus on undertaking strategies to minimise the most likely threat/s to juvenile mortality,

6.2.3 Tracking dispersing sub-adults

My study determined the fine-scale movement patterns of adults over a relatively short time period (up to 42 days) at three sub-populations. However, little is known regarding the movements of sub-adults (250 to 950 g). The high genetic diversity within the Lamb Range suggests the sub-populations are connected, with around 20% dispersal of male sub-adults (Pope et al. 2012). Research into the movements of sub-adults may help verify this and determine the location of dispersal corridors. Managers could then focus on maintaining or improving habitat quality of these corridors to maximise connectivity between sub-populations. It is important that sub-populations remain connected as isolated and small populations tend to have low genetic diversity (Schwartz et al. 2003; Mimura & Aitken 2009; Pacioni et al. 2013), low viability (Spradling et al. 2010) and are often the first to disappear (Gedir et al. 2015).

6.3 Conclusion

This study provided comprehensive baseline information on the population density, movement patterns and habitat requirements of *B. tropica*. Managers can use this information to tailor management strategies to improve habitat quantity and quality for *B. tropica*. Management has often been reactive, with actions implemented once a decline is observed (Rodrigues 2006). However, declines can be difficult to accurately detect (Lurz et al. 2008), especially since many populations are not regularly or consistently monitored (Oakley et al. 2003). Consequently, substantial or catastrophic declines often occur before control measures are undertaken (Plumptre 2000). This is especially the case when threats, such as disease (Daszak et al. 2011) or increased predation, have a severe and rapid impact upon the population (Fancourt 2014). It is thus crucial for management to be pre-emptive and focus on preventing declines before they occur and safe-guarding populations against extinction (Norris & Harper 2003; Biebly et al. 2008; Weldon et al. 2013).

Bettongia tropica is an example of a species where pro-active, rather than reactive, management has been undertaken within the core population. This strategy appears successful, with the *B. tropica* population on the Lamb Range so far remaining stable. The Lamb Range has had a relatively stable climate, which may have assisted the persistence of *B. tropica*. However, environmental changes resulting from climate change are predicted to worsen with time (Steffen et al. 2017) and are predicted to exacerbate or increase the number of threats operating upon species (Didham et al. 2007; Bellard et al. 2012). This may result in unstable weather patterns or more predators intruding into the Lamb Range (Burbidge & Woinarski 2016), which my models show may threaten the viability of *B. tropica*. It is thus important to continue and improve habitat management as recommended and to undertake monitoring of *B. tropica* and potential competitors and predators.

Conserving *B. tropica* may provide conservation benefits for other species within *Eucalyptus* woodlands. Protecting keystone species (Jonnson & Holbrook 2014), such as *B. tropica* (Nuske 2017) may also benefit the health and viability of the entire ecosystem and the species dependent on the ecosystem (Norris & Harper 2003). Maximising the conservation benefit from one management program is especially important considering climate change could have dire consequences for many species, including species that are not currently threatened (Jetz et al. 2007) and it is not feasible to individually manage all species. Therefore, continuing to increase the population viability and recovery of a keystone species such as *B. tropica* is a high conservation priority.

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Appendix A. Base model of life-history parameters and age class mortalities used in population viability analyses of *Bettongia tropica* on the Lamb Range, north-eastern Queensland.

Scenario settings	**Data input**	**Justification**
Duration of simulations (years)	100	
Number of iterations	1000	
Number of populations	4	Vernes and Pope (2006) showed that Davies, Tinaroo, Emu and Bridle Creeks all had viable populations. All four were modelled as a metapopulation.
Dispersal		
Dispersing Class	males aged 1 year	
% Surviving Dispersers	87%, but no dispersal into saturated populations	See below for discussion of survivorship
Percent dispersing/immigrating	20%	Pope et al. (2012) showed 80% of males are sedentary, whilst 20% disperse. Bridle Creek and Tinaroo Creek are the most northerly and southerly populations, with 20% of individuals modelled to disperse to adjacent populations at Davies Creek and Emu Creek respectively. Davies Creek and Emu Creek provide 10% dispersal to populations located to north and south.
Life-history parameters		
Inbreeding	No	
Mating system	Short-term monogamy or polygyny	Pope et al. (2012) defined *B. tropica* mating system as 'overlap promiscuity,' however it may be 'serial monogamy'.
Female breeding age (years)	1	Vernes and Pope (2002) estimated earliest age of reproduction for females was at 9-12 months; Johnson and Delean (2001) suggested captive *B. tropica* females can breed at 1 year.
Male breeding age (years)	1	Males estimated to reach sexual maturity at same age as females (1 year) (Vernes & Pope 2002).
Maximum breeding age (years)	5	Vernes and Pope (2002) recorded individuals alive at 4.9 years of age, so it is estimated that animals can breed to 5 years.
Maximum age (including non-breeding senescence)	7	Seebeck and Rose (1989) suggested that potoroids live up to (perhaps beyond) 7 years in the wild. However, older animals (≥ 8 years) in a captive colony of *Aepyprymnus rufescens* at University of New England (unpublished) could not produce young.
Sex ratio at birth (% males)	50	Vernes and Pope (2002) found no significant difference in sex ratio at birth.

Number of broods per year	3	Johnson and Delean (2001) recorded continuous breeding in a captive population, as is typical of other potoroids (Seebeck & Rose 1989). Vernes and Pope (2002) recorded *B. tropica* pouch life of 106 days, with young born in all months. A female can thus theoretically rear three successive pouch young to permanent pouch emergence each year.
Number of progenies per brood	1	Single young have only ever been recorded (Vernes & Pope 2002), although twins may occur in extremely low rates (as found in other macropod species).
Percentage of females breeding each year	96	Vernes and Pope (2002) found that of 120 captures of adult females, 115 (96%) were carrying a pouch young at the time of capture.
Standard deviation (SD) in percent of females breeding	3.9	Using VORTEX 10 and data from Vernes and Pope (2002), a SD of 3.9 was estimated (8%/2.06 SD units (over 4 years)
Of females breeding, percentage producing 1, 2, or 3 offspring?	1 offspring = 8 2 offspring = 34 3 offspring = 58	The likelihood of a female having 1, 2 or 3 young/year was calculated from Table 2 in Vernes and Pope (2002). 8% of females were estimated to have had 1 young (and lost the others), 34% had two young (but lost the third) and 58% carried all 3 young to permanent pouch emergence.
Age class mortalities (percent for males and females including environmental variation/standard deviation)		
0-1 year	48 (SD = 10)	Vernes and Pope (2002) recaptured 6 of 29 pouch young as sub-adults, indicating 79% of pouch young did not survive. About 50% did not survive until permanent emergence from the pouch. Therefore, assumed mortality was 40%. Of sub-adults tagged (21 animals: 9 females, 12 males) only 6 females (6/9 = 67%) and 3 males (3/12 = 25%) were recaptured as adults. Pope et al. (2012) estimated that male:female dispersal is 80:20 biased towards males. Mortality of sub-adults was therefore estimated at 13% (67+20 = 87% survival). 40% mortality from pouch to sub-adult, and 13% from sub-adult to adult yields average mortality of approx. 48%.
1+ years	15 (SD = 2)	Adult survivorship probability has been estimated at ≥80% (Vernes & Pope 2002). Adult mortality was therefore estimated as 15% (85% survivorship), with low (2%) standard deviation.
All adult males breeding	Yes	
Start at stable age distribution	Yes	
Initial population size (N)	BC = 105 DC = 225 EC = 300 TD = 435	Each population was treated as a 30 km^2 cell (5 km long x 6 km wide - the width of the dry end of wet sclerophyll occupied by *B. tropica* on the Lamb Range). Applying maximum densities calculated by Vernes and Pope (2006), initial population sizes for each location are: Bridle Creek (BC): 30 km^2 x 3.5 bettongs/km^2 = 105 animals; Davies Creek (DC): 30 km^2 x 7.5 ± 1.20 bettongs/km^2 = 225 ± 26 animals; Emu Creek (EC): 30 km^2 x 10 bettongs/km^2 = 300 animals; Tinaroo Creek (TC): 30 km^2 x 14.5 bettongs/km^2 = 435 animals. Population densities were calculated by undertaking Jolly-Seber analysis of *B. tropica* captures at

		each site, with 10 three-night trapping sessions conducted between November 1994 and December 1996. Sampling effort varied between sites, with 125 trap nights conducted at Bridle Creek, 4,267 at Davies Creek, 130 at Emu Creek and 334 at Tinaroo Creek. It is thus acknowledged that differences in sampling effort may have influenced population abundance estimates.
Carrying capacity (K)	As above	Observations 17 years ago suggest the carrying capacity was equal to the initial population size. Although the current carrying capacity might be lower, this is the best estimate available.
Standard deviations in carrying capacity	10%	A 10% deviation allows for population fluctuation.
Trend in carrying capacity	No	
Harvest of individuals	No	
Supplementation	No	
Specify exact distribution	Yes	

Appendix B. Presence/absence matrices of *Bettongia tropica* individuals at Davies Creek, Emu Creek and Tinaroo Creek based on cage trapping mark-recapture data.

Table B.1. Presence/absence matrix of *Bettongia tropica* individuals at Davies Creek based on mark-recapture data. A ‘1’ indicates presence, whilst ‘0’ indicates absence. ‘S’ represents trapping session, with 1 to 9 indicating the first to ninth trapping session. ‘D’ represents trap night and the number relates to the first to fourth night of trapping within the trapping session (e.g. S1D1 is the first night of the first trapping session). The number of captures is listed in the last column. The orange shading highlights the first capture for each individual, whilst the purple shading highlights individuals’ presence. The last 5 digits of the microchip number are shown.

Micro-chip number	Sex	S1D1	S1D2	S1D3	S1D4	S2D1	S2D2	S2D3	S2D4	S3D1	S3D2	S3D3	S3D4	S4D1	S4D2	S4D3	S4D4	S5D1	S5D2	S5D3	S5D4	S6D1	S6D2	S6D3	S6D4	S7D1	S7D2	S7D3	S7D4	S8D1	S8D2	S8D3	S8D4	S9D1	S9D2	S9D3	S9D4	Captures
24253	F	**1**	1	0	0	0	0	1	0	0	1	0	0	1	0	1	1	1	0	1	1	1	0	0	0	0	1	0	1	0	0	0	1	1	0	1	0	16
24651	M	**1**	1	0	0	0	0	0	0	1	0	0	0	1	1	1	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10
24139	M	**1**	0	0	0	0	0	0	0	1	0	1	1	1	1	1	1	1	1	0	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	25
25096	F	**1**	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
24646	F	**1**	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	5
34853	M	0	**1**	1	1	1	0	0	0	1	1	0	1	1	1	1	1	0	0	1	0	0	0	1	0	0	0	0	0	1	1	1	1	1	0	0	1	19
E4720	M	0	0	**1**	1	1	1	0	0	0	0	1	0	1	0	1	1	1	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	13
25135	M	0	0	**1**	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4
35187	M	0	0	**1**	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	1	0	1	0	0	1	0	1	1	0	0	0	0	1	0	1	1	12
24213	M	0	0	0	**1**	1	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5
25129	F	0	0	0	0	**1**	0	0	0	1	0	0	0	1	0	1	0	1	0	0	1	0	0	0	0	1	0	0	0	0	1	0	1	0	1	0	1	11
24454	F	0	0	0	0	**1**	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	1	1	0	0	1	1	0	0	0	1	0	0	9
24386	M	0	0	0	0	0	0	**1**	0	0	0	0	1	1	1	1	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	8
24424	F	0	0	0	0	0	0	**1**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
25433	M	0	0	0	0	0	0	0	**1**	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	1	1	1	1	1	1	1	1	1	13
25229	M	0	0	0	0	0	0	0	**1**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
24982	F	0	0	0	0	0	0	0	0	**1**	0	0	0	1	0	0	1	0	0	0	1	0	1	0	0	1	0	0	1	1	1	0	1	0	1	0	0	11
24463	M	0	0	0	0	0	0	0	0	0	**1**	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	5
25002	F	0	0	0	0	0	0	0	0	0	0	0	**1**	0	1	1	0	0	0	1	1	0	0	0	0	0	1	0	0	1	1	1	1	0	1	1	0	12
25190	M	0	0	0	0	0	0	0	0	0	0	0	**1**	0	1	0	1	0	0	0	0	0	0	0	0	1	0	1	0	1	1	1	0	1	0	0	1	10
24011	M	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
24879	M	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	1	1	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	7
24765	F	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2

Micro-chip number	Sex	S1D1	S1D2	S1D3	S1D4	S2D1	S2D2	S2D3	S2D4	S3D1	S3D2	S3D3	S3D4	S4D1	S4D2	S4D3	S4D4	S5D1	S5D2	S5D3	S5D4	S6D1	S6D2	S6D3	S6D4	S7D1	S7D2	S7D3	S7D4	S8D1	S8D2	S8D3	S8D4	S9D1	S9D2	S9D3	S9D4	Captures
23973	M	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
24787	F	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
24570	M	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	3
25290	F	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	4
31782	M	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	3
24972	M	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
53368	M	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2
25195	M	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
07099	F	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	1	0	1	0	0	0	0	1	4
24889	F	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	0	0	0	0	0	0	0	0	1
07252	M	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	1	0	0	0	0	1	0	1	0	4
24649	F	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	1	0	0	0	0	0	1	0	1	4
24243	F	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	0	0	0	0	0	0	0	1
24520	M	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	1	1	1	0	0	0	0	0	4
03932	F	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	1	1	1	0	0	0	0	4
24762	M	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	0	0	0	0	1
03909	M	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	1	0	0	0	0	2
12738	M	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	0	0	1
38116	M	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	1
38113	M	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	1

Table B.2. Presence/absence matrix of *Bettongia tropica* individuals at Emu Creek based on mark-recapture data. A ‘1’ indicates presence, whilst ‘0’ indicates absence. ‘S’ represents trapping session, with 1 to 9 indicating the first to ninth trapping session. ‘D’ represents trap night and the number relates to the first to fourth night of trapping within the trapping session (e.g. S1D1 is the first night of the first trapping session). The number of captures is listed in the last column. The orange shading highlights the first capture for each individual, whilst the purple shading highlights individuals’ presence. The last 5 digits of the microchip number are shown.

Micro-chip number	Sex	S1D1	S1D2	S1D3	S1D4	S2D1	S2D2	S2D3	S2D4	S3D1	S3D2	S3D3	S3D4	S4D1	S4D2	S4D3	S4D4	S5D1	S5D2	S5D3	S5D4	S6D1	S6D2	S6D3	S6D4	S7D1	S7D2	S7D3	S7D4	S8D1	S8D2	S8D3	S8D4	S9D1	S9D2	S9D3	S9D4	Captures
23900	M	**1**	1	0	0	0	0	1	1	1	1	1	0	1	1	1	1	1	1	1	1	0	1	1	1	1	0	0	1	1	1	0	1	1	1	0	0	25
25242	M	**1**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	0	6
24595	M	**1**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
25008	M	0	**1**	1	0	0	1	0	1	0	1	0	0	0	1	0	1	1	1	1	0	0	0	0	0	1	0	1	0	1	0	1	1	0	1	1	1	18
25395	M	0	**1**	0	1	1	1	0	0	1	0	0	1	1	1	0	0	0	1	1	0	1	0	0	0	1	1	0	1	0	0	1	1	0	1	1	0	18
24224	F	0	**1**	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
24626	F	0	**1**	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	1	0	1	0	8
24143	M	0	**1**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
24786	F	0	0	**1**	0	1	1	0	0	1	1	1	1	1	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	13
24892	M	0	0	0	0	**1**	0	1	1	0	1	1	1	1	0	1	0	1	0	1	1	0	0	0	0	1	1	0	0	0	1	1	1	0	0	0	1	17
24878	F	0	0	0	0	**1**	0	0	1	0	1	0	0	0	0	0	1	0	1	0	1	0	0	0	0	1	0	0	1	1	1	1	1	0	0	1	1	14
10781	M	0	0	0	0	**1**	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
25015	F	0	0	0	0	0	**1**	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	4
25285	M	0	0	0	0	0	**1**	0	0	0	0	1	0	1	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6
24753	M	0	0	0	0	0	0	**1**	0	1	0	1	1	1	1	0	1	1	1	1	1	1	1	0	0	1	0	1	1	1	1	1	1	1	1	0	1	23
24837	M	0	0	0	0	0	0	**1**	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
23897	F	0	0	0	0	0	0	0	**1**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
53370	M	0	0	0	0	0	0	0	**1**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
25149	F	0	0	0	0	0	0	0	0	0	**1**	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
24474	F	0	0	0	0	0	0	0	0	0	**1**	0	0	0	1	0	1	1	1	1	0	0	0	0	0	0	1	0	0	1	1	1	0	1	1	1	0	13
25438	F	0	0	0	0	0	0	0	0	0	**1**	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
24868	F	0	0	0	0	0	0	0	0	0	**1**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
25393	M	0	0	0	0	0	0	0	0	0	**1**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
25379	F	0	0	0	0	0	0	0	0	0	0	**1**	1	1	0	0	0	1	0	1	1	0	1	0	0	1	1	0	1	1	1	1	1	1	1	1	0	17
25061	M	0	0	0	0	0	0	0	0	0	0	**1**	0	1	0	1	1	1	1	0	1	1	0	0	0	0	1	0	0	0	0	1	1	0	1	1	0	13
24232	F	0	0	0	0	0	0	0	0	0	0	0	**1**	1	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5
24898	F	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0	1	6
24748	F	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	1	0	0	1	8
24183	M	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3

Micro-chip number	Sex	S1D1	S1D2	S1D3	S1D4	S2D1	S2D2	S2D3	S2D4	S3D1	S3D2	S3D3	S3D4	S4D1	S4D2	S4D3	S4D4	S5D1	S5D2	S5D3	S5D4	S6D1	S6D2	S6D3	S6D4	S7D1	S7D2	S7D3	S7D4	S8D1	S8D2	S8D3	S8D4	S9D1	S9D2	S9D3	S9D4	Captures
25438	F	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
31905	M	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	1	1	0	0	0	0	0	0	0	1	1	0	0	0	1	1	0	0	1	0	1	9
24261	M	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	4
24479	M	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
31863	F	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	1	0	1	0	1	0	0	1	0	0	0	0	1	1	0	1	1	1	0	0	10
31891	M	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	1	0	0	0	0	1	1	0	0	1	1	0	0	0	0	0	0	6
53371	M	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
24779	F	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	4
24391	F	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	0	1	0	1	1	1	0	1	1	0	1	0	1	0	1	10
24249	M	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
53311	F	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	0	0	0	0	1	0	1	1	0	1	0	1	1	0	7
07195	M	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
53365	M	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
24126	F	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	0	0	1	0	0	0	1	0	1	0	0	4
07083	M	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2
07304	M	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	0	0	0	0	0	0	0	0	0	0	1
07185	M	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	1	1	0	1	0	0	0	0	1	0	5
24203	M	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	1	0	0	1	1	0	1	1	1	0	1	8
24846	M	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	1	1	0	0	0	0	0	1	4
94393	F	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	0	1	0	0	1	1	1	0	5
25101	M	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	0	0	1	0	0	0	0	0	2
24942	F	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	1	1	1	0	1	1	0	0	0	6
24577	M	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	1	0	0	1	1	1	1	1	1	8
07196	F	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	1	1	1	0	0	1	1	1	7
03899	F	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	0	0	0	0	0	1
25203	M	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	0	0	0	0	0	1
07320	M	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	1	1	0	0	0	3
12748	M	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	1	1	0	0	0	3
25167	F	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	1	0	0	1	1	4
24136	M	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	1	0	0	2
35100	M	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	0	1
07118	M	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	1	1	0	3
38095	F	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	1
25098	F	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	1
00000	F	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	1

Table B.3. Presence/absence matrix of *Bettongia tropica* individuals at Tinaroo Creek based on mark-recapture data. A '1' indicates presence, whilst '0' indicates absence. 'S' represents trapping session, with 1 to 9 indicating the first to ninth trapping session. 'D' represents trap night and the number relates to the first to fourth night of trapping within the trapping session (e.g. S1D1 is the first night of the first trapping session). The number of captures is listed in the last column. The orange shading highlights the first capture for each individual, whilst the purple shading highlights individuals' presence. The last 5 digits of the microchip number are shown.

Micro-chip number	Sex	S1D1	S1D2	S1D3	S1D4	S2D1	S2D2	S2D3	S2D4	S3D1	S3D2	S3D3	S3D4	S4D1	S4D2	S4D3	S4D4	S5D1	S5D2	S5D3	S5D4	S6D1	S6D2	S6D3	S6D4	S7D1	S7D2	S7D3	S7D4	S8D1	S8D2	S8D3	S8D4	S9D1	S9D2	S9D3	S9D4	Captures
25179	M	**1**	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
24834	F	**1**	0	1	0	1	0	0	1	1	0	1	1	0	1	1	1	1	1	1	1	1	1	0	1	1	0	0	1	1	1	1	1	1	1	0	0	25
23980	F	**1**	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	1	1	0	0	1	1	0	1	1	0	1	0	0	1	0	0	1	1	0	0	15
24446	F	0	**1**	0	1	1	0	1	0	1	0	1	0	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	1	1	0	1	1	1	1	1	17
24954	F	0	**1**	0	0	1	0	1	0	1	1	1	0	1	0	1	1	1	0	0	0	0	1	0	0	1	0	1	1	1	1	0	1	1	1	1	1	21
24503	F	0	**1**	0	0	1	0	1	0	0	0	1	0	1	0	0	1	1	0	0	1	1	0	0	0	0	1	0	0	1	1	1	1	1	1	1	0	17
24531	F	0	**1**	0	0	0	0	1	0	1	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	1	1	0	1	1	0	1	0	1	1	1	1	16
24619	M	0	**1**	0	0	0	0	1	0	0	0	0	1	1	0	1	1	1	1	1	0	1	1	1	0	0	1	1	0	1	0	0	1	1	1	1	1	20
24866	F	0	0	**1**	1	0	0	1	1	1	0	1	0	1	1	1	0	1	1	1	1	1	1	0	1	1	1	1	1	1	0	1	1	1	1	1	1	27
22644	M	0	0	**1**	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
25330	F	0	0	**1**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
24897	M	0	0	0	**1**	0	0	1	1	0	1	0	1	0	1	0	1	0	1	1	1	0	1	0	1	0	1	1	0	1	1	1	1	1	1	1	1	22
25294	M	0	0	0	0	**1**	1	0	1	0	1	0	0	0	1	1	1	0	1	1	0	0	1	1	0	1	0	0	0	0	0	1	0	1	1	0	0	15
25329	M	0	0	0	0	**1**	0	1	0	0	0	1	0	1	0	0	0	1	1	1	0	0	0	0	0	0	1	0	0	1	1	1	0	0	0	0	0	11
24120	F	0	0	0	0	**1**	0	1	0	0	0	0	0	1	0	0	0	1	0	0	1	1	1	0	1	0	1	0	0	1	1	0	1	1	0	1	0	14
24791	F	0	0	0	0	**1**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
24354	M	0	0	0	0	0	**1**	1	0	1	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9
24910	M	0	0	0	0	0	**1**	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4
24749	M	0	0	0	0	0	0	**1**	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	6
24188	M	0	0	0	0	0	0	**1**	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	5
24827	F	0	0	0	0	0	0	**1**	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	7
10779	F	0	0	0	0	0	0	**1**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
10782	F	0	0	0	0	0	0	0	**1**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
25407	F	0	0	0	0	0	0	0	0	**1**	1	0	1	1	1	0	1	0	1	1	0	1	1	0	0	1	0	1	0	1	1	0	1	1	1	1	1	19
24993	M	0	0	0	0	0	0	0	0	**1**	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
24766	F	0	0	0	0	0	0	0	0	**1**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
25147	M	0	0	0	0	0	0	0	0	0	**1**	1	0	1	0	0	1	0	0	0	1	0	0	0	0	1	0	1	0	1	1	0	1	0	0	1	0	11
25116	F	0	0	0	0	0	0	0	0	0	**1**	0	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5
25191	F	0	0	0	0	0	0	0	0	0	**1**	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3

Micro-chip number	Sex	S1D1	S1D2	S1D3	S1D4	S2D1	S2D2	S2D3	S2D4	S3D1	S3D2	S3D3	S3D4	S4D1	S4D2	S4D3	S4D4	S5D1	S5D2	S5D3	S5D4	S6D1	S6D2	S6D3	S6D4	S7D1	S7D2	S7D3	S7D4	S8D1	S8D2	S8D3	S8D4	S9D1	S9D2	S9D3	S9D4	Captures
24902	F	0	0	0	0	0	0	0	0	0	**1**	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	5
24168	F	0	0	0	0	0	0	0	0	0	**1**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
24720	M	0	0	0	0	0	0	0	0	0	0	**1**	0	1	0	0	0	1	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	6
25146	M	0	0	0	0	0	0	0	0	0	0	**1**	0	0	1	1	0	1	1	0	1	0	0	0	0	1	1	0	1	1	1	0	1	1	1	1	0	15
24422	F	0	0	0	0	0	0	0	0	0	0	**1**	0	0	1	1	0	1	0	1	0	0	0	0	0	1	0	1	0	0	0	1	1	0	1	0	1	11
53366	M	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	1	0	0	1	6
53309	F	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	1	0	1	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	1	1	0	1	9
53373	M	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4
53310	F	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	1	1	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	6
24838	F	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
53372	F	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	4
24564	M	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
24941	M	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	1	0	1	0	0	1	0	0	1	0	0	0	0	1	1	0	0	1	8
10783	M	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
24602	M	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
53312	F	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
53369	F	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
53313	F	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
24498	F	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	4
53367	M	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
94386	F	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
24702	F	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2
07312	M	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
24935	F	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	0	0	0	0	0	0	0	0	0	1
24605	M	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	1	0	0	0	0	1	0	1	0	0	0	4
24385	M	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	1	1	1	0	0	1	1	1	0	7
24301	M	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	1	0	0	0	0	0	0	0	0	2
24212	M	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	1	1	0	0	0	1	1	0	5
94390	F	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	1	0	1	1	1	1	0	0	6
94396	M	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	0	0	0	0	0	0	0	1
24640	F	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	0	0	0	0	0	0	1
24996	F	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	1	0	1	0	0	0	1	4
12733	F	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	1	0	0	1	0	0	0	3
12753	F	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	0	0	0	0	1
12736	M	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	1	0	1	1	1	0	5
12746	F	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	1	0	0	1	3
12732	M	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	0	1	0	2

Micro-chip number	Sex	S1D1	S1D2	S1D3	S1D4	S2D1	S2D2	S2D3	S2D4	S3D1	S3D2	S3D3	S3D4	S4D1	S4D2	S4D3	S4D4	S5D1	S5D2	S5D3	S5D4	S6D1	S6D2	S6D3	S6D4	S7D1	S7D2	S7D3	S7D4	S8D1	S8D2	S8D3	S8D4	S9D1	S9D2	S9D3	S9D4	Captures
12723	F	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	0	0	1	2
12747	M	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	0	0	1	2
12751	M	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	0	0	0	1
12757	M	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	0	0	0	1
25410	F	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	0	0	1
38103	M	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	0	0	1
07051	M	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	0	0	1
07440	F	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	0	1
12761	M	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	1	0	0	2
38094	F	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	1
24118	F	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	1	0	2
38112	M	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	1
12744	F	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	1
38104	M	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	1
25594	M	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	1

Appendix C. Validating the model assumptions of Pollock's robust design.

The Pollock's robust design model has two assumptions: (1) the trapped population represents the target population, and (2) there is an equal probability of capturing individuals (Chapter 3). To test these assumptions, a preliminary robust design model was constructed in RStudio.

Testing assumption one: assessing for large residuals and calculating model goodness of fit

Large residuals indicate the population does not accurately represent the population, with large residuals needing to be removed. To assess the model residuals, Pearson's residuals were plotted against the frequency of capture of *B. tropica* individuals. To assess the model fit, a goodness of fit of the robust design models was undertake (Baillargeon & Rivest 2007). A fit of ≥0.80 was deemed suitable (Lettink & Armstrong 2003).

Pearson's residuals ≥3 were considered outliers (Huffman & Szafron 2017) and removed. At Davies Creek and Tinaroo Creek, there was one outlier, with Emu Creek having two outliers (Figure C.1). Once outliers were removed, the model fit at all sites improved (Table C.1) and residuals were more evenly distributed (Figure C.1aii, bii and cii).

Table C.1. Goodness of fit with and without outliers (Pearson's residuals ≥3) included in the robust design models.

	Outliers included	Outliers removed
Davies Creek	0.665	0.998
Emu Creek	0.923	0.990
Tinaroo Creek	0.328	0.961

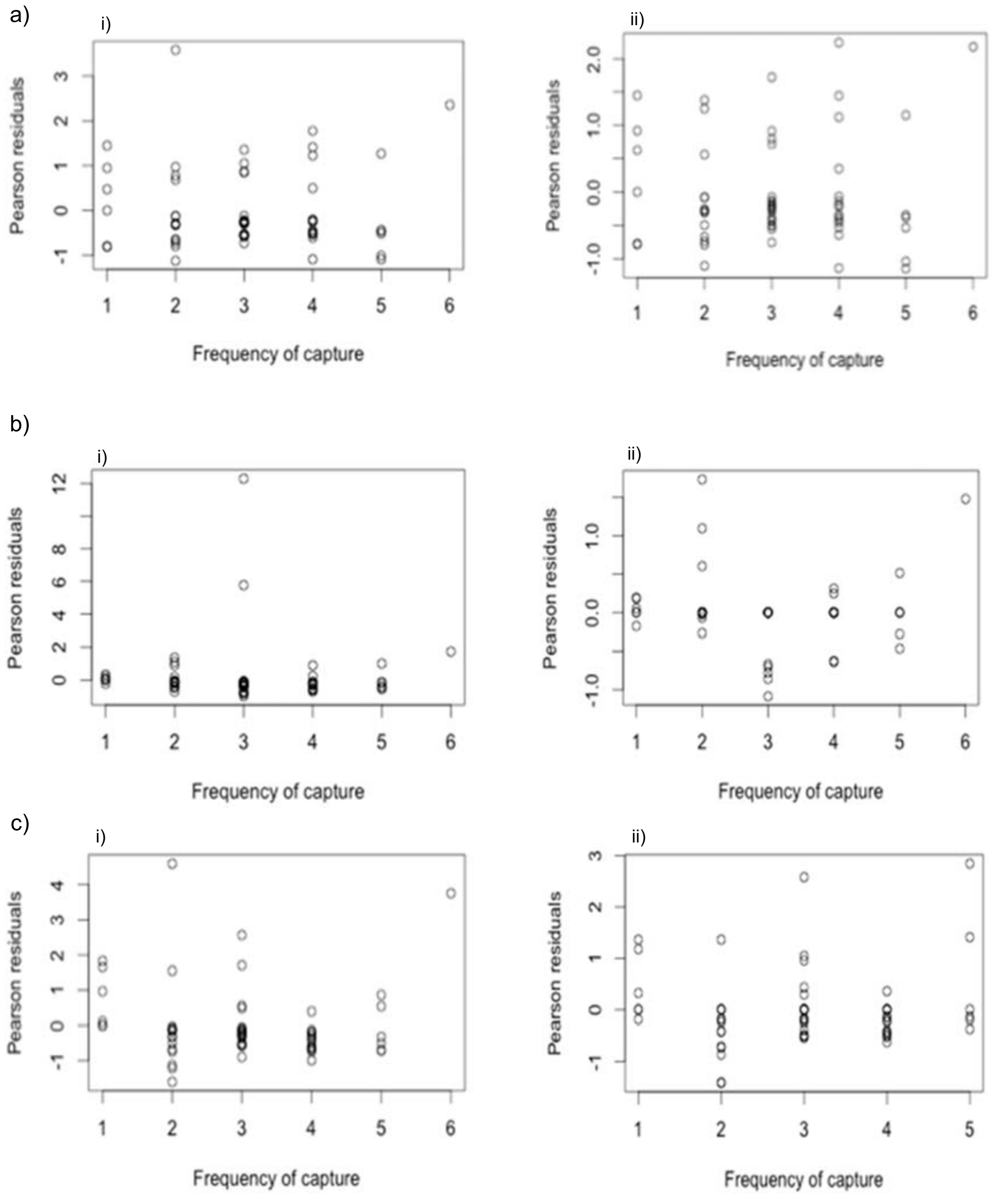

Figure C.1. Model diagnostics for population abundance at (a) Davies Creek, (b) Emu Creek and (c) Tinaroo Creek, showing Pearson's residuals in relation to frequency of capture (i) prior to large residuals being removed and (ii) after residuals ≥3 were removed, with no outliers present.

Testing assumption two: assessing for trap effect

To assess for trap effect, robust design models (without outliers) were created (1) without trap effect (null model), (2) with trap effect and (3) with homogeneous trap effect (Baillargeon & Rivest 2007). Models with the lowest Akaike's Information Criterion (AIC) values were deemed to be the best fit and models within two AIC values were assumed to be of equal fit (Burnham & Anderson 2004;

Symonds & Moussalli 2011). AIC is a measure of the relative quality of the model (Burnham & Anderson 2004; Symonds & Moussalli 2011).

Models without trap effect were better fitting at Davies Creek and Tinaroo Creek (lower AIC values), although models with trap effect were within 2 AIC values of the null model (C2). At Emu Creek, best fitting models incorporated trap effect (Table C2). However, since large residuals were removed and all null models had a high goodness of fit, population abundance models were considered valid and accurate (Baillargeon & Rivest 2007).

Table C.2. Robust design models of *Bettongia tropica* sub-populations at Davies Creek, Emu Creek and Tinaroo Creek, comparing models with no trap effect (null model), trap effect and homogeneous trap effect. Models with the lowest Akaike Information Criterion (AIC) value (highlighted in bold), or within 2 AIC values of the lowest value (indicated by an asterisk), were considered to be the best fit. Degrees of freedom (df) and standard error (deviance) for each model are shown.

	AIC	df	Deviance
Davies Creek:			
null model	**245.45**	488	126.74
trap effect	247.44*	487	126.73
homogeneous trap effect	253.82	482	123.11
Emu Creek:			
null model	231.56	487	93.02
trap effect	230.12	486	89.57
homogeneous trap effect	**219.09**	481	68.54
Tinaroo Creek:			
null model	**281.28**	487	143.65
trap effect	283.06*	486	143.42
homogeneous trap effect	289.02	481	139.34

Appendix D. Calculating effective trapping area of each site.

The effective trapping area was calculated by adding the mean home range radius of a male bettong (431 m) to all sides of each cage trap location. By measuring from each cage trap location means the cage trap locations are assumed to be the centre of the individuals' home range. This is unlikely to be the case for all individuals and it is noted that the effective trapping area is an estimate of the true area used by individuals.

As detailed in Chapter 4, Global Positioning System (GPS) collars were fitted to 51 *B. tropica* between February 2015 and 2016. The area of each collared individual's home range was plotted on Google Earth®. The diameter of each home range was measured in Google Earth® using the line tool. Home ranges were not symmetrical and the longest diameter for each home range was measured. The radius was calculated by halving the diameter. The mean radius of males and females was calculated separately, with the average radius of home ranges utilised by males being 431 m ± 19.77 m (mean ± standard error) whilst females averaged 245 m ± 16.09 m.

I used the home range diameter of males to calculate the effective trapping area. Using the home range of males may result in the effective trapping area being overestimated, especially since the home range radius was measured using the longest straight line of the home range. This may result in the population density being underestimated. This is because the density is calculated as abundance/effective trapping area and using the maximum effective area produces a lower density than if the effective trapping area was smaller. This approach was chosen so that the population density was a conservative estimate. Additionally, choosing 431 m also enabled population density estimates to be compared with results from Vernes and Pope (2006), who calculated the effective trapping area using a home range radius of 430 m based on their radio-tracking data.

At Tinaroo Creek, a river that is 10 m to 50 m wide borders the study site. Seventeen *B. tropica* individuals were GPS collared at Tinaroo (Chapter 4). By plotting their home ranges on Google Earth®, it was determined that no individual crossed the river, despite eight travelling to ≤10 m of the river edge and another within 40 m. The river thus appears to impose a movement barrier to *B. tropica*. When calculating the effective trapping area at Tinaroo Creek, I therefore only measured up to the river (Figure 3.2). It was assumed that individuals that were trapped in cages near the river were likely to be on the periphery of their home range and may travel further inland than the radius measurement (431 m). To determine the distance individuals may have travelled inland, the distance between the river and each cage trap was measured and this distance subtracted from the 431 m radius. The resulting number was then added to the radius (431 m) (i.e. if a cage trap was only 200 m from the river, 662 m was used (431 m + (431-200)), rather than 431 m). This new measurement was then used to delineate the boundary for the effective trapping area.

Appendix E. Influence of site and gender on the number of *Bettongia tropica* individuals and trap success during each cage trapping session.

Repeated measures ANOVAs with Tukey honest significance difference (HSD) post-hoc tests (adjusted with Bonferroni correction) were undertaken to assess the influence of site and gender on (1) the number of individuals captured, and (2) the number of captures of *B. tropica*. Captures refers to the total number of times *B. tropica* were cage trapped.

The number of *B. tropica* individuals and total captures of *B. tropica* differed between sites (individuals: $F_{2,48} = 6.621$, $p<0.001$; captures: $F_{2,48} = 6.621$, $p = 0.00289$), with significantly more individuals and captures recorded at Tinaroo Creek than at Emu Creek (individuals: $p<0.001$; captures: $p = 0.00190$). The number of individuals and captures were similar between Tinaroo Creek and Davies Creek (individuals: $p = 0.117$; captures: $p = 0.212$) and Davies Creek and Emu Creek (individuals: $p = 0.0730$; captures: $p = 0.174$).

Overall, the individuals and captures of males and females were similar (individuals: $F_{1,48} = 0.008$, $p = 0.927$; captures: $F_{1,48} = 0.036$, $p = 0.849$). There was an overall interaction between site and gender (individuals: $F_{2,48} = 2.205$, $p = 0.121$; captures: $F_{2,48} = 1.601$, $p = 0.212$). However, the number of female individuals differed between Davies Creek and Tinaroo Creek ($p = 0.00158$), as did the number of captures of females ($p = 0.00893$).

Table E.1. Number of individuals and captures of *Bettongia tropica* at Davies Creek, Emu Creek and Tinaroo Creek during each of the nine trapping sessions between November 2014 and 2016.

Site	Trapping session	Season	Male individuals	Male captures	Female individuals	Female captures	Total individuals	Number of captures
Davies Creek	Nov. 2014	Wet	6	8	4	7	10	15
	Feb. 2015	Wet	5	7	4	5	11	12
	May 2015	Dry	10	13	6	8	16	21
	Aug. 2015	Dry	11	24	10	18	21	42
	Nov. 2015	Dry	12	21	11	15	22	37
	Feb. 2016	Wet	8	11	4	4	12	15
	May 2016	Wet	6	12	7	10	13	22
	Aug. 2016	Dry	12	26	11	28	23	54
	Nov. 2016	Dry	8	19	10	15	18	34
Total	**Nov. 2014-2016**						**46**	**251**
	Nov. 2014	Wet	6	9	3	3	8	12

Emu Creek	Feb. 2015	Wet	7	12	6	7	8	19
	May 2015	Dry	10	18	10	15	20	33
	Aug. 2015	Dry	12	17	11	19	23	46
	Nov. 2015	Dry	16	32	9	18	25	50
	Feb. 2016	Wet	10	14	6	7	16	21
	May 2016	Wet	16	29	14	22	30	51
	Aug. 2016	Dry	19	38	15	34	34	72
	Nov. 2016	Dry	16	31	19	35	35	66
Total	**Nov. 2014-Nov. 2016**						**65**	**370**
Tinaroo Creek	Nov. 2014	Wet	5	8	7	9	12	17
	Feb. 2015	Wet	9	15	10	16	19	31
	May 2015	Dry	13	21	13	21	26	42
	Aug. 2015	Dry	15	28	17	33	32	61
	Nov. 2015	Dry	12	27	20	37	32	64
	Feb. 2016	Wet	8	14	15	30	23	45
	May 2016	Wet	13	21	17	26	30	47
	Aug. 2016	Dry	21	36	23	44	44	83
	Nov. 2016	Dry	17	36	24	47	41	83
Total	**Nov. 2014-Nov. 2016**						**84**	**473**

Appendix F. Number of individuals and density estimates of *Bettongia tropica* obtained using the Jolly-Seber methodology based on mark-recapture data.

The number of individuals at each study site was calculated using the Jolly-Seber method for all trapping sessions, except the first and last session. Population density estimates were subsequently estimated. Davies Creek recorded the lowest density, with on average of 7.76 ± 0.63 bettongs/km^2 (Table F.1). The highest population density of *B. tropica* was recorded at Tinaroo Creek, with 15.05 ± 1.25 bettongs/km^2, which was around double that attained at Davies Creek (Table E.1). At Emu Creek, an estimated 8.74 ± 0.29 bettongs/km^2 occurred (Table F.1).

Table F.1. Population abundance and density estimates of *Bettongia tropica* populations at Davies Creek, Emu Creek and Tinaroo Creek. Population estimates were calculated using the Jolly-Seber methodology and include the associated standard error. Abundance and density estimates are unable to be computed for the first and last trapping sessions.

	Season	Population abundance	Density estimates (individuals/km^2)
Davies Creek			
November 2014	Wet	(not computable)	(not computable)
February 2015	Wet	22.37 ± 2.63	6.90 ± 0.82
May 2015	Dry	20.97 ± 0.06	6.47 ± 0.02
August 2015	Dry	24.58 ± 1.04	7.58 ± 0.33
November 2015	Dry	25.00 ± 0.20	7.72 ± 0.06
February 2016	Wet	27.43 ± 2.01	8.47 ± 0.62
May 2016	Wet	28.05 ± 4.58	8.66 ± 1.41
August 2016	Dry	27.67 ± 3.72	8.54 ± 1.15
November 2016	Dry	(not computable)	(not computable)
Mean estimates		**25.15 ± 2.03**	**7.76 ± 0.63**
Emu Creek			
November 2014	Dry	(not computable)	(not computable)
February 2015	Wet	19.00 ± 0.00	5.74 ± 0.00
May 2015	Wet	24.00 ± 0.00	7.25± 0.00
August 2015	Dry	27.00 ± 0.09	8.16 ± 0.02
November 2015	Dry	32.13 ± 1.61	9.71 ± 0.48
February 2016	Wet	30.80 ± 8.87	9.30 ± 1.17
May 2016	Wet	33.66 ± 1.09	10.17 ± 0.33
August 2016	Dry	36.00 ± 0.09	10.88 ± 0.02
November 2016	Dry	(not computable)	(not computable)
Mean estimates		**28.94 ± 0.96**	**8.74 ± 0.29**

Tinaroo Creek			
November 2014	Dry	(not computable)	(not computable)
February 2015	Wet	39.40 ± 12.66	15.10 ± 4.84
May 2015	Wet	36.67 ± 2.57	14.05 ± 0.98
August 2015	Dry	38.74 ± 0.39	14.84 ± 0.15
November 2015	Dry	33.00 ± 0.70	12.64 ± 0.27
February 2016	Wet	41.58 ± 3.94	15.93 ± 1.51
May 2016	Wet	38.83 ± 2.27	14.87 ± 0.87
August 2016	Dry	46.74 ± 0.39	17.91 ± 0.15
November 2016	Dry	(not computable)	(not computable)
Mean estimates		**39.28 ± 3.27**	**15.05 ± 1.25**

Appendix G. Methodology for re-trapping *Bettongia tropica* to remove collars.

Removing collars

To re-trap collared bettongs, cages were placed where the collared *B. tropica* was previously caught, with 10 to 20 cages placed 50 m to 200 m apart in a grid configuration (example Figure G.1).

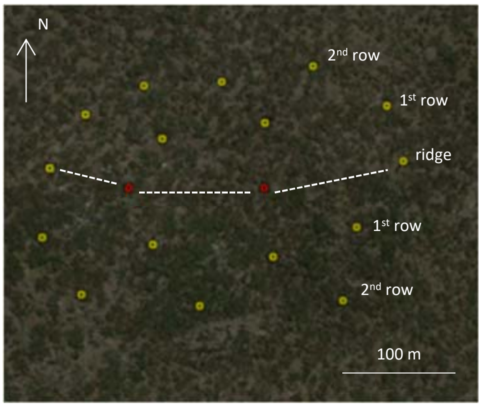

Figure G.1. Example of where cage traps were positioned at Tinaroo Creek to re-trap a collared *Bettongia tropica*. Cages were placed where the collared bettong had previously been trapped (red circles) and at additional locations (yellow circles) along the ridgeline (delineated by the dotted line) and in two rows either side of the ridgeline.

Bettongia tropica were also radio-tracked on foot to their nest and 10 cage traps were deployed 50 m to 100 m apart in a grid configuration around the nesting site (Figure G.2). The deployment of cages around a nesting site increased the chance of trapping *B. tropica* when they emerged from their nest to forage. *Bettongia tropica* have multiple nests (section 4.4.2) and after the first night of follow-up trapping, if *B. tropica* were not re-trapped, *B. tropica* would be again tracked to their nest. If the nest was in an area where cages were not already deployed, a further 10 cages would be placed in the area. This was continued until each collared *B. tropica* was re-trapped and collars removed. A maximum of 50 cages were deployed at each site during each follow-up session.

VHF signals could be obtained up to 700 m away, but local topography and obstructions, such as boulders, frequently reduced this distance considerably. Once a signal was obtained, the bettong’s location could generally be determined within 20 minutes. Redeployment of the collars gradually weakened the VHF antenna, which became prone to breaking. If the antenna had broken, VHF signals could generally only be obtained within about 50 m of the collared bettong. Trapping to remove collars was ceased if individuals were not trapped after eight nights of cage trapping, which occurred only twice.

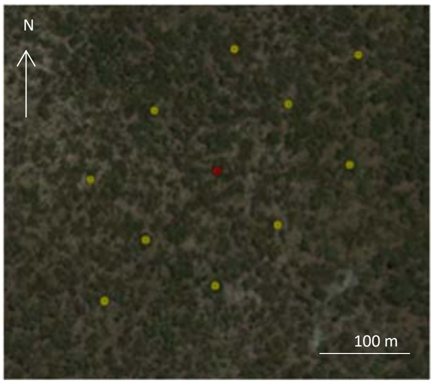

Figure G.2. An example of a grid configuration of cage traps at Davies Creek, with cage traps (yellow circles) positioned around a nest site (red circle) of the collared *Bettongia tropica*.

Appendix H. Methodology and results of home range estimated using all GPS fixes and for 12, 15, 20, 25 and 30 days of data.

Methodology

I calculated the 95% and 99% utilisation distribution (UD) home range of collared *B. tropica* for six time periods: 12, 15, 20, 25, 30 days and for all days of data. For each analysis, collars that recorded fewer days than the time period were excluded. Using 12 days of data meant two female individuals from each site were included in the analysis. The other time periods were selected so there was 5 days between each time period (excluding between 12 and 15 days). To ensure even comparisons between individuals, the first day (24 hour period) started at 6 pm on the night following when *B. tropica* was collared. Starting at 6 pm removed any bias associated with *B. tropica* being collared at different times. I selected 6 pm because all *B. tropica* emerged from their nesting area just before 7 pm. A programming error meant that the GPS collar on one *B. tropica* (943094320424120) only recorded data between 4 pm and midnight. Therefore, this individual could not be included in analysis.

I used a one-way ANOVAs and Kruskal-Wallis analysis to compare the home range calculated for each time period with the home range calculated using all data (which is considered the most accurate). All sites were analysed separately. To ensure a balanced comparison, the individuals with less data than the specified time period were also removed from the all data (e.g. if comparing 12 days of data and there were 10 individuals with 12 days of data, only the 10 individuals were included in the all days of data analysis). I also plotted the mean and standard error at all sites and for males and females for both the 95% UD and 99% UD for all the time periods (Figure H.1, H.2 and H.3).

Results

There was no difference between home ranges calculated using 12, 15, 20, 25 or 30 days of data compared to using all days of data (Table H.1). The UD 99% home ranges were considered the most suitable for analyses, as this range is the most inclusive for management purposes. The 99% UD home ranges also contained no disjunct sections (all sections of an animal's home range were connected). The 99% UD was therefore selected to be used.

Table H.1. Results from ANOVA and Kruskal-Wallis tests comparing 99% and 95% home range of *Bettongia tropica* calculated using all days of GPS data and 12, 15, 20, 25 and 30 days of data. All Kruskal-Wallis tests used one degree of freedom.

	Davies Creek	Emu Creek	Tinaroo Creek
95% home range			
All vs. 12 days	$\chi^2 = 0.40$, $p = 0.529$	$F_{1,18} = 1.087$, $p = 0.311$	$\chi^2 = 0.158$, $p = 0.691$
All vs. 15 days	$\chi^2 = 0.923$, $p = 0.337$	$F_{1,18} = 0.009$, $p = 0.926$	$\chi^2 = 0.0215$, $p = 0.884$
All vs. 20 days	$\chi^2 = 0.103$, $p = 0.749$	$F_{1,16} = 0.069$, $p = 0.796$	$\chi^2 = 0.00591$, $p = 0.939$
All vs. 25 days	$F_{1,8} = 0.036$, $p = 0.855$	$F_{1,10} = 0.025$, $p = 0.887$	$\chi^2 = 0.00591$, $p = 0.939$
All vs. 30 days	$F_{1,6} = 0.062$, $p = 0.811$	$F_{1,6} = 0.366$, $p = 0.567$	$\chi^2 = 0.000834$, $p = 0.977$
99% home range			
All vs. 12 days	$F_{1,14} = 1.55$, $p = 0.233$	$F_{1,18} = 1.428$, $p = 0.248$	$\chi^2 = 0.304$, $p = 0.581$
All vs. 15 days	$F_{1,10} = 1.305$, $p = 0.28$	$F_{1,18} = 0.173$, $p = 0.682$	$\chi^2 = 0.00592$, $p = 0.939$
All vs. 20 days	$F_{1,10} = 0.125$, $p = 0.731$	$F_{1,16} = 0.003$, $p = 0.955$	$\chi^2 = 0.000657$, $p = 0.980$
All vs. 25 days	$F_{1,8} = 0.27$, $p = 0.617$	$F_{1,10} = 0.328$, $p = 0.579$	$\chi^2 = 0.000657$, $p = 0.980$
All vs. 30 days	$F_{1,6} = 0.236$, $p = 0.645$	$F_{1,6} = 0.395$, $p = 0.553$	$\chi^2 = 0.0473$, $p = 0.828$

By comparing the error bars (Figure H.1) and home range estimates across all sites and genders (Table H.2, H.3 and H.4), 15 days of data appeared to produce the most reliable results. Using 15 days of data were considered most suitable to enable even comparison between sites and genders. Analysis using 15 days of data had relatively small error bars, generally overlapped with the error bars of the home ranges calculated using all data and were similar to home ranges using all data (Figure H.1; Table H.2, H.3 and H.4). Additionally, selecting 15 days meant that at least one female at each site was included in the analysis. This enabled comparisons of females between sites and genders. Home ranges calculated using 12 days of data tended to be smaller than those estimated from all data (Table H.2, H.3 and H.4). Home ranges estimated using 20, 25 and 30 days of data at Davies Creek were substantially larger than those calculated using all data (Figure H.1; Table H.2, H.3 and H.4). Male home ranges were calculated from the first 25 and 30 days of data were substantially smaller than estimates obtained using all data (Figure H.1; Table H.2, H.3 and H.4). The sample sizes for the 20, 25 and 30 day estimates were much reduced (for 25 and 30 days less than half the original sample size was retained).

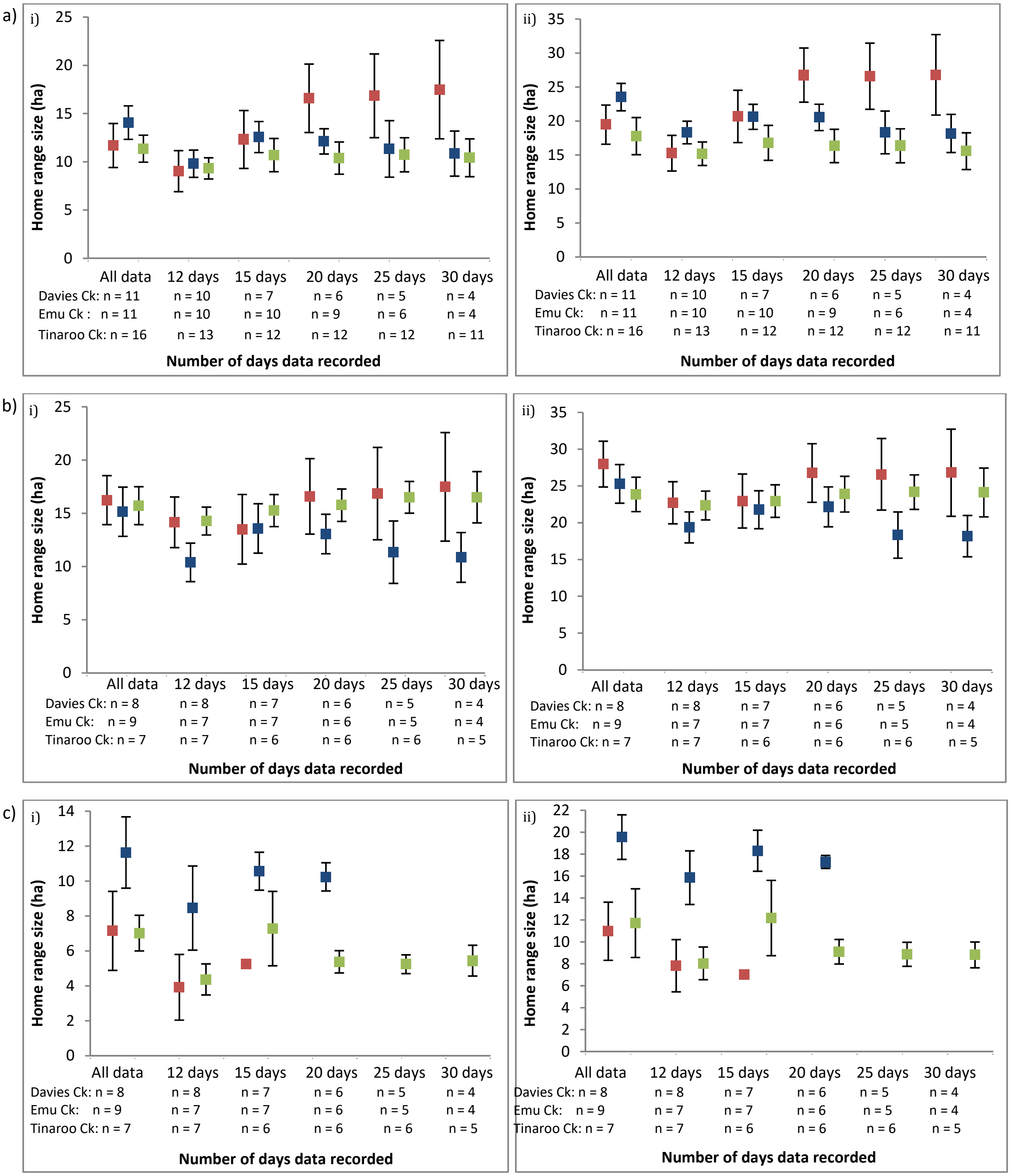

Figure H.1. Comparison of (a) all, (b) male and (c) female *Bettongia tropica* home ranges (mean and standard error bars) at Davies Creek (red), Emu Creek (blue) and Tinaroo Creek (green) calculated from all GPS data and data from the first 12, 15, 20, 25 and 30 days, using (i) 95% and (ii) 99% utilisation distributions.

Table H.2. Comparison of home range sizes of *Bettongia tropica* at Davies Creek, with home ranges calculated using 95% and 99% utilisation distribution (UD). Home ranges were estimated from all GPS fixes and for the first 12, 15, 20, 25 and 30 days of data. All estimates are in hectares. Means, with standard errors, are shown in bold. Microchip numbers of individuals are shown under ID. A dash (-) indicates there were insufficient days of data to compute the home range.

					All GPS fixes		First 12 days		First 15 days		First 20 days		First 25 days		First 30 days	
ID	Sex	Month collared	Season	Days	95% UD	99% UD	95% UD	99% UD	95% UD	99% UD	95% UD	99% UD	95% UD	99% UD	95% UD	99% UD
25229	M	Feb. 2015	Wet	25	10.27	23.41	11.73	23.29	9.85	19.34	9.88	20.87	10.27	23.41	-	-
E4720	M	Feb. 2015	Wet	23	12.88	26.11	12.51	20.67	11.26	21.35	14.51	28.64	-	-	-	-
24139	M	May 2015	Dry	13	8.76	15.96	9.28	14.35	-	-	-	-	-	-	-	-
24651	M	May 2005	Dry	13	21.96	36.30	16.21	27.50	-	-	-	-	-	-	-	-
23973	M	Aug. 2015	Dry	41	10.98	16.93	8.53	13.40	6.92	14.00	10.19	15.13	10.04	14.69	10.41	14.80
24213	M	Aug. 2015	Dry	36	17.69	34.68	11.97	18.45	10.32	17.66	13.87	23.43	8.00	18.09	8.08	19.67
24386	M	Aug. 2015	Dry	38	26.96	39.26	29.74	38.41	29.28	39.45	33.27	43.72	31.77	42.14	30.06	40.99
135187	M	Nov. 2015	Dry	32	20.36	31.13	13.24	25.58	13.33	25.89	17.81	28.74	21.02	30.67	21.38	31.72
Mean				**27.63 ± 3.99**	**16.23 ± 2.30**	**27.97 ± 3.11**	**14.15 ± 2.38**	**22.71 ± 2.86**	**13.49 ± 3.27**	**22.95 ± 3.67**	**16.59 ± 3.55**	**26.76 ± 3.98**	**16.85 ± 4.34**	**26.59 ± 4.86**	**17.49 ± 5.10**	**26.80 ± 5.92**
24982	F	May 2015	Dry	13	8.32	11.47	5.80	10.21	-	-	-	-				
24646	F	Nov. 2015	Dry	8	10.35	15.29	-	-	-	-	-	-				
25096	F	Nov. 2015	Dry	16	2.78	6.16	2.05	5.46	5.26	7.03	-	-				
Mean				**12.33 ± 2.33**	**7.15 ± 2.26**	**10.97 ± 2.65**	**3.92 ± 1.88**	**7.83 ± 2.38**	**5.26**	**7.03**	**-**	**-**	**-**	**-**	**-**	**-**

Table H.3. Comparison of home range sizes of *Bettongia tropica* at Emu Creek, with home ranges calculated using 95% and 99% utilisation distribution (UD). Home ranges were estimated from all GPS fixes and for the first 12, 15, 20, 25 and 30 days of data. All estimates are in hectares. Means, with standard errors, are shown in bold. Microchip numbers of individuals is shown under ID. A dash (-) indicates there were insufficient days of data to compute the home range.

					All GPS fixes		First 12 days		First 15 days		First 20 days		First 25 days		First 30 days	
ID	Sex	Month collared	Season	Days	95% UD	99% UD	95% UD	99% UD	95% UD	99% UD	95% UD	99% UD	95% UD	99% UD	95% UD	99% UD
24892	M	Feb. 2015	Wet	28	8.46	20.50	7.28	19.70	6.83	19.11	10.62	22.76	4.90	14.84	-	-
24395	M	May 2015	Dry	10	30.56	41.31	-	-	-	-	-	-	-	-	-	-
25393	M	May 2015	Dry	22	15.26	28.88	13.24	26.60	19.39	30.80	19.79	32.43	-	-	-	-
24183	M	Aug. 2015	Dry	32	14.74	23.96	7.97	13.98	10.53	18.15	11.14	19.91	14.26	21.45	11.21	19.83
24753	M	Nov. 2015	Dry	36	15.99	21.14	14.06	21.88	17.48	22.11	13.38	20.87	15.20	20.51	15.93	20.16
431905	M	Nov. 2015	Dry	39	6.52	12.82	7.86	13.40	8.22	13.40	6.97	12.09	3.87	8.20	4.61	9.98
25008	M	Nov. 2015	Dry	32	13.81	24.59	17.93	25.60	18.98	27.03	16.43	24.86	18.47	26.59	11.66	22.73
24261	M	Feb. 2016	Wet	19	11.92	23.93	4.37	14.39	5.43	14.85	-	-	-	-	-	-
25061	M	Feb. 2016	Wet	11	19.06	30.42	-	-	-	-	-	-	-	-	-	-
Mean				**25.44 ± 3.51**	**15.15 ± 2.31**	**25.28 ± 2.62**	**10.39 ± 1.80**	**19.36 ± 2.11**	**12.41 ± 2.28**	**20.78 ± 2.39**	**13.05 ± 1.86**	**22.15 ± 2.72**	**11.34 ± 2.93**	**18.32 ± 3.14**	**10.85 ± 2.34**	**18.17 ± 2.81**
25149	F	May-15	Dry	25	7.94	14.36	9.11	16.28	9.57	14.92	10.22	16.10	7.94	14.36	-	-
25015	F	Aug. 2015	Dry	23	13.49	21.06	12.26	19.86	12.74	21.37	8.85	17.91	-	-	-	-
25379	F	Feb. 2016	Wet	7	16.51	24.00	-	-	-	-	-	-	-	-	-	-
24626	F	Feb. 2016	Wet	24	8.60	18.80	3.99	11.42	9.39	18.66	11.65	17.85	-	-	-	-
Mean				**19.75 ± 4.27**	**11.64 ± 2.04**	**19.55 ± 2.03**	**8.45 ± 2.41**	**15.86 ± 2.45**	**10.57 ± 1.09**	**18.31 ± 1.87**	**10.24 ± 0.84**	**17.29 ± 0.59**	**7.94**	**14.36**	**-**	**-**

Table H.4. Comparison of home range sizes of *Bettongia tropica* at Tinaroo Creek, with home ranges calculated using 95% and 99% utilisation distribution (UD). Home ranges were estimated from all GPS fixes and for the first 12, 15, 20, 25 and 30 days of data. All estimates are in hectares. Means, with standard errors, are shown in bold. Microchip numbers of individuals are shown under ID. A dash (-) indicates there were insufficient days of data to compute the home range. *Bettongia tropica* 24210 was excluded from analyses as GPS data only recorded between 4 pm and midnight. *Bettongia tropica* 24954/10780* was collared twice, with only the first collaring data (February 2015) included in the averages.

					All GPS fixes		First 12 days		First 15 days		First 20 days		First 25 days		First 30 days	
ID	Sex	Month collared	Season	Days	95% UD	99% UD	95% UD	99% UD	95% UD	99% UD	95% UD	99% UD	95% UD	99% UD	95% UD	99% UD
24354	M	Feb. 2015	Wet	30	8.00	12.28	7.74	11.89	8.28	12.71	8.44	12.91	9.07	13.50	8.54	13.02
24446	M	Feb. 2015	Wet	14	15.54	24.05	12.58	22.56	-	-	-	-	-	-	-	-
25294	M	Aug. 2015	Dry	31	19.30	29.31	16.90	28.57	16.05	27.03	16.76	27.97	17.55	28.95	23.36	33.38
24897	M	Aug. 2015	Dry	26	13.82	24.37	16.35	25.97	18.85	27.47	19.19	29.05	18.47	28.12	-	-
25146	M	Aug. 2015	Dry	31	19.20	25.56	18.10	22.54	16.60	21.91	17.01	22.60	18.29	23.47	14.97	23.30
24619	M	Aug. 2015	Dry	31	21.63	31.04	13.44	23.09	14.58	24.49	16.12	27.26	17.74	27.58	18.16	27.28
24188	M	Nov. 2015	Dry	38	12.46	20.35	14.76	21.79	17.16	24.05	17.04	23.50	17.86	23.30	17.49	23.56
Mean				**28.71 ± 2.79**	**15.71 ± 1.78**	**23.85 ± 2.34**	**14.27 ± 1.31**	**22.34 ± 1.96**	**15.25 ± 1.51**	**22.94 ± 2.21**	**15.76 ± 1.52**	**23.88 ± 2.43**	**16.50 ± 1.49**	**24.15 ± 2.35**	**16.50 ± 2.41**	**24.11 ± 3.32**
24954/10780*	F	Feb. 2015*	Wet	32	3.25	6.09	1.96	4.49	2.65	5.38	2.73	5.67	3.32	5.97	4.68	7.22
24531	F	May 2015	Dry	30	3.61	6.36	3.50	5.51	4.32	6.77	4.81	7.22	4.70	6.97	4.49	7.08
24954/10780*	F	Nov. 2015	Dry	37	5.47	10.56	3.93	9.53	5.7	10.82	5.78	10.91	5.35	10.57	5.51	9.87
24834	F	Nov. 2015	Dry	38	12.57	17.50	7.05	13.53	7.70	13.93	7.37	14.07	7.25	13.88	10.30	14.42
24120	F	Nov. 2015	Dry	3	2.90	6.08	-	-	-	-	-	-	-	-	-	-
24941	F	Feb. 2016	Wet	34	2.33	4.85	3.50	6.15	4.38	7.81	4.29	7.35	4.11	6.68	3.58	5.93
24827	F	Feb. 2016	Wet	36	5.91	8.26	3.40	5.87	5.48	7.24	5.17	7.44	5.06	7.30	3.56	6.20
24210	F	Feb. 2016	Wet	19	21.03	34.53	-	-	-	-	-	-	-	-	-	-
23980	F	Feb. 2016	Wet	11	7.08	11.50	-	-	-	-	-	-	-	-	-	-
24866	F	Feb. 2016	Wet	36	6.00	11.37	7.24	11.16	6.26	10.23	7.50	11.07	6.90	10.71	6.00	10.98
Mean				**27.60 ± 4.18**	**7.02 ± 1.02**	**11.71 ± 3.13**	**4.37 ± 0.89**	**8.04 ± 1.49**	**7.28 ± 2.13**	**12.18 ± 3.43**	**5.38 ± 0.64**	**9.10 ± 1.12**	**5.24 ± 0.54**	**8.87 ± 1.10**	**5.45 ± 0.88**	**8.81 ± 1.17**

Appendix I. Verification for using 50% utilisation distribution to calculate nesting areas of *Bettongia tropica*.

Nesting areas calculated using the 50% UD were a more accurate representation of the region *Bettongia tropica* used for nesting. Estimates obtained using 95% and 99% UD were substantially larger (often larger than home range estimates) and are thus not representative of where bettongs nested (Figures I.1, I.2 and I.3; Table I.1).

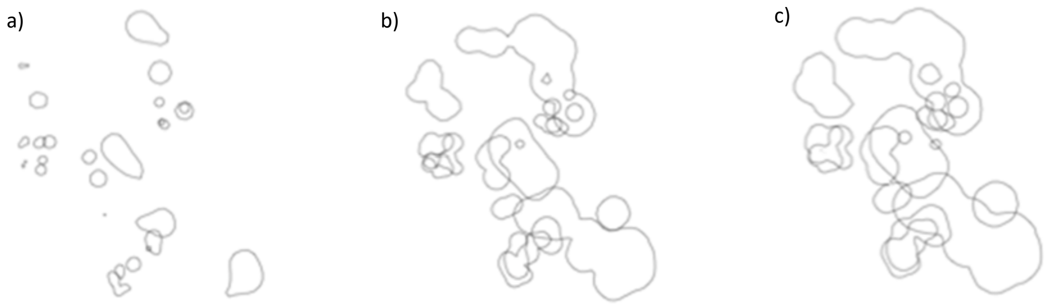

Figure I.1. Nesting areas of collared *Bettongia tropica* individuals at Davies Creek, with areas calculated using (a) 50% utilisation distribution (UD), (b) 95% UD and (c) 99% UD.

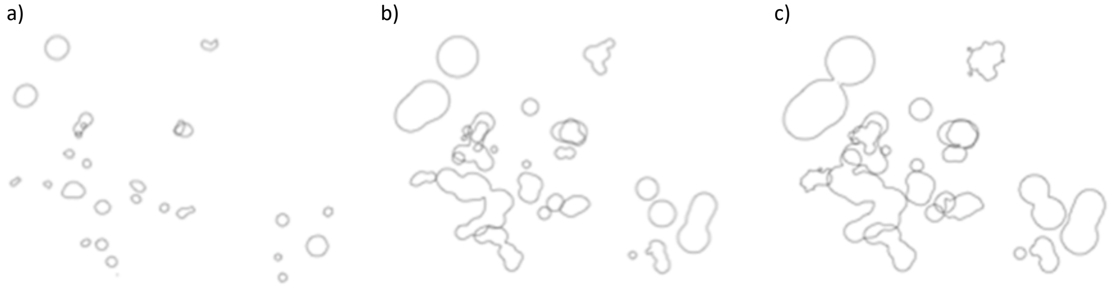

Figure I.2. Nesting areas of collared *Bettongia tropica* individuals at Emu Creek, with areas calculated using (a) 50% utilisation distribution (UD), (b) 95% UD and (c) 99% UD.

Figure I.3. Nesting areas of collared *Bettongia tropica* individuals at Tinaroo Creek, with areas calculated using (a) 50% utilisation distribution (UD), (b) 95% UD and (c) 99% UD.

Table I.1. Nesting areas of *Bettongia tropica* at Davies Creek, Emu Creek and Tinaroo Creek. Nesting areas were calculated using 50%, 95% and 99% utilisation distribution (UD) from 15 days and all days of data. Mean sizes ± standard error are shown in bold. *Bettongia tropica* 24954/10780* was collared twice, with only the first collaring data (February 2015) included in the means.

						15 days of data			All days of data		
Site	Bettong ID	Sex	Month collared	Season	Days	50% UD (ha)	95% UD (ha)	99% UD (ha)	50% UD (ha)	95% UD (ha)	99% UD (ha)
Davies Creek	25229	M	Feb. 2015	Wet	25	0.90	14.50	25.03	1.57	6.42	8.87
Davies Creek	E4720	M	Feb. 2015	Wet	23	1.80	17.68	29.98	3.93	19.77	30.39
Davies Creek	24139	M	May 2015	Dry	13	2.02	22.72	36.38	1.28	8.11	12.46
Davies Creek	24651	M	May 2005	Dry	13	4.37	23.32	39.01	5.77	29.31	41.58
Davies Creek	23973	M	Aug. 2015	Dry	41	0.36	15.59	25.93	0.26	2.64	4.85
Davies Creek	24213	M	Aug. 2015	Dry	36	1.27	14.32	25.03	0.92	4.79	6.81
Davies Creek	24386	M	Aug. 2015	Dry	38	0.78	13.15	23.74	0.88	8.30	12.77
Davies Creek	135187	M	Nov. 2015	Dry	32	3.25	29.18	45.78	7.44	34.54	47.08
Davies Creek	24982	F	May 2015	Dry	13	1.47	19.20	31.13	1.47	7.79	12.00
Davies Creek	24646	F	Nov. 2015	Dry	8	0.66	10.35	20.34	0.66	3.76	5.49
Davies Creek	25096	F	Nov. 2015	Dry	16	0.60	11.61	22.18	0.60	2.87	4.38
					Mean ± SE	**1.59 ± 0.37**	**17.4 ± 1.74**	**29.50 ± 2.39**	**2.25 ± 0.72**	**11.66 ± 3.35**	**16.97 ± 4.63**
Emu Creek	24892	M	Feb. 2015	Wet	28	0.11	11.58	21.47	0.19	1.89	3.39
Emu Creek	24395	M	May 2015	Dry	10	0.71	17.85	29.59	0.71	4.15	6.64
Emu Creek	25393	M	May 2015	Dry	22	3.38	23.97	39.05	2.08	12.01	18.14
Emu Creek	24183	M	Aug. 2015	Dry	32	0.36	13.12	23.62	0.33	2.40	3.83
Emu Creek	24753	M	Nov. 2015	Dry	36	1.62	15.10	27.64	1.33	6.14	8.92
Emu Creek	431905	M	Nov. 2015	Dry	39	0.22	13.84	23.63	0.40	3.27	5.60
Emu Creek	25008	M	Nov. 2015	Dry	32	3.24	28.97	43.30	1.93	12.97	18.97
Emu Creek	24261	M	Feb. 2016	Wet	19	0.72	9.05	19.87	0.92	4.52	6.39

Site	Bettong ID	Sex	Month collared	Season	Days	50% UD (ha)	95% UD (ha)	99% UD (ha)	50% UD (ha)	95% UD (ha)	99% UD (ha)
Emu Creek	25061	M	Feb. 2016	Wet	11	0.46	16.42	28.38	0.46	2.72	5.06
Emu Creek	25149	F	May-15	Dry	25	0.14	13.97	24.87	0.17	1.23	2.37
Emu Creek	25015	F	Aug. 2015	Dry	23	0.38	14.45	25.42	0.43	2.77	4.91
Emu Creek	25379	F	Feb. 2016	Wet	7	3.33	24.15	37.64	3.33	15.82	24.11
Emu Creek	24626	F	Feb. 2016	Wet	24	0.80	18.98	30.89	0.91	3.82	5.75
					Mean ± SE	**1.19 ± 0.35**	**17.03 ± 1.57**	**28.87 ± 1.98**	**1.01 ± 0.26**	**5.67 ± 1.32**	**8.77 ± 1.93**
Tinaroo Creek	24354	M	Feb. 2015	Wet	30	1.03	13.04	24.11	0.89	4.90	7.41
Tinaroo Creek	24446	M	Feb. 2015	Wet	14	3.92	25.50	40.45	3.92	18.77	29.27
Tinaroo Creek	25294	M	Aug. 2015	Dry	31	2.50	20.94	34.90	2.35	9.89	14.63
Tinaroo Creek	24897	M	Aug. 2015	Dry	26	0.52	11.62	22.02	0.84	4.30	6.49
Tinaroo Creek	25146	M	Aug. 2015	Dry	31	1.30	18.84	32.07	1.37	7.12	11.38
Tinaroo Creek	24619	M	Aug. 2015	Dry	31	2.10	23.30	36.31	2.10	11.25	16.91
Tinaroo Creek	24188	M	Nov. 2015	Dry	38	0.22	15.22	26.29	0.38	2.44	4.30
Tinaroo Creek	24954/10780*	F	Feb. 2015	Wet	32	0.24	7.97	17.19	0.32	2.40	3.83
Tinaroo Creek	24531	F	May 2015	Dry	30	0.30	14.68	24.93	0.27	1.57	2.61
Tinaroo Creek	24954/10780*	F	Nov. 2015	Dry	37	5	0.36	10.9	21.10	0.35	1.91
Tinaroo Creek	24834	F	Nov. 2015	Dry	38	8	1.05	16.60	27.34	0.91	5.08
Tinaroo Creek	24120	F	Nov. 2015	Dry	3	2	1.16	14.97	24.18	1.16	5.35
Tinaroo Creek	24941	F	Feb. 2016	Wet	34	5	0.63	11.32	21.86	0.43	2.69
Tinaroo Creek	24827	F	Feb. 2016	Wet	36	7	0.38	9.65	19.10	0.43	2.58
Tinaroo Creek	24210	F	Feb. 2016	Wet	19	6	1.67	28.08	45.60	1.67	7.72
Tinaroo Creek	23980	F	Feb. 2016	Wet	11	6	0.66	13.78	24.16	0.66	3.09
Tinaroo Creek	24866	F	Feb. 2016	Wet	36	5	0.32	8.74	18.55	0.78	3.84
					Mean ± SE	**1.12 ± 0.25**	**15.89 ± 1.50**	**27.44 ± 2.05**	**1.15 ± 0.24**	**5.81 ± 1.11**	**8.88 ± 1.71**

Appendix J. Cage trapping details from when collars were deployed and retrieved from *Bettongia tropica*.

Table J.1. Cage trapping details of collared *Bettongia tropica* at Davies Creek. Trap number is the trap where the bettong was caught on the day it was collared. Days of data refers to the number of days that the GPS collar recorded data.

Bettong microchip	Sex	Month collared	Season	Weight when collared (g)	Radio-tracking frequency	Trap number	Date deployed	Time released	Date retrieved	Days of data
943094320425229	M	Feb-15	Wet	1270	150.750	A5	7/02/15	1:15	4/03/15	25
FXDA4A683E4720	M	Feb-15	Wet	1325	150.931	B6	5/02/15	1:42	6/03/15	23
943094320425433	M	Feb-15	Wet	1310	150.970	I1	7/02/15	3:10	21/02/15	0
943094320424139	M	May-15	Dry	1330	150.970	F4	31/05/15	1:56	19/07/15	12
943094320424651	M	May-15	Dry	1240	150.831	I5	31/05/15	3:10	20/07/15	12
943094320424982	F	May-15	Dry	1170	150.871	B5	31/05/15	4:07	21/07/15	12
943094320424386	M	Aug-15	Dry	1330	150.790	G5	31/07/15	3:20	6/09/15	38
943094320424213	M	Aug-15	Dry	1130	150.750	F6	2/08/15	2:50	6/09/15	36
943094320423973	M	Aug-15	Dry	1100	150.991	B7	31/07/15	4:25	9/09/15	41
985170000135187	M	Nov-15	Dry	1240	150.871	A1	13/11/15	0:25	16/12/15	32
943094320424646	F	Nov-15	Dry	1285	150.710	A6	12/11/15	2:03	18/12/15	16
943094320425096	F	Nov-15	Dry	1280	150.750	F7	13/11/15	2:15	16/12/15	8
943094320424879	M	Feb-16	Wet	1280	150.750	F4	6/02/16	2:50	Not found	0
943094320424454	F	Feb-16	Wet	1260	150.931	F2	5/02/16	0:22	16/03/16	1.5

Table J.2. Cage trapping details of collared *Bettongia tropica* at Emu Creek. Trap number is the trap where the bettong was caught on the day it was collared. Days of data refers to the number of days that the GPS collar recorded data.

Bettong microchip	Sex	Month collared	Season	Weight when collared (g)	Radio-tracking frequency	Trap number	Date deployed	Time released	Date retrieved	Days of data
943094320424892	M	Feb-15	Wet	1380	150.991	A3	21/02/15	1:35	20/03/15	28
943094320423900	M	Feb-15	Wet	1380	150.871	A1	21/02/15	0:10	26/02/15	0
943094320425393	M	May-15	Dry	1290	150.910	H2	21/05/15	2:10	3/07/15	22
943094320424395	M	May-15	Dry	1360	150.670	B6	20/05/15	0:35	30/06/15	10
943094320425149	F	May-15	Dry	1360	150.710	A6	21/05/15	1:47	3/07/15	25
943094320424183	M	Aug-15	Dry	1260	151.141	H7	19/08/15	4:50	20/09/15	32
943094320423900	M	Aug-15	Wet	1380	150.871	A1	20/08/15	1:19	25/08/15	0
943094320425015	F	Aug-15	Wet	1400	150.710	F7	19/08/15	0:40	18/09/15	23
943094320424232	F	Feb-15	Wet	1400	150.710	F7	19/02/15	3:04	25/03/15	0
943094320424753	M	Nov-15	Dry	1240	150.991	C1	2/11/15	0:20	11/12/15	36
943094320425061	M	Nov-15	Dry	1280	150.931	C7	2/11/15	1:10	10/12/15	0
943094320431905	M	Nov-15	Dry	1120	150.831	D2	2/11/15	1:55	8/12/05	39
943094320425008	M	Nov-15	Dry	1220	150.97	E2	2/11/15	2:15	8/12/05	32
943094320424261	M	Feb-16	Wet	1280	150.831	E4	13/02/16	0:26	17/03/16	19
943094320425061	M	Feb-16	Wet	1260	150.710	C7	13/02/16	1:36	18/03/16	11
943094320424626	F	Feb-16	Wet	1300	150.790	C6	13/02/16	1:56	18/03/16	24
943094320425379	F	Feb-16	Wet	1380	150.670	A1	14/02/16	0:14	20/03/16	7
943094320707195	M	Feb-16	Wet	1300	150.871	A2	13/02/16	3:15	Not found	0

Table J.3. Cage trapping details of collared *Bettongia tropica* at Tinaroo Creek. Trap number is the trap where the bettong was caught on the day it was collared. Days of data refers to the number of days that the GPS collar recorded data.

Bettong microchip	Sex	Month collared	Season	Weight when collared (g)	Radio-tracking frequency	Trap number	Date deployed	Time released	Date retrieved	Days of data
943094320424446	M	Feb-15	Wet	1290	150.670	F3	1/03/15	2:47	1/04/15	14
943094320424354	M	Feb-15	Wet	1280	150.910	D2	2/03/15	3:10	1/04/15	30
24954/10780*	F	Feb-15	Wet	1170	150.790	H2	1/03/15	0:30	4/04/15	32
943094320424531	F	May-15	Dry	1280	150.991	F4	10/05/15	3:05	9/06/15	30
943094320424993	M	May-15	Dry	960	150.750	H3	10/05/15	2:00	12/05/15	0
943094320424834	F	May-15	Dry	1270	150.931	E2	10/05/15	0:10	9/06/15	0
943094320424897	M	Aug-15	Dry	1340	151.180	D1	31/08/15	1:50	2/10/15	26
943094320424619	M	Aug-15	Dry	1370	150.670	C3	1/09/15	1:30	2/10/15	31
943094320425146	M	Aug-15	Dry	1245	151.221	H6	1/09/15	1:22	2/10/15	31
943094320425294	M	Aug-15	Dry	1255	150.970	H1	1/09/15	2:20	2/10/15	31
943094320424188	M	Nov-15	Dry	1190	151.221	H7	23/10/15	1:27	19/11/15	38
943094320424834	F	Nov-15	Dry	1290	150.670	E2	23/10/15	0:25	18/11/15	38
943094320424120	F	Nov-15	Dry	1400	150.790	E7	23/10/15	1:05	20/11/15	3
24954/10780*	F	Nov-15	Dry	1300	151.141	H3	23/10/15	2:08	18/11/15	37
943094320424941	F	Feb-16	Wet	1315	151.141	E3	26/02/16	0:31	4/04/16	34
943094320424827	F	Feb-16	Wet	1300	150.970	E4	26/02/16	0:50	4/04/16	36
943094320424120	F	Feb-16	Wet	1515	150.910	H7	26/02/16	1:33	7/04/16	19
943094320423980	F	Feb-16	Wet	1440	150.991	B5	26/02/16	3:19	5/04/16	11
943094320424866	F	Feb-16	Wet	1160	151.221	C2	26/02/16	3:41	4/04/16	36

*Bettong number 24954/10780 was microchipped twice.

Appendix K. Home range size, core nesting and foraging areas and number of nesting areas used by *Bettongia tropica* at each site.

Table K.1. Home range size, core nesting and foraging areas and number of nesting areas used by *Bettongia tropica* at Davies Creek for all GPS fixes recorded and for the first 15 days. Means, with standard errors, are shown in bold.

				All GPS fixes							First 15 days of data				
Bettong ID	Sex	Month collared	Season	Days	GPS fixes	Nesting areas (count)	50% UD nesting (ha)	50% UD foraging (ha)	95% UD (ha)	99% UD (ha)	Nesting areas (count)	50% UD nesting (ha)	50% UD foraging (ha)	95% UD (ha)	99% UD (ha)
25229	M	Feb. 2015	Wet	25	3002	9	0.97	5.77	10.27	23.41	4	0.90	4.06	9.85	19.34
E4720	M	Feb. 2015	Wet	23	2139	6	0.37	6.36	12.88	26.11	4	1.80	6.08	11.26	21.35
24139	M	May 2015	Dry	13	2110	4	0.37	4.55	8.76	15.96	<15 days	<15 days	<15 days	<15 days	<15 days
24651	M	May 2005	Dry	13	1979	7	0.29	11.05	21.96	36.30	<15 days	<15 days	<15 days	<15 days	<15 days
23973	M	Aug. 2015	Dry	41	5002	5	0.57	5.08	10.98	16.93	3	0.36	4.08	6.92	14.00
24213	M	Aug. 2015	Dry	36	4493	9	0.10	6.92	17.69	34.68	5	1.27	4.91	10.32	17.66
24386	M	Aug. 2015	Dry	38	4335	6	0.28	10.18	26.96	39.26	3	0.78	16.36	29.28	39.45
135187	M	Nov. 2015	Dry	32	3825	13	3.00	11.20	20.36	31.13	4	3.25	10.15	13.33	25.89
Mean				**27.63 ± 3.99**	**3361 ± 428**	**7.38 ± 1.02**	**0.74 ± 0.30**	**7.64 ± 0.96**	**16.23 ± 2.30**	**27.97 ± 3.11**	**3.88 ± 0.31**	**1.39 ± 0.42**	**7.61 ± 1.98**	**13.49 ± 3.27**	**22.95 ± 3.67**
24982	F	May 2015	Dry	13	1445	5	1.76	5.59	8.32	11.47	<15 days	<15 days	<15 days	<15 days	<15 days
24646	F	Nov. 2015	Dry	8	991	7	0.45	4.06	10.35	15.29	<15 days	<15 days	<15 days	<15 days	<15 days
25096	F	Nov. 2015	Dry	16	2157	4	0.01	3.00	2.78	6.16	3	0.60	1.06	5.26	7.03
Mean				**12.33 ± 2.33**	**1513 ± 339**	**5.33 ± 0.88**	**0.74 ± 0.52**	**4.22 ± 0.75**	**7.15 ± 2.26**	**10.97 ± 2.65**	**3**	**0.60**	**1.06**	**5.26**	**7.03**

Table K.2. Home range size, core nesting and foraging areas and number of nesting areas used by *Bettongia tropica* at Emu Creek for all GPS fixes recorded and for the first 15 days. Means, with standard errors, are shown in bold.

				All GPS fixes							First 15 days of data				
Bettong ID	Sex	Month collared	Season	Days	GPS fixes	Nesting areas (count)	50% UD nesting (ha)	50% UD foraging (ha)	95% UD (ha)	99% UD (ha)	Nesting areas (count)	50% UD nesting (ha)	50% UD foraging (ha)	95% UD (ha)	99% UD (ha)
24892	M	Feb. 2015	Wet	28	3102	5	0.09	2.54	8.46	20.50	4	0.11	3.32	6.83	19.11
24395	M	May 2015	Dry	10	1250	3	0.37	7.92	30.56	41.31	<15 days	<15 days	<15 days	<15 days	<15 days
25393	M	May 2015	Dry	22	2601	5	0.61	3.39	15.26	28.88	5	3.38	9.13	19.39	30.80
24183	M	Aug. 2015	Dry	32	3885	7	0.08	5.37	14.74	23.96	4	0.36	4.12	10.53	18.15
24753	M	Nov. 2015	Dry	36	4350	8	0.38	6.18	15.99	21.14	4	1.62	5.47	17.48	22.11
431905	M	Nov. 2015	Dry	39	5069	6	0.74	3.21	6.52	12.82	4	0.22	2.51	8.22	13.40
25008	M	Nov. 2015	Dry	32	4768	8	0.46	7.54	13.81	24.59	5	3.24	6.35	18.98	27.03
24261	M	Feb. 2016	Wet	19	1710	5	0.46	4.39	11.92	23.93	4	0.72	4.97	5.43	14.85
25061	M	Feb. 2016	Wet	11	1412	4	0.73	7.52	19.06	30.42	<15 days	<15 days	<15 days	<15 days	<15 days
Mean				**25.44 ± 3.51**	**3127 ± 490**	**5.67 ± 0.58**	**0.44 ± 0.08**	**5.34 ± 0.69**	**15.15 ± 2.31**	**25.28 ± 2.62**	**4.28 ± 0.18**	**1.38 ± 0.53**	**5.12 ± 0.83**	**12.41 ± 2.28**	**20.78 ± 2.39**
25149	F	May-15	Dry	25	2537	3	0.54	2.27	7.94	14.36	3	0.14	2.29	9.57	14.92
25015	F	Aug. 2015	Dry	23	2536	2	0.78	4.70	13.49	21.06	3	0.38	4.90	12.74	21.37
25379	F	Feb. 2016	Wet	7	1412	3	0.13	4.91	16.51	24.00	<15 days	<15 days	<15 days	<15 days	<15 days
24626	F	Feb. 2016	Wet	24	2710	6	0.94	3.52	8.60	18.80	4	0.80	2.34	9.39	18.66
Mean				**19.75 ± 4.27**	**2299 ± 299**	**3.50 ± 0.87**	**0.60 ± 0.18**	**3.85 ± 0.61**	**11.64 ± 2.04**	**19.55 ± 2.03**	**3.33 ± 0.33**	**0.44 ± 0.19**	**3.18 ± 0.86**	**10.57 ± 1.09**	**18.31 ± 1.87**

Table K.3. Home range size, core nesting and foraging areas and number of nesting areas used by *Bettongia tropica* at Tinaroo Creek for all GPS fixes recorded and for the first 15 days. *Bettongia tropica* 24954/10780 was collared twice, with only the first collaring data (February 2015) included in the means. *Bettongia tropica* 24210 only recorded between 12 am and 3 am, with the number of GPS fixes recorded by the collared excluded in the mean calculation. Means, with standard errors, are shown in bold.

				All GPS fixes						First 15 days of data					
Bettong ID	Sex	Month collared	Season	Days	GPS fixes	Nesting areas (count)	50% UD nesting (ha)	50% UD foraging (ha)	95% UD (ha)	99% UD (ha)	Nesting areas (count)	50% UD nesting (ha)	50% UD foraging (ha)	95% UD (ha)	99% UD (ha)
24354	M	Feb. 2015	Wet	30	3612	6	1.31	4.59	8.00	12.28	4	1.03	2.55	8.28	12.71
24446	M	Feb. 2015	Wet	14	1328	3	0.39	6.39	15.54	24.05	<15 days	<15 days	<15 days	<15 days	<15 days
25294	M	Aug. 2015	Dry	31	4052	6	0.55	11.54	19.30	29.31	4	2.50	12.36	16.05	27.03
24897	M	Aug. 2015	Dry	26	3245	6	1.15	8.16	13.82	24.37	4	0.52	8.58	18.85	27.47
25146	M	Aug. 2015	Dry	31	3900	5	1.06	6.62	19.20	25.56	3	1.30	5.88	16.60	21.91
24619	M	Aug. 2015	Dry	31	3946	10	0.69	9.36	21.63	31.04	5	2.10	7.98	14.58	24.49
24188	M	Nov. 2015	Dry	38	4516	6	0.16	6.75	12.46	20.35	4	0.22	7.75	17.16	24.05
Mean				**28.7 ± 2.79**	**3514 ± 393**	**6.00 ± 0.79**	**0.76 ± 0.16**	**7.63 ± 0.86**	**15.71 ± 1.78**	**23.85 ± 2.34**	**4.0 ± 0.26**	**1.28 ± 0.36**	**7.52 ± 1.32**	**15.25 ± 1.51**	**22.94 ± 2.21**
24954/ 10780	F	Feb. 2015	Wet	32	3348	7	0.29	2.33	3.25	6.09	4	0.24	1.32	2.65	5.38
24531	F	May 2015	Dry	30	3648	4	0.17	2.47	3.61	6.36	4	0.30	0.90	4.32	6.77
24954/ 10780	F	Nov. 2015	Dry	37	4460	5	0.21	3.21	5.47	10.56	6	0.36	1.88	5.72	10.82
24834	F	Nov. 2015	Dry	38	4682	8	0.48	5.29	12.57	17.50	4	1.05	4.50	7.70	13.93
24120	F	Nov. 2015	Dry	3	296	2	0.72	1.12	2.90	6.08	<15 days	<15 days	<15 days	<15 days	<15 days
24941	F	Feb. 2016	Wet	34	4382	5	0.81	2.00	2.33	4.85	4	0.63	1.20	4.38	7.81
24827	F	Feb. 2016	Wet	36	4588	7	0.63	3.60	5.91	8.26	4	0.38	1.65	5.48	7.24
24210	F	Feb. 2016	Wet	19	739*	6	2.92	6.41	21.03	34.53	Date recorded incorrectly				
23980	F	Feb. 2016	Wet	11	1161	6	0.54	3.72	7.08	11.50	<15 days	<15 days	<15 days	<15 days	<15 days
24866	F	Feb. 2016	Wet	36	4227	5	0.51	3.74	6.00	11.37	5	0.32	2.82	6.26	10.23
Mean				**27.60 ± 4.18**	**3421 ± 534**	**5.50 ± 0.54**	**0.78 ± 0.27**	**3.39 ± 0.55**	**7.02 ± 1.02**	**11.71 ± 3.13**	**4.43 ± 0.30**	**0.49 ± 0.13**	**2.06 ± 0.56**	**7.28 ± 2.13**	**12.18 ± 3.43**

Appendix L. Permanova post-hoc tests comparing habitat at nesting and foraging areas with habitat at random areas.

Table L.1. Post-hoc results from permanova comparing nesting and random areas between Davies Creek (DC), Emu Creek (EC) and Tinaroo Creek (TC). Habitat data from all sites was combined into one analysis. Significant values (using Bonferroni correction) are highlighted in bold.

	Grass trees (/20 m^2)	Grass cover (%)	Cockatoo grass (/m^2)	Rock cover (%)	Tree height (m)	Slope (º)	CWD cover^ (%)	Soil resistance (mPa)	Tree basal area (m^2)	Bare soil cover (%)	Soil moisture (%)
Kruskal-Wallis result	$\chi^2 = 45.47$ **$p<0.001$**	$\chi^2 = 63.57$, **$p<0.001$**	$\chi^2 = 21.09$ **$p<0.001$**	$\chi^2 = 5.49$, $p = 0.359$	$\chi^2 = 14.44$, **$p = 0.0125$**	$\chi^2 = 42.41$, **$p<0.001$**	$\chi^2 = 19.53$, **$p<0.01$**	$\chi^2 = 50.45$, **$p<0.001$**	$\chi^2 = 43.41$, **$p<0.01$**	$\chi^2 = 7.84$, $p = 0.165$	$\chi^2 = 26.68$, **$p<0.001$**
DC nesting vs. DC random	0.587	**<0.001**	1.00	1.00	1.00	**<0.001**	1.00	**<0.001**	**<0.001**	1.00	1.00
DC nesting vs. EC nesting	1.00	1.00	1.00	1.00	0.486	1.00	1.00	**<0.001**	0.523	1.00	**<0.01**
DC nesting vs. EC random	1.00	**<0.001**	0.0674*	1.00	**0.015**	0.994	1.00	**<0.001**	1.00	1.00	1.00
DC nesting vs. TC nesting	**<0.001**	**<0.001**	1.00	1.00	0.475	1.00	1.00	**0.0436**	1.00	1.00	**0.022**
DC nesting vs. TC random	1.00	**<0.001**	1.00	1.00	**0.020**	1.00	0.297	1.00	**<0.001**	1.00	**0.0179**
DC random vs. EC nesting	1.00	**0.0280**	1.00	1.00	1.00	**<0.001**	0.931	1.00	**0.0140**	1.00	**<0.01**
DC random vs. EC random	0.833	1.00	0.565	1.00	1.00	**0.0112**	1.00	1.00	**<0.01**	1.00	1.00
DC random vs. TC nesting	**<0.001**	1.00	0.244	1.00	1.00	**<0.001**	1.00	0.510	**<0.01**	0.59	0.122
DC random vs. TC random	0.735	0.103	1.00	1.00	1.00	**<0.01**	1.00	**<0.01**	1.00	1.00	0.100
EC nesting vs. EC random	1.00	0.0784*	0.175	1.00	1.00	0.700	0.0632*	1.00	1.00	1.00	0.154
EC nesting vs. TC nesting	**<0.001**	0.0671*	0.675	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
EC nesting vs. TC random	1.00	**<0.001**	1.00	1.00	1.00	1.00	**<0.01**	0.0544*	0.123	1.00	1.00
EC random vs. TC nesting	**<0.001**	1.00	**<0.001**	0.43	1.00	0.699	0.111	0.0861	1.00	1.00	1.00
EC random vs. TC random	1.00	**0.0331**	0.807	1.00	1.00	1.00	1.00	**<0.001**	**0.0209**	1.00	0.904
TC nesting vs. TC random	**<0.001**	0.0534*	0.202	1.00	1.00	1.00	**0.0179**	1.00	**0.0154**	0.73	1.00

^CWD = coarse woody debris

*Result approaches significance

Table L.2. Habitat variables *Bettongia tropica* selected at foraging and random areas. Foraging and random habitat were compared between Davies Creek (DC), Emu Creek (EC) and Tinaroo Creek (TC). Significant values (using Bonferroni correction) are highlighted in bold.

	Grass trees (/20 m^2)	Grass height (cm)	Cockatoo grass (/m^2)	Rock cover (%)	Tree height (m)	Slope (°)	CWD cover^ (%)	Soil resistance (mPa)	Tree basal area (m^2)	Bare soil cover (%)	Soil moisture (%)	Canopy cover (%)	No. of bettong diggings
Kruskal-Wallis result	χ^2 = 25.52 **p<0.001**	χ^2 = 41.23, **p<0.001**	χ^2 = 58.86 **p<0.001**	χ^2 = 5.86, p = 0.330	χ^2 = 24.94, **p<0.001**	χ^2 = 64.50, **p<0.001**	χ^2 = 26.58, **p<0.001**	χ^2 = 50.98, **p<0.001**	χ^2 = 53.22, **p<0.001**	χ^2 = 21.05, **p<0.001**	χ^2 = 16.29 **p<0.01**	χ^2 = 60.21, **p<0.001**	χ^2 = 49.03, **p<0.001**
DC foraging vs. DC random	0.673	1.00	**<0.01**	1.00	0.081	**<0.001**	1.00	**<0.01**	**<0.01**	1.00	1.00	1.00	**<0.001**
DC foraging vs. EC foraging	1.00	1.00	0.872	1.00	1.00	1.00	0.224	**<0.001**	1.00	1.00	0.059	1.00	0.0172
DC foraging vs. EC random	**<0.01**	0.0765	**<0.001**	1.00	0.056	**<0.001**	1.00	**<0.001**	0.776	1.00	1.00	1.00	**<0.001**
DC foraging vs. TC foraging	1.00	0.0181	1.00	0.80	1.00	0.0684	1.00	1.00	1.00	1.00	0.338	**<0.001**	0.0381
DC foraging vs. TC random	0.329	1.00	0.282	1.00	0.147	**<0.001**	0.419	1.00	0.0764	0.054	0.010	**<0.001**	**<0.001**
DC random vs. EC foraging	0.103	1.00	**<0.001**	1.00	0.068	**<0.001**	**<0.01**	1.00	**<0.001**	1.00	0.586	1.00	0.236
DC random vs. EC random	1.00	**<0.01**	1.00	1.00	1.00	1.00	1.00	1.00	**<0.001**	1.00	1.00	1.00	1.00
DC random vs. TC foraging	1.00	**<0.001**	0.0168	1.00	0.0310	0.147	1.00	0.204	0.228	0.890	1.00	**<0.001**	0.191
DC random vs. TC random	1.00	1.00	1.00	1.00	1.00	1.00	1.00	**<0.01**	1.00	0.0120	0.157	**<0.001**	1.00
EC foraging vs. EC random	**<0.001**	0.0167	**<0.001**	1.00	**0.047**	**<0.01**	**0.0148**	1.00	1.00	1.00	1.00	1.00	0.0537
EC foraging vs. TC foraging	0.442	**<0.01**	0.666	0.71	1.00	1.00	**<0.01**	**<0.01**	0.0800*	1.00	1.00	**<0.01**	1.00
EC foraging vs. TC random	0.0403	1.00	**<0.001**	1.00	0.123	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.065	1.00	**<0.01**	1.00
EC random vs. TC foraging	0.576	1.00	**<0.001**	0.97	0.021	0.494	1.00	0.0140	0.0357	0.205	1.00	**<0.001**	0.0439
EC random vs. TC random	1.00	**<0.001**	0.412	1.00	1.00	1.00	1.00	**<0.001**	**<0.001**	**<0.001**	1.00	**<0.001**	0.888
TC foraging vs. TC random	1.00	**<0.001**	0.517	1.00	0.058	0.0120	1.00	1.00	1.00	1.00	1.00	1.00	1.00

^CWD = coarse woody debris
*Result approaches significance