Integrated analysis of the movement and ecology of wild dingoes in the arid zone

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Abstract

The behaviour and use of space by mammalian predators influences the structure and function of ecosystems. Mammalian predators are often highly mobile, and in resource limited environments they need to move through spatially distinct habitats in search of prey, water, refuge, and conspecifics. This increases connectivity between ecosystems and can have important ecological implications for food web stability. Underlying a predator's decision to move is the need to balance requirements for energy acquisition and expenditure.

Advances in remote monitoring technology are increasing our ability to gain detailed, quantitative insights into the movement ecology and ecophysiology of wild animals. However, methodological and analytical complexities have impeded the integration of different biologging tools. In this thesis I explored the biology of Australia's largest terrestrial predator, the dingo *Canis dingo*, and adopted an integrative approach to studying the ecology of wild individuals.

My research focused on the genetics, behaviour, resource selection, and energetics of a population of dingoes in remote central Australia. The population exhibited high genetic purity (mean purity > 90%) and clear phenotypic variation in coat colour. Genetic analysis of 83 individuals revealed high levels of relatedness, and both promiscuous and monogamous mating strategies. Morphological analysis of prey remains in dingo scats collected from our study site showed European rabbits *Oryctolagus cuniculus* dominated their diet, which was mirrored in a meta-analysis of the diet of dingoes across the 5.4 million km^2 arid zone. Whenever food availability boomed during resource pulses, hyperabundant small and medium sized mammals became their primary prey. Dingoes showed considerable dietary similarities throughout the arid zone, despite some sites being separated by a distance equivalent to that between Spain and Russia.

Using captive dingoes fitted with accelerometers, we developed a classification model that predicted 14 behaviours from accelerometry data collected at the very low frequency of 1

Hz. The high accuracy (mean = 87%) of these predictions, even at a low sampling frequency, suggests that reliable, fine-scale behavioural observations of wild animals can be made over a longer period than was previously thought possible. To investigate resource use at both the individual and population level, we obtained > 150,000 GPS locations from 18 dingoes over a two year period. At the population level, dingoes selected strongly for watercourses and avoided salt lakes, which is not surprising considering the survival of canids in desert ecosystems is contingent upon access to free water and refuges. Interestingly, there was extreme individual variation in space use by dingoes, as well as seasonal differences in activity patterns where females shifted their behaviour from crepuscular to diurnal during the pup whelping and rearing seasons.

We recorded accelerometry data from seven wild dingoes, and were able to apply our classification model to predict fine time-scale behaviours. We then used these behaviours to create activity-specific time-energy budgets by incorporating energetic data previously reported in the literature. This is one of the first attempts at integrating location, accelerometry, and energetic data, and allowed the comprehensive assessment of the daily costs of living in a wild canid. Our results revealed that ambient temperature (T_a) drives the activity and energetics of dingoes in the arid zone, with substantially lower activity when external temperatures were high, equating to lower daily energy expenditure in summer than in winter. Moreover, the negative relationship between dingo activity and T_a during the day implies that high heat gain from solar radiation is a factor that limits diurnal activity in an arid environment.

Thesis Declaration

I certify that this work contains no material which has been accepted for the award of any other degree or diploma in my name, in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text. In addition, I certify that no part of this work will, in the future, be used in a submission in my name, for any other degree or diploma in any university or other tertiary institution without the prior approval of the University of Adelaide and where applicable, any partner institution responsible for the joint-award of this degree.

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I acknowledge the support I have received for my research through the provision of an Australian Government Research Training Program Scholarship.

Sincerely,

Jack Tatler

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The very first person who needs acknowledgement is Shannon Currie. Thank you for your unwavering support and encouragement, your brain and your friendship every single day throughout this rollercoaster ride. I would be in a straitjacket if it were not for you. Thanks for my forever motto: ‘The early dingo catches the rabbit’.

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Chapter 1. Introduction

Animal movement and space use are important ecological processes that are shaped by individual and population level responses to the patchy distribution of resources in the environment (Kolasa and Pickett, 1991, Boyce and McDonald, 1999). In theory, animals in heterogeneous landscapes should increase their fitness by using areas with the best or most abundant resources in preference to areas where resources are lacking (Leake, 1961, Southwood, 1977). Selection for certain resources occurs when an animal uses a resource in excess of its availability in the landscape; a reflection of the mechanistic link between an animal's behaviour and its location in the environment (Manly et al., 1993).

Space use and movement patterns employed by animals are non-random and stem from their need to balance energy use with energy acquisition. Movement is the major contributor to energy expenditure in mobile vertebrates with many behavioural and physiological mechanisms employed to reduce daily costs of living (Schmidt-Nielsen, 1972, Tatner, 1986). The considerable energetic costs of movement can be elevated for certain taxa, particularly when inhabiting harsh environments, given the challenge of acquiring adequate resources to survive whilst maintaining homeostasis (Schmidt-Nielsen, 1997, Fuller et al., 2014). Moreover, behavioural traits such as sociality and territoriality, can contribute considerably to an animal's daily energy expenditure given their influence over movement patterns and space use. The high metabolic rates of medium-sized and large carnivores makes survival in resource-limited systems, like deserts, especially challenging, and often requires adaptive traits such as behavioural thermoregulation (Carbone et al., 2007, Terrien et al., 2011, Karasov, 2015). Indeed, the energetic cost associated with movement can account for the bulk of a carnivore's daily energy expenditure (Carbone et al., 2007). Defining energy expenditure for free-ranging predators using traditional approaches has proven difficult. For example, the doubly labelled water (DLW) and heart-rate methods demand physiological expertise and rely on invasive and expensive techniques that often require individuals to be recaptured over time. While time-energy budgets are effective at estimating daily energy expenditure (Weathers et al., 1984), the inability to continuously monitor behaviours in wild animals has impeded the application of this method outside of captivity.

Today, animal movement can be reliably captured non-invasively by accelerometers (ACC), which are lightweight externally-fitted devices that measure changes in acceleration. Commonly, ACC data are translated into specific behaviours through classification algorithms and converted into overall dynamic body acceleration (ODBA), a measure of activity. Overall dynamic body acceleration has proven a useful proxy for quantifying energy expenditure in many species (Wilson et al., 2006, Halsey et al., 2009a). The use of ODBA to estimate energy expenditure in wild animals has overtaken DLW in recent years, however, it still requires laboratory calibration of the relationship between ODBA and energy expenditure. Furthermore, it may not accurately predict energy expenditure outside of the range of behaviours for which calibrations exist. In turn, the use of ACC to determine specific behaviours of animals has allowed quantitative measurements that detail how animals behave and react over fine time scales. The capacity for defining and quantifying behaviours of wild animals (using ACC) permits activity-specific energy budgets to be constructed where it was previously impossible, thus creating a new method for estimating energy expenditure in wild animals. If GPS information is captured simultaneously with ACC data, then there is scope to quantify and interpret detailed patterns of animal behaviour and energy expenditure in the landscape.

Mammalian predators exert top down pressure on prey populations, which can strongly influence the structure and function of ecosystems (Soulé et al., 2003). Berger et al. (2001) showed the extent to which large carnivores can affect ecological communities, with a trophic cascade resulting from the local anthropogenic extinction of grizzly bears *Ursus arctos* and wolves *Canis lupus*. Strongly interacting species (e.g., mammalian predators) are often used as bio-indicators in the event of human-induced ecosystem disruption. Given their important functional role in ecosystems, it is particularly concerning that the biggest driver of change in predator populations is anthropogenic disturbance (Weber and Rabinowitz, 1996). Unfortunately, the extent to which terrestrial systems have been modified is so extreme that it is almost impossible to fully disentangle human and non-human effects on animal behaviour and movement ecology.

The family *Canidae* consists of 36 species, many of which are top order predators (Macdonald, 2007). The dingo *Canis dingo* (Meyer, 1793) is Australia's largest terrestrial predator and occupies a range of habitats from alpine mountains and the wet tropics, to the driest deserts (Fleming et al., 2001). Dingoes have a highly flexible, generalist diet, although medium-sized and large mammals usually make up the bulk of their prey (Doherty et al., 2018). Understanding the diet of dingoes is important because they are implicated as both friend and foe to threatened native mammals (Allen and Fleming, 2012, Allen and Leung, 2012, Letnic et al., 2012). Akin to most canids, dingoes display a complex social system that is governed by a dominance hierarchy, though the level of gregariousness is flexible depending on both intrinsic and extrinsic factors (Thomson, 1992c, Fleming et al., 2001, Macdonald, 2007). Considered to be cooperative breeders, the mating strategy of dingoes is widely regarded as monogamous, but extra-pair copulations have been observed in captivity (Catling et al., 1992).

Dingoes are an ecologically and economically important, iconic species. Since their arrival c. 5,000 years ago (Savolainen et al., 2004) until the arrival of Europeans c. 230 years ago, dingoes were apex predators across the Australian mainland. The predation of sheep by dingoes resulted in the species being declared a pest, which instigated intensive control programs that continue to this day (Fleming et al., 2001, Philip, 2018). Dingoes readily hybridise with domestic dogs and, given the extent to which interbreeding has been found throughout Australia, their unique evolutionary lineage is at risk of extinction (Stephens et al., 2015). Further, the difficulty of identifying dingoes from their hybrids based on external characteristics means that genetic techniques are necessary to accurately identify pure dingoes (Banks et al., 2003).

Thesis Overview

Extensive anthropogenic disturbance and widespread hybridisation with domestic dogs has hindered our ability to study intact populations of dingoes in the wild. As a result, most of our basic understanding of dingo biology (e.g., phenotypic variation, mating strategies) stems from perturbed or captive populations. In *Chapter 2* we used molecular analysis to test dingo ancestry (i.e., purity) in a remote and relatively undisturbed population of dingoes in central Australia. We also explored their mating strategy using a pedigree constructed from genetic data, and examined how phenotypic variation was influenced by age, sex, heterozygosity, and relatedness. The population displayed high levels of dingo ancestry that had no relationship to the four coat colour morphs we observed. All individuals (n = 83) were closely related to each other; with all but one individual a full-sibling or parent/offspring. Our pedigree showed both long-term monogamy and promiscuity occur in the population, suggesting that mating strategies of dingoes are more complex than previously thought.

Dingoes have a highly flexible diet that enables them to meet daily energetic requirements, even in the resource limited deserts of central Australia, where irregular rainfall drives extreme fluctuations in mammal assemblages. In *Chapter 3* we first conducted a case study on dingo diet at the study site, Kalamurina Sanctuary, located in central Australia. We then included this new information within a meta-analysis of the mammalian component of dingo diet in Australia's arid zone, an area covering c. 5.4 million km^2. We used 25 datasets to quantify the effects of resource booms and anthropogenic disturbance on diet. Dingoes primarily consumed medium-sized (35 – 5500 g) and large (> 5500 g) mammals, whereas most small mammals (< 35 g) were consumed infrequently, or not at all. The composition of their diet changed dramatically during resource booms to exploit irruptive prey species (small to medium-sized mammals) whilst the consumption of large mammals decreased significantly. Surprisingly, the diet of dingoes was very consistent in space, despite > 2,500 km separating some populations.

With the overarching goal of determining fine-scale behaviours in wild dingoes, in *Chapter 4* we described an approach to classifying behaviours from tri-axial accelerometer data recorded from captive dingoes. A major trade-off exists between the duration of data collection and the sampling frequency of an ACC device, where duration is usually sacrificed for high sampling frequency due to the perceived increase in behavioural classification accuracy. Further, a multitude of approaches to behavioural classification have complicated and slowed its use in the wider scientific community. We used a comprehensive approach to building a classification model to assess whether we could predict multiple observed behaviours (n = 14) from ACC data recorded at the very low sampling frequency of 1 Hz. We tested the importance of predictor variable selection and moving window size for the classification of each behaviour and overall model performance, with the aim of producing a simple, but accurate, model. We provided evidence that low-frequency ACC data can still yield accurate classifications of a range of behaviours from lying down to playing. In addition, we showed that a Random Forest model of relatively low complexity has the potential to mitigate some major challenges associated with establishing meaningful ecological conclusions from accelerometry data.

Determining how and why predators move through their environment is a central focus of many ecological studies as it informs how ecosystems function and change as a result of fluctuating predator abundance; or following disturbances such as fire, drought, or climate change. For *Chapter 5*, we obtained > 150,000 GPS locations from 18 dingoes (13 female, 5 male) over a two-year period and fitted separate resource selection models for each individual to explore their movement ecology. We then used a meta-analytic approach to identify population-level responses to their environment. Dingoes exhibited polarising preferences for resources depending on the individual, sex, and time of year. In addition, our assessment of daily and seasonal activity patterns showed females shifted their activity from crepuscular to diurnal during the pup-whelping and rearing seasons, whereas males remained primarily crepuscular year round.

The aim in *Chapter 6* was to display the scope of quantitative data that can be acquired from integrating two commonly used remote monitoring tools (ACC and GPS) with previous energetic research. To demonstrate this we estimated the daily energy expenditure of wild dingoes using accelerometer informed time-energy budgets. The challenges of measuring daily energy demands of free-ranging and highly active predators, like dingoes, has resulted in a poor understanding of how environmental variables and physiological capacity affect their movement and use of space. Our classification model from *Chapter 3* was used to classify three broad behaviours from ACC data recorded from seven wild dingoes, where the energetic cost of each behaviour was estimated using equations from the literature. We also used location (GPS) data from each individual to explore their energetic landscape. Our integrative approach provided robust estimates of daily energy expenditure in wild dingoes. We found that solar radiation and ambient temperature drove their location and behaviour in space. Furthermore, their less active lifestyle in summer was indicative of a behavioural thermoregulation strategy that resulted in significantly lower daily energy expenditure compared to the winter months.

Thesis Structure

The data chapters in this thesis (Chapters 2 - 6) have been written in journal format, for publication. I have chosen to write in the first person plural, although I am the primary author and major contributor to each chapter (see ‘Statements of Authorship’). See specific chapters for their current publication status at the time of submission.

Statement of Authorship

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Name of Principal Author (Candidate)	Jack Tatler		
Contribution to the Paper	Planned and developed the research, collected the data, developed the models and analysed the data, wrote the manuscript.		
Overall percentage (%)	80%		
Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.		
Signature		Date	18/03/2019

Co-Author Contributions

By signing the Statement of Authorship, each author certifies that:

i. the candidate's stated contribution to the publication is accurate (as detailed above);

ii. permission is granted for the candidate in include the publication in the thesis; and

iii. the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

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Contribution to the Paper	Contributed to the development of the modelling and statistical analysis, revised and edited the manuscript.		
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Chapter 2. Phenotypic variation in coat colour and mating strategy in a wild population of pure dingoes *Canis dingo*

Jack Tatler, Thomas A. A. Prowse, David A. Roshier, and Phillip Cassey

Appendix: Supplementary material accompanying this chapter can be found in Appendix 1 of this thesis.

ABSTRACT

Phenotypic diversity occurs in natural populations as a result of the interaction between an individual’s genotype and the environment. Nevertheless, individual variation in phenotypic traits such as coat colour and body size are routinely used to differentiate between ‘pure’ dingoes *Canis dingo* and dingo-dog hybrids. Extensive anthropogenic impacts and widespread hybridisation with domestic dogs has hindered our ability to study intact dingo populations and, therefore, most of our basic understanding of dingo biology (e.g., phenotypic variation, mating systems, and genetic diversity) stems from observational studies on perturbed populations. We sampled a relatively undisturbed population of dingoes, from arid Australia, to determine their purity and genetic diversity. We explored their mating strategy using a pedigree built from genetic data and examined how phenotypic variation was influenced by age, sex, heterozygosity, and relatedness. Coat colour was our measure of phenotype and our population displayed four types (sandy, black & tan, white, and sable). All dingoes (n = 83) possessed a high level of dingo ancestry (mean purity > 90%) and were closely related to each other; with all but one individual related as full-sibling or parent-offspring. Our pedigree shows both monogamous and promiscuous mating strategies exist within an undisturbed population. Variation in coat colour or body size cannot be used to infer a dingo’s level of purity because the phenotype of pure dingoes is intrinsically variable. The breeding system of dingoes was long thought to be monogamous, but we provide genetic evidence for numerous mating strategies including both long-term monogamy and extreme promiscuity.

INTRODUCTION

Phenotypic diversity occurs in all sexually reproducing natural populations, and is one of the basic tenets of evolution by natural selection (Fisher, 1958). Intraspecific variation in phenotypic traits such as pelage and body size is a result of the interaction between genotype and environment, and is therefore predicted to vary within and between populations throughout time and space. Phenotypic differences within a population are considered important for generating variation in individual attributes such as habitat preference, competitive ability, anti-predator defence, parasite load, and diet (Hayes and Jenkins, 1997, Bolnick et al., 2003, Lankau and Strauss, 2007). Although strong ecological effects of phenotypic variation have been identified, few broad commonalities have emerged (Bolnick et al., 2011).

Admixture between wild and domestic animals is largely viewed as a detrimental process because it threatens the long term persistence of wild species, and can contribute to population and species extinction (Levin et al., 1996, Rhymer and Simberloff, 1996). In addition to genetic assimilation, hybridisation can result in a different set of phenotypes that alter the functional role of a species (Stronen et al., 2012). In north-eastern North America the larger body size of coyotes *Canis latrans* is a product of their hybridisation with wolves *Canis lupus*, enabling them to hunt larger prey species than their western counterparts and occupy a different ecological niche (Stronen et al., 2012). There are a number of examples of human-facilitated hybridisation around the world, with domestic dogs *Canis familiaris* the primary threat to wild canids. Australia's only canid, the dingo *Canis dingo*, arrived from Asia *c.* 5000 years ago and was once distributed across the entire continent (Savolainen et al., 2004, Fillios and Taçon, 2016, Balme et al., 2018). Since European arrival, however, rapid and widespread hybridisation with domestic dogs has resulted in only the most remote parts of central Australia containing pure individuals (Stephens et al., 2015).

Dingoes are medium-sized generalist predators and one of Australia's most provocative species. They hold considerable cultural significance to indigenous Australians, represented in their Dreaming narratives and prehistoric art (Cahir and Clark, 2013). More recently, European colonisation introduced extensive pastoralism, which relegated dingoes to a pest species (Fleming et al., 2001). Nevertheless, dingoes are an apex predator and maintain a functional role in a variety of ecosystems. Dingoes are the closest extant relative of grey wolves and an ancient, phylogenetically distinct breed of domestic dog (Savolainen et al., 2004, Crowther et al., 2014). However, their genetic and phenotypic similarity to domestic dogs perpetuates their uncertain taxonomic position, which in turn promotes discordance around their conservation status and management in Australia.

Introduced to northern Australia by Australasian seafarers, dingoes spread rapidly throughout the continent and soon occupied a broad variety of ecosystems from alpine habitat to tropical rainforests and arid deserts (Fleming et al., 2001). Environmental gradients across their distribution are reflected by their phenotypic variation, with substantial intra and inter-population differences in body size (mean weight varies from 13 – 19 kg; Allen and Leung, 2014), coat colour (e.g., sandy, white, black and tan; Fleming et al., 2001), and social behaviour (e.g., pack sizes from 2 – 23; Thomson, 1992c). Indeed it is this natural individual variation that can be mistaken for hybridisation and promotes the stereotypical view that pure dingoes display a certain set of phenotypic traits (i.e., sandy coat with white tips to tail and feet), despite several studies reporting otherwise (Newsome and Corbett, 1985, Corbett, 1995, Newsome et al., 2013c). Inability to distinguish dingoes and their hybrids based on phenotype alone has created the need for genetic approaches to test purity (Banks et al., 2003, Stephens, 2011).

The social behaviour of dingoes differs from other canids in that it is driven by the availability of resources, and therefore can be highly variable between populations (Corbett and Newsome, 1987a, Thomson, 1992c). When there is a surplus of food (e.g., anthropogenic resource subsidies) dingoes can form large social groups of related individuals (Thomson, 1992c, Newsome et al., 2013c), or when only smaller sized prey are available their group size decreases (Newsome et al., 1983, Robertshaw et al., 1985a). Interactions between conspecifics is also influenced by relatedness, with several studies reporting a hierarchical social system dominated by a breeding pair, not unlike wolves and coyotes (Moehlman, 1989, Thomson, 1992c, Thomson et al., 1992). Breeding success may also be influenced by aspects of dingo sociality such as infanticide, which can be a major cause of death for the offspring of subdominant females (Corbett, L.K. 1988). Although the mating system of wild dingoes is not well understood, ecological inference from observational studies indicate they are cooperative breeders, where a monogamous breeding pair is supported by related individuals, which are often their young (Thomson, 1992a, Asa and Valdespino, 1998). However, a number of studies on captive and wild dingoes suggest subordinate dingoes can also produce offspring and therefore their mating system may not be strictly monogamous (Corbett, 1988, Catling et al., 1992, Newsome et al., 2013c).

Pervasive human impacts and widespread hybridisation have created few, if any, regions in Australia where populations of pure dingoes persist without disturbance. Despite advances in our understanding of dingo ecology and genetics, there is little information on free-ranging dingoes beyond the influence of anthropogenic disturbance (i.e., lethal control, pastoralism, resource subsidies). Here, we sampled a relatively undisturbed population of dingoes from arid central Australia to determine their purity and genetic diversity. We used genetic data to build pedigrees in order to explore their mating strategy, and examined phenotypic variation from direct observations. Given the history of low anthropogenic disturbance in remote central Australia we predicted that the population of dingoes would display a high level of purity. We expected coat colour to be variable and unrelated to purity. We were also interested in whether genetic diversity explained differences in coat colour. We expected our genetic pedigree to reveal a high level of monogamy given the population was likely to exhibit a stable social structure. This study presents an exceptional opportunity to investigate the biology of a remote, unperturbed population of wild canids.

METHODS

Study area

The study was conducted between April 2016 and May 2018 at Kalamurina, a 667,000 Ha wildlife sanctuary situated between the north shore of Kati Thanda-Lake Eyre and the southern boundary of the Simpson Desert Regional Reserve, South Australia (27°48'S, 137°40'E; Fig. 2.1). Kalamurina lies at the intersection of three of Australia’s central deserts: the Simpson, Tirari, and Sturts Stony Desert. The site adjoins protected areas to the north and south to create a 6,406,400 km^2 contiguous area that is managed for conservation. The site has a short history of low grazing pressure and sporadic dingo control, which ceased in 2007 when it was purchased by the Australian Wildlife Conservancy (AWC). Destocking and regular control of introduced species (e.g., camels, feral cats) by AWC, coupled with the re-establishment of natural hydrological processes, has restored much of the landscape. Neighbouring properties to the east and west operated as cattle stations during the study, where lethal control of dingoes was employed opportunistically.

The region’s climate is arid, characterised by very hot summers and mild winters; mean temperatures ranging from 23.1 - 37.9 ˚C in the hottest month (January) and 5.9 - 19.7 ˚C in the coldest month (July; Bureau of Meteorology, 2017). Kalamurina is one of the driest areas in the country with a median annual rainfall of 133.5 mm (Bureau of Meteorology, 2017). It is located in the Simpson-Strzelecki Dunes Bioregion and the dominant landform is sand dunes (<18 m), with scattered dryland river floodplains, claypans and salt lakes. The dune crests and flanks are dominated by Sandhill Canegrass *Zygochloa paradoxa* with an over storey of scattered shrubs including species of *Acacia* and *Hakea.* The dune swales are characterised by Chenopod shrubland where the main vegetation are species of *Acacia*, *Eremophila*, and *Atriplex*. Extensive coolabah *Eucalyptus coolabah* woodlands exist along the banks and floodplains of the larger watercourses.

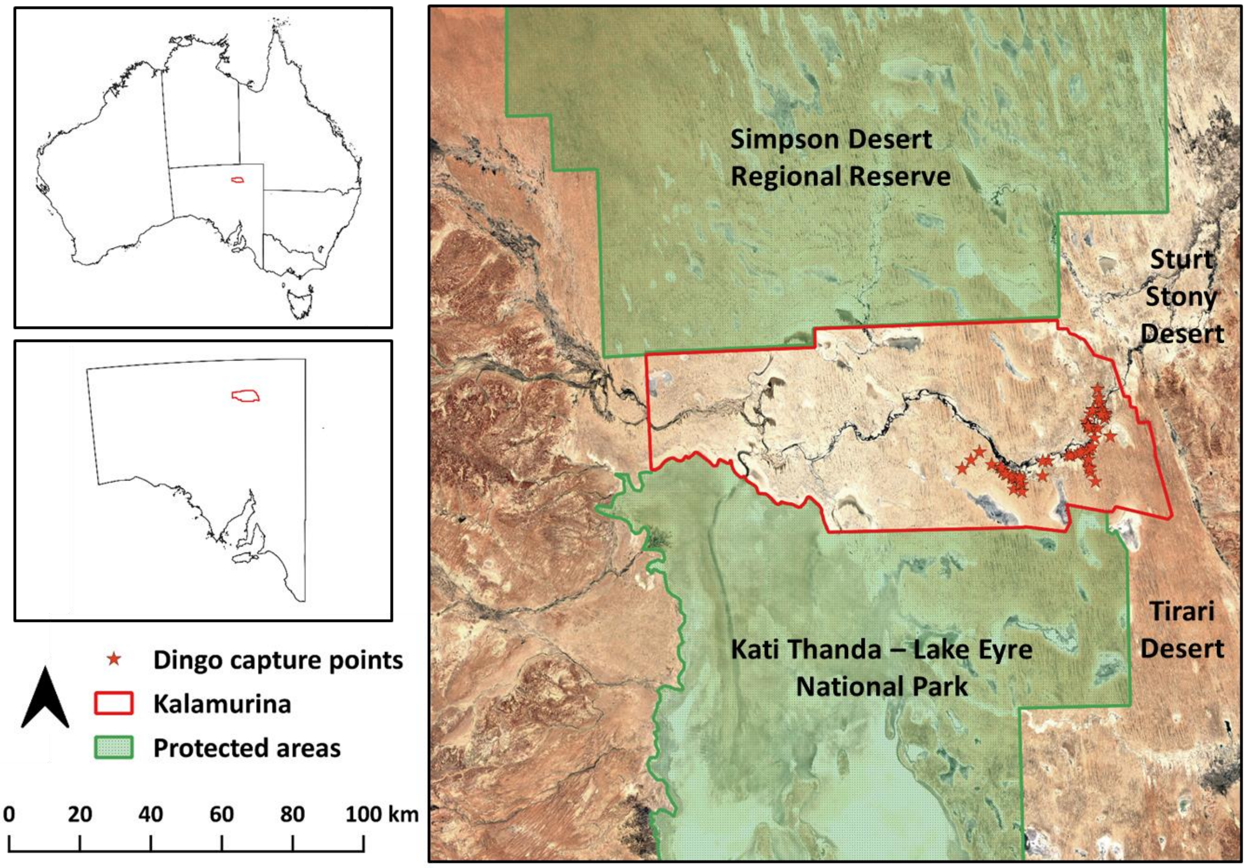

Figure 2.1. Location of study site in central Australia and where dingoes were sampled during this study, from 2016 – 2018 (n = 84). Red stars indicate the locations where dingoes were caught throughout the study and the red outline indicates the boundary of Kalamurina.

Trapping and handling of animals

Dingoes were captured using Victor Soft Catch® #3 leg-hold traps modified with Paws-I-Trip pans and a Jake Chain Rig (Professional Trapp Supplies, Molendinar, Queensland). These traps and modifications are designed to reduce the impact on the trapped limb (Meek et al., 1995). All traps were set within close proximity (< 20 m) to tracks and checked twice daily within three hours of sunrise and sunset. Initially, captured dingoes were controlled using a ketch-all pole and then restrained on a holding board by straps across their waste, shoulders, and neck. Once secured, the ketch-all pole was released and the trap removed. We recorded capture location, weight (to the nearest 0.25 kg), age class, sex, coat colour, identifying marks and body condition. The age of each individual was approximated by examining their body size, tooth wear and presence/ extent of grey fur. Dingoes were then categorised into four distinct age classes: sub-adult, young adult, adult, and older adult. Coat colour was defined broadly as sandy (light yellow to orange), white, black and tan (combination of black, tan, and/or white), and sable (sandy with a dorsal strip of black-tipped hairs). Despite a positive correlation with weight, body condition provides a valuable assessment of general health (e.g., disease, parasite load, injuries). We scored dingoes between 1 and 5, with 1 indicating poor condition and 5 representing excellent. A small hair sample (< 20 hairs with follicles attached) was taken for DNA analysis and kept refrigerated below 4 ˚C.

Purity testing

All laboratory analyses were performed by Helix Molecular Solutions (Perth, Western Australia). DNA was amplified at 23 microsatellite markers to obtain a unique DNA fingerprint, which was then examined for the likelihood that it had come from a dingo or a domestic dog ancestor using the computer program Structure (Pritchard et al., 2000). An overall percentage of dingo DNA present in the sample is obtained from the mean of 10 Structure analyses, with pure dingoes scoring > 90 % and 80 – 90% representing ‘probable’ pure dingoes (see Stephens et al., 2015 for a full explanation of percentage scores and dingo purity). Purity scoring was conducted by Zoological Genetics (Adelaide, South Australia).

Relatedness and Pedigree analysis

For relatedness testing we amplified our DNA samples at an additional 11 microsatellite markers (n = 34). Pairwise relatedness (r) and corresponding p-values were calculated using the symmetrical Queller-Goodnight estimator (Queller and Goodnight, 1989) implemented in Kingroup version 2 (Konovalov et al., 2004) for each pair of individuals. Expected relatedness for first order relatives (parent-offspring or full siblings) is c. 0.5. Full sibling reconstruction was performed using the descending ratio algorithm and samples were sorted into putative groups of first order relatives (kin groups). Pedigree reconstruction was carried out using a likelihood-based parentage analysis in the software program Cervus 3.0.7 (Kalinowski et al., 2007). We used each individual's age at capture and capture date to differentiate the cohort into approximate generations before we defined our set of candidate parents and offspring. For example, older adult dingoes trapped in session 1 (April 2016) could only be considered as candidate parents and not offspring, whereas sub adult dingoes trapped in session 5 (May 2018) could only be offspring and never a candidate parent. The simulated parameters were 10,000 simulated offspring, 38 candidate mothers, 47 candidate fathers, 80% of the candidate parents sampled, and an error rate of 1%.

Statistical analyses

All statistical analyses were conducted in the R software environment for statistical and graphical computing (version 3.5.1; R Core Team, 2017). We tested the effect of age and sex on the weight of dingoes using a generalised linear model (GLM) with a Gaussian error distribution. We also analysed the effect of age, coat colour, sex, and purity on the body condition score using a GLM with a Poisson error distribution. Finally, we used quasi-binomial GLMs to explore: 1) the effect of coat colour, age, and sex on the purity (proportion of dingo ancestry) of dingoes, and 2) the relationship between coat colour and genetic diversity (H_E).

Table 2.1. Number of dingoes sampled at Kalamurina displaying different coat colours. Mean weights are presented for each age class and sex. Females and males and presented in brackets, respectively.

	Sandy	Black & Tan	Sable	White	*N*	Mean Weight (kg)
Sub adult	17 (11, 6)	3 (1, 2)	3 (1, 2)	0	23 (13, 10)	11 (11, 13)
Young adult	18 (5, 13)	4 (1, 3)	4 (2, 2)	0	26 (8, 18)	14.5 (11.5, 15.5)
Adult	14 (6, 8)	2 (1, 1)	0	4 (1, 3)	20 (8, 12)	18 (17.5, 18.5)
Older adult	12 (7, 5)	2 (1, 0)	2 (1, 1)	0	15 (9, 6)	17 (15.5, 18.5)

RESULTS

Eighty-four individual dingoes (38 females and 46 males) were captured and released from five sampling sessions (c. 700 traps nights) at Kalamurina, with one mortality incurred in our last session (Table A1.1). There was a minor age bias with fewer older dingoes captured, though the sex ratio was mostly even (Table 2.1). Age had the biggest effect on the weight of dingoes with sub and young adults weighing significantly less than adults (Fig. 2.2). Young adult males weighed significantly more than young adult females (mean ± se; males = 15.5 ± 0.44 kg, females = 11.66 ± 0.5 kg, $p < 0.05$) and males weighed more than females in general, though it was not significant ($\beta = 0.98$, $p = 0.35$). Dingoes were in average condition (3.3 ± 0.12) with the lowest scores consistently recorded by sub adults. However, there was no significant relationship between body condition and age, sex, or coat colour (Table A1.2). Some evidence for an age bias in coat colour was evident with white coats only recorded in adults, whereas the sable colouration was never observed in adults in this study. Dingoes with sandy coats were the most common regardless of age (73.5% of all individuals).

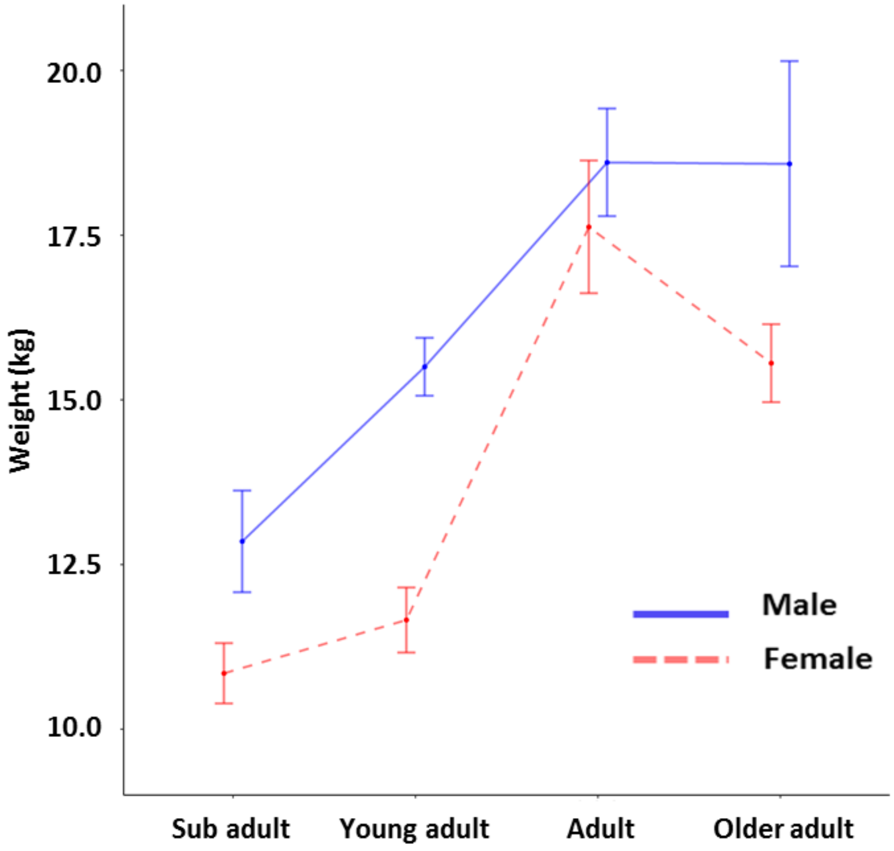

Figure 2.1. Mean weights (± se) of dingoes in each age class, separated by sex. Sample size = sub-adult male (10) and female (13), young adult male (18) and female (8), adult male (12) and female (8), and older adult male (6) and female (9).

Purity and relatedness

We obtained purity scores for 84 dingoes, though one sample gave spurious results (purity score and relatedness) and was removed from the analyses (leaving *n* = 83). The mean purity of dingoes at Kalamurina was high (91.4% ± 0.5%) and it did not change based on the dingo's coat colour (i.e., there was no relationship between purity and phenotypic variation; Fig. 2.3). We also found no effect of sex, age or weight on purity (Table A1.3). All 83 dingoes were closely related to at least one other, with only one individual yielding an *r* score < 0.2 (i.e., it was a cousin or uncle, rather than a parent, offspring, or sibling). We found 18 kin groups, the largest consisted of nine individuals and represented all age classes and both sexes (Table 2.2). The maximum capture distance between first-order relatives was 32 km (mean = 12.3 km).

Table 2.2. The number of dingoes with different coat colours in each kin group (first-order relatives). Capture distance represents the maximum distance between individuals in each kin group, regardless of the session they were captured in. Although dingoes that were not assigned to a kin group were related, they were not first order relatives.

Kin group	Sandy	Black & Tan	Sable	White	Max. capture distance (km)
1	-	2	-	-	1.50
2	1	-	-	1	15.0
3	2	-	-	-	3.50
4	4	-	2	-	5.00
5	2	-	-	-	4.50
6	1	1	-	-	25.0
7	2	-	-	-	18.5
8	4	-	-	-	5.50
9	3	-	-	-	1.50
10	1	1	-	-	1.00
11	3	3	1	-	9.50
12	4	1	-	-	18.5
13	2	-	-	-	30.0
14	4	-	-	1	32.0
15	3	-	1	1	4.50
16	2	-	-	-	25.0
17	2	-	-	-	14.5
18	3	-	6	-	7.00
Not assigned	15	2	3	1	-

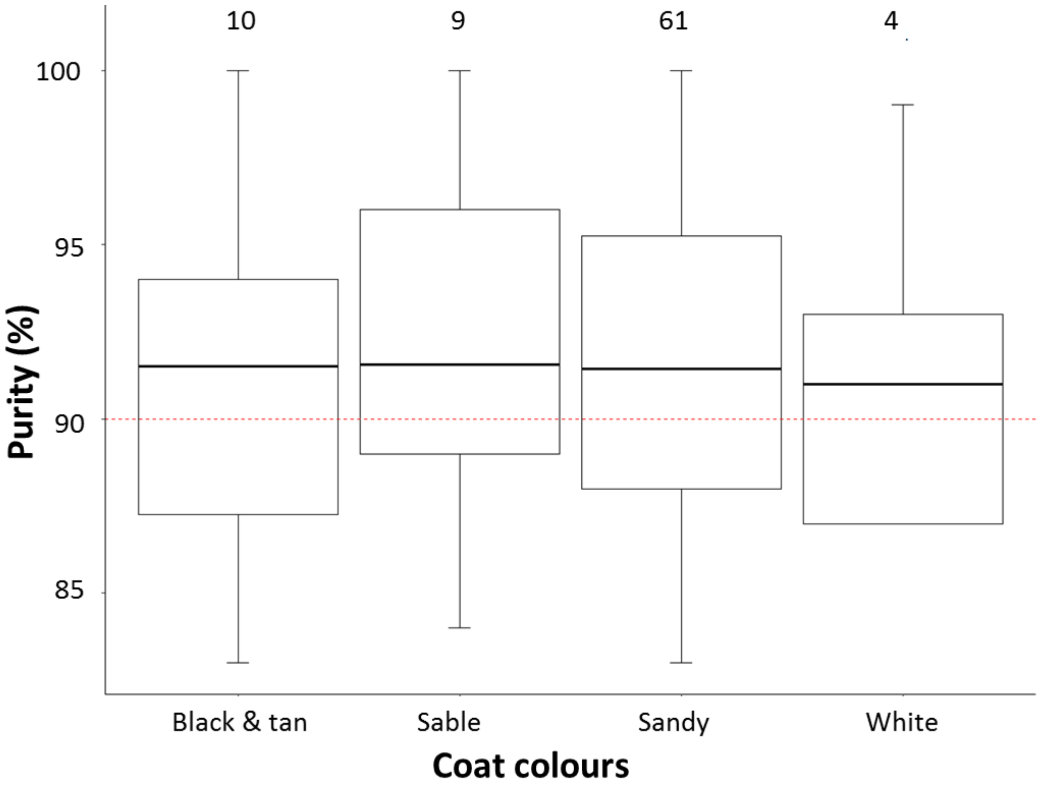

Figure 2.2. The purity scores for different phenotypes (coat colours) from 83 dingoes sampled at Kalamurina between 2016 and 2018. Each boxplot shows the range of purity scores within each coat colour category. The solid line represents the mean, lower and upper hinges correspond to the first and third quartiles, and the whiskers extent to the minimum and maximum scores. Numbers above each boxplot indicate the sample size, and the horizontal dashed-line shows the percentage purity above which individuals are classified as pure dingoes. Between 80 – 90% indicates a probable dingo (i.e., likely no domestic dog-like alleles present).

Dingo pedigree and genetic diversity

Of the 74 successfully sequenced offspring both parents could be identified with high confidence in 20 cases, and one parent for a further 23. This resulted in > 70% of our samples being placed in the pedigree (Fig A1.1). We found six dams and three sires dominated our pedigree, displaying parentage to 73% of all offspring. Our pedigree demonstrated that the mating system for dingoes at Kalamurina is primarily promiscuous, with only one monogamous pair identified (JT320 & JT53). This monogamous pair produced offspring over at least three generations (Fig. 2.3A), and all of their offspring were trapped within c. 4 km from each other. Conversely, many of the other breeding dingoes each mated with more than one individual. For example, a single male (JT08, 25 kg) mated with four different females in one breeding season and sired five offspring, all of which were trapped within c. 6.5 km of each other six and 12 months later (Fig. 2.3B). Although the inbreeding coefficient for our population was low at 0.012, three offspring had inbreeding coefficients of 0.25, which was the result of incestuous breeding between sire and grandam (sire's dam). All inbred offspring were male with black and tan coats.

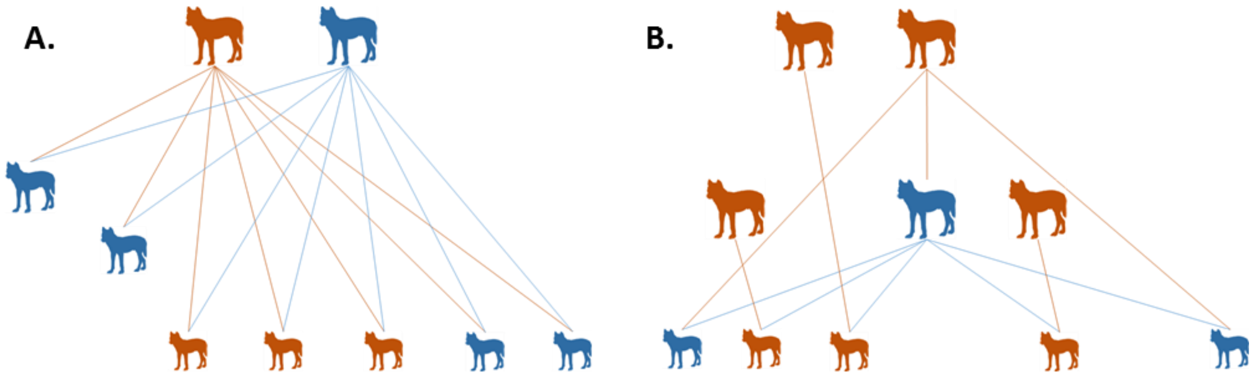

Figure 2.3. Pedigree analysis revealing two different breeding strategies from a population of pure dingoes at Kalamurina. (A) shows a monogamous pair that have produced three generations of offspring, and (B) is an example of male promiscuity in our population where one male (central) sired offspring to four females in the same breeding season. Generations are represented by different levels and sexes are blue (male) and orange (female). Lines indicate parentage.

Genetic diversity

Overall genetic diversity was low (mean H_E = 0.51; Table 2.3). Dingoes with the phenotype for a black and tan coat exhibited the lowest mean H_E (0.47), but we found no significant relationship between coat colour and H_E.

Table 2.3. Genetic diversity of the 34 microsatellite loci used to measure purity and relatedness. We used a total of 84 samples. k *= number of alleles at the locus, N = number of individuals typed at the locus,* H_O *= observed heterozygosity,* H_E *= expected heterozygosity, PIC = polymorphic information content, NE-1P = non-exclusion probability for one candidate parent, NE-2P = non-exclusion probability for identity of two unrelated individuals, NE-PP = non-exclusion probability for a candidate parent pair, NE-I = non-exclusion probability for identity of two unrelated individuals, NE-SI = non-exclusion probability for identity of two unrelated siblings.*

Locus	*k*	N	H_O	H_E	PIC	NE-1P	NE-2P	NE-PP	NE-I	NE-SI
AHT103	6	83	0.627	0.691	0.645	0.721	0.544	0.353	0.140	0.442
FH2247	11	84	0.821	0.839	0.815	0.494	0.324	0.149	0.047	0.344
m13c19	2	81	0.049	0.048	0.047	0.999	0.976	0.955	0.907	0.953
FH2257	5	83	0.711	0.649	0.580	0.774	0.621	0.452	0.191	0.475
CXX434	3	83	0.193	0.176	0.162	0.985	0.918	0.853	0.694	0.836
CXX460	5	83	0.253	0.328	0.297	0.946	0.836	0.722	0.483	0.708
FH2199	19	82	0.841	0.891	0.876	0.368	0.225	0.076	0.023	0.313
AHT109	8	84	0.714	0.729	0.686	0.677	0.498	0.307	0.114	0.416
CXX109	4	84	0.238	0.239	0.226	0.971	0.876	0.777	0.593	0.780
FH2079	3	82	0.244	0.287	0.248	0.959	0.874	0.791	0.548	0.744
CXX410	3	83	0.036	0.036	0.035	0.999	0.982	0.965	0.930	0.965
m13tt	2	82	0.329	0.323	0.27	0.948	0.865	0.783	0.512	0.717
CXX402	2	84	0.143	0.173	0.157	0.985	0.921	0.861	0.700	0.839
FH2313	6	84	0.738	0.769	0.726	0.635	0.456	0.274	0.093	0.391
CXX30	5	84	0.357	0.417	0.361	0.913	0.800	0.678	0.397	0.642
CPH2	3	83	0.024	0.024	0.024	1.000	0.988	0.976	0.953	0.976
FH2346	14	83	0.843	0.865	0.844	0.439	0.279	0.115	0.035	0.329
AHT125	6	83	0.651	0.717	0.664	0.703	0.531	0.351	0.132	0.426
CXX406	5	84	0.250	0.230	0.219	0.973	0.879	0.782	0.605	0.787
FH2293	13	83	0.807	0.885	0.868	0.389	0.240	0.088	0.026	0.317
VIASD10	4	84	0.452	0.410	0.374	0.915	0.782	0.642	0.384	0.642
LEI008	3	83	0.277	0.278	0.259	0.962	0.857	0.751	0.541	0.747

FH2138	15	82	0.744	0.827	0.801	0.514	0.343	0.162	0.053	0.352
ladeC213	4	13	0.308	0.403	0.363	0.922	0.785	0.640	0.400	0.656
FH2168	14	83	0.783	0.819	0.802	0.502	0.329	0.135	0.047	0.355
FH3591	5	84	0.083	0.082	0.08	0.997	0.958	0.919	0.845	0.921
WanV142	4	84	0.56	0.667	0.611	0.757	0.59	0.413	0.166	0.46
FH3295	6	84	0.726	0.676	0.618	0.739	0.574	0.391	0.161	0.454
FH3413	14	80	0.813	0.852	0.83	0.464	0.3	0.128	0.04	0.337
Ren195	4	83	0.289	0.261	0.247	0.965	0.862	0.754	0.56	0.76
FH2537	8	78	0.769	0.798	0.767	0.571	0.393	0.205	0.069	0.371
FH3278	5	84	0.69	0.721	0.665	0.708	0.537	0.363	0.132	0.425
Ren47D	6	84	0.524	0.55	0.472	0.845	0.718	0.571	0.28	0.547
Ren229	7	84	0.738	0.787	0.748	0.604	0.426	0.244	0.081	0.379
Overall	6.59	80.94	0.489	0.513	0.482	0.775	0.650	0.518	0.349	0.583

DISCUSSION

The strong signal of dingo ancestry present in each of the sampled dingoes indicates a pure population. Individuals displayed considerable differences in their coat colour yet this phenotypic variation was not related to their purity nor genetic diversity. Indeed the low variability in our estimates of purity (due to the lack of introgression) throughout the population impeded our ability to find any biological trait that influenced their genetic purity. This implies that pure dingoes can exhibit considerable variation in their appearance within a single population, and consequently it is unlikely that there is an archetypal dingo phenotype. Describing the relationship between genetics and colouration in mammals is complex, with more than 150 genetic loci involved in pigmentation (Hubbard et al., 2010). Moreover, mutations at these loci may produce colour variations similar to that of hybridisation (Randi, 2011).

The population of dingoes in this study have been free from pervasive human impacts, such as lethal control and pastoralism, for a decade. In addition, the study site is distinct from most of the continent in that it has only ever experienced very low levels of (post-Indigenous) anthropogenic disturbance. The remoteness of a dingo population was found by Stephens et al. (2015) to reflect the level of hybridisation, with the most widespread examples of hybridisation occurring in populated coastal areas near human settlement. Corbett (1995) theorised that social stability (destabilised by human actions) might be negatively correlated with hybridisation between dingoes and dogs, which has also been suggested for other canids such as wolves (Rutledge et al., 2010) and foxes (Sacks et al., 2011). Although social behaviour was not explicitly explored in this study, low levels of human interference suggest the population could have maintained a stable social structure and thus another buffer to hybridisation. Moreover, this dingo population persists in one of Australia's hottest and driest regions where free water is largely restricted to the Warburton Creek (a single source of bore water also lies adjacent to the Warburton Creek). The shortage of free water and harsh climatic conditions are likely to present an environmental barrier to movement and thus further reduce chances of introgression from roaming domestic dogs, which can have poor survivorship in the wild (Geffen et al., 2011, Stephens et al., 2015). These factors are likely to have worked synergistically to mitigate hybridisation and preserve the purity of the dingo population.

Species with complex social structures often possess innate behaviours that mitigate introgression and inbreeding (Sacks et al., 2011, Bohling and Waits, 2015). Many canids express kin recognition and evade inbreeding through strict social hierarchies that permit only one pair in a social group to breed in a given season (Geffen et al., 2011). Moreover, maturing offspring will often be forced to disperse into new areas by dominant individuals in order to reduce kin encounter rate. In canids, dispersal is often solitary and sex biased, and dispersal distance can be highly variable (Moehlman, 1989). In dingoes, dispersal is prompted by locally limited resources and the vacancy of adjacent areas (Thomson et al., 1992). The primary limiting resource for dingoes at Kalamurina is access to water and this is likely to impede their ability to disperse, explaining the high levels of relatedness that was observed between individuals. Inbreeding has been found in every population of dingoes (Stephens, 2011) though the observed levels of inbreeding was lower in our population than might be expected given the number of kin groups and their close spatial association with one another (Table 2.2; Geffen et al., 2011). Low levels of inbreeding despite exposure to related individuals is consistent with cooperative breeding in canids, where their social behaviour impedes breeding between related individuals (e.g., Koenig et al., 1999, Jamieson et al., 2009).

Observational accounts of sociality and mating system in dingoes suggest they are similar to grey wolves in that they follow a hierarchy and are cooperative breeders (Corbett, 1988, Newsome et al., 2013c). Thomson (1992c) tracked 34 dingoes across 3 years in arid Australia and reported five main packs that consisted of a dominant breeding pair and their offspring of various years. Although not well understood, observational studies suggest the dingo mating system is monogamous (Corbett, 1988), and we did find some evidence to support this. However, promiscuity appeared to be the primary mating strategy for dingoes at Kalamurina (Fig. 2B). The lack of genetic based pedigrees for dingo populations may be shadowing the frequency of extra-pair copulations akin to what has been reported in other 'monogamous' species such as humans *Homo sapiens* (Small, 1992), saddle-back tamarins *Saguinus fuscicollis* (Terborgh and Goldizen, 1985), and aardwolves *Proteles cristatus* (Richardson, 1987). Further, recent genetic-based investigations have revealed that other members of the canid family may not be genetically monogamous as previously thought, but possess a flexible mating structure similar to that of socially monogamous birds (Moehlman, 1989, Hughes, 1998, Baker et al., 2004, Kitchen et al., 2006).

It has often been proposed that promiscuous breeding is a strategy to avoid inbreeding (e.g., Brooker et al., 1990, Sillero-Zubiri et al., 1996, Tregenza and Wedell, 2000), and empirical studies have shown it can provide genetic benefits to females (reviewed in Kempenaers, 2007). The baseline level of genetic diversity for dingoes in Australia is low, presumably due to a small number of founder animals (Savolainen et al., 2004, Stephens, 2011), which is consistent with our findings. Low genetic variation is predicted to lower individual fitness and population adaptability (Lande, 1988), which may warrant concern for the future conservation of dingoes. Paetkau et al. (1998) identified a gradient of genetic diversity in brown bears *Ursos arctos* that was much lower on the fringes of their range and in populations with limited connectivity. Connectivity between dingo populations is severely limited throughout much of Australia due to human settlement and human-wildlife conflict, and in the most remote parts of their range the flow of genes between populations is likely to be heavily impeded by the combination of lethal control and harsh climatic conditions. However, this reduction in connectivity between populations may be beneficial to their conservation given their primary threatening process requires gene flow (hybridisation).

Phenotypic variation is well documented among and between dingo populations. Coat colour is often used to distinguish pure dingoes from dingo-dog hybrids though recent genetic testing has shown pure dingoes may exhibit a number of coat colours and patterns. Newsome et al. (2013c) used genetic analyses to show two different coat colours (ginger, and black and tan) were present in pure dingoes, while eight different coat colours (including ginger, and black and tan) were observed in sympatric dogs. Sable colouration and white ticking are often reported to only occur in dogs and dingo hybrids however, we provide evidence that pure dingoes may also carry this phenotype. Body weight of adult dingoes can be highly variable depending on geographic location and available resources (see Allen and Leung, 2014), and we reported some of the heaviest weights for a dingo population (Table 2.1). The primary prey item of dingoes in this study was European rabbits (c. 1.6 kg; Tatler et al., 2019), which indicates that it is not the size of the prey items that dictate the body size of dingoes. Akin to wolves, intact populations of dingoes are likely to be intrinsically regulated and therefore we might expect a male sex bias (Wolff, 1997, Phung et al., 2018). However, the similar sex ratio observed in our study is consistent with other studies on dingoes (e.g., Thomson, 1992c, Robley et al., 2010, Newsome et al., 2013c) as well as coyotes *Canis latrans*, a medium-sized canid with many traits comparable to dingoes (Moehlman, 1989).

CONCLUSIONS

Variation in coat colour or body size cannot be used to infer a dingo's level of purity because the phenotype of pure dingoes is intrinsically variable. Remoteness, environmental barriers and social stability are likely to act synergistically and additively as barriers to hybridisation. The breeding system of dingoes was long thought to be monogamous but we provide genetic evidence for a flexible mating strategy within a population that ranges from long-term monogamy to promiscuity, which is consistent with emerging research on other 'monogamous' species.

Statement of Authorship

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Contribution to the Paper	Planned and developed the research, collected and collated the data, developed the models and analysed the data, wrote the manuscript.		
Overall percentage (%)	80%		
Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.		
Signature		Date	18/03/2019

Co-Author Contributions

By signing the Statement of Authorship, each author certifies that:

iv. the candidate's stated contribution to the publication is accurate (as detailed above);

v. permission is granted for the candidate in include the publication in the thesis; and

vi. the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

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Contribution to the Paper	Developed the research, contributed to the development of the modelling and statistical analysis, revised and edited the manuscript.		
Signature		Date	18/03/2019

Chapter 3. Resource pulses affect prey selection and reduce dietary diversity of dingoes in arid Australia

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Appendix: Supplementary material accompanying this chapter can be found in Appendix 2 of this thesis.

ABSTRACT

In Australia, dingoes *Canis dingo* are the largest terrestrial predator and contribute to ecological processes and functions throughout their continental distribution. Their generalist diet enables daily energetic requirements to be met even in the resource-limited deserts of central Australia, where irregular rainfall drives extreme inter-annual fluctuations in mammal assemblages. Given predation is a primary driver of declining mammal populations and failed reintroductions, it is necessary to understand the dietary intake of the continents apex predator if conservation outcomes are to be achieved. We performed a meta-analysis of the mammalian composition of the dingo's diet throughout Australia's arid-zone, an area covering c. 5.4 million km^2. We used 25 datasets from 12 studies to measure the effects of resource booms and anthropogenic disturbance (e.g., pastoralism) on diet. We explored whether the probability of prey species occurring in the diet was related to their size and/or prevailing conditions. We also investigated the similarities in diet between dingo populations from across the arid-zone and how this was affected by opposing land uses. Dingoes primarily consumed medium-sized (35 – 5500 g) and large (> 5500 g) mammals, whereas most small mammals (< 35 g) were consumed infrequently, or not at all. The composition of their diet changed dramatically during resource booms to exploit irruptive prey species such as long-haired rats (native; 144 g) and house mice (introduced; 20 g). During resource booms, the consumption of large mammals decreased significantly whilst the occurrence of medium-sized mammals remained high. The diversity of species consumed by dingoes during boom periods was significantly lower than non-boom periods. The dingo's heightened consumption of hyper-abundant species has the potential to temporarily release many non-target species from direct predation pressure during boom times. This could be advantageous for remnant and reintroduced populations of mammals, which are especially susceptible to predation.

INTRODUCTION

Ecological communities can be severely disrupted by changes to the abundance and distribution of predators, and synergistic impacts can result when other anthropogenic stressors are present (Estes et al., 2011). In Australia, the acute and pervasive environmental impacts of European arrival are evident in the aberrant structure of many extant ecological communities. Dingoes *Canis dingo* are Australia's largest terrestrial predator (c. 16 kg) and persist across a gradient of anthropogenic disturbance throughout their continental distribution (Fleming et al., 2014). Though relentless human-wildlife conflict continues to alter their abundance and distribution (Fleming et al., 2014), dingoes have the potential to drive biological processes in a diverse range of ecosystems.

Dingoes are generalist predators with a highly flexible diet that enables them to meet daily energetic requirements even in the resource-limited deserts of central Australia. Akin to other opportunistic predators, dingoes routinely scavenge and, where available, make use of anthropogenic food sources that can comprise a considerable portion of their diet (Newsome et al., 2014). The composition of dingo diet varies temporally and spatially, and a wide range of mammal species are considered potential prey. The frequency at which different mammalian prey occur in dingo diet is often heavily skewed towards one or two preferred species in a given area, regardless of their availability (Newsome et al., 1983). In a study by Robertshaw et al. (1985b), the swamp wallaby *Wallabia bicolor* (c. 15 kg) occurred in > 30% of dingo scats and this did not vary despite fluctuations in the local abundance of wallabies. In contrast, acute exploitation of novel prey and surplus killing of mammals has been recorded by dingoes in the arid zone (Moseby et al., 2011, Bannister et al., 2016).

The persistence of dingoes in Australia is largely attributed to a flexible foraging strategy that is dynamically modified to suit the prevailing conditions. Robertshaw et al. (1985b) reported a versatile feeding behaviour from their temperate study site, where a solitary lifestyle and diet of small to medium-sized mammals alternated with pack hunting and predation of large mammals. Though the potential prey of dingoes includes a variety of taxa from insects to crocodiles *Crocodylus johnsoni* (Somaweera et al., 2011), mammals typically occur in more than 70% of diet samples (e.g. Corbett and Newsome, 1987b, Marsack and Campbell, 1990, Thomson, 1992b). The mammalian composition of dingo diet varies considerably across their continent-wide distribution, with clear distinctions between bioclimatic zones (Doherty et al., 2018). Further, irregular rainfall within Australia's arid zone drives extreme fluctuations in prey assemblages and availability (e.g., Letnic and Dickman, 2006, Pavey et al., 2008). Many small and medium-sized mammal species respond to these short-lived flushes of primary productivity with a population irruption (boom), causing dingoes (Spencer et al., 2017) and other predators such as raptors (McDonald and Pavey, 2014), and feral cats *Felis catus* (Pettigrew, 1993, Yip et al., 2015), to alter their diet and exploit hyper-abundant prey.

Following the disappearance of the thylacine *Thylacinus cynocephalus* as the continent's apex consumer (Prowse et al., 2014, White et al., 2018), dingoes have coexisted alongside, and presumably preyed on, a suite of medium-sized marsupials and rodents for almost 3000 years. In the last 200 years, the arid interior of Australia has seen extreme declines and extinctions of mammals weighing between 35 g and 5500 g, termed the "critical weight range" (CWR; Burbidge and McKenzie, 1989). Of the c. 55 species of CWR mammals extant in the arid zone at the time of European colonisation (late eighteenth century), 12 are now extinct, 16 have been extirpated from the arid zone, and most of the remainder are in decline (Fig. 3.1). Given dingoes are apex predators with a variable prey base, and are implicated as both friend and foe to CWR mammals (e.g., Letnic et al., 2009, Allen and Fleming 2012), describing their dietary intake can provide an insight into the state of extant faunal communities. This is particularly important in the arid zone where the remaining biota are struggling to persist under the pervasive impacts of anthropogenic disturbance including invasive species, mammalian predators, altered fire regimes, feral herbivores, and pastoralism (Woinarski et al., 2014).

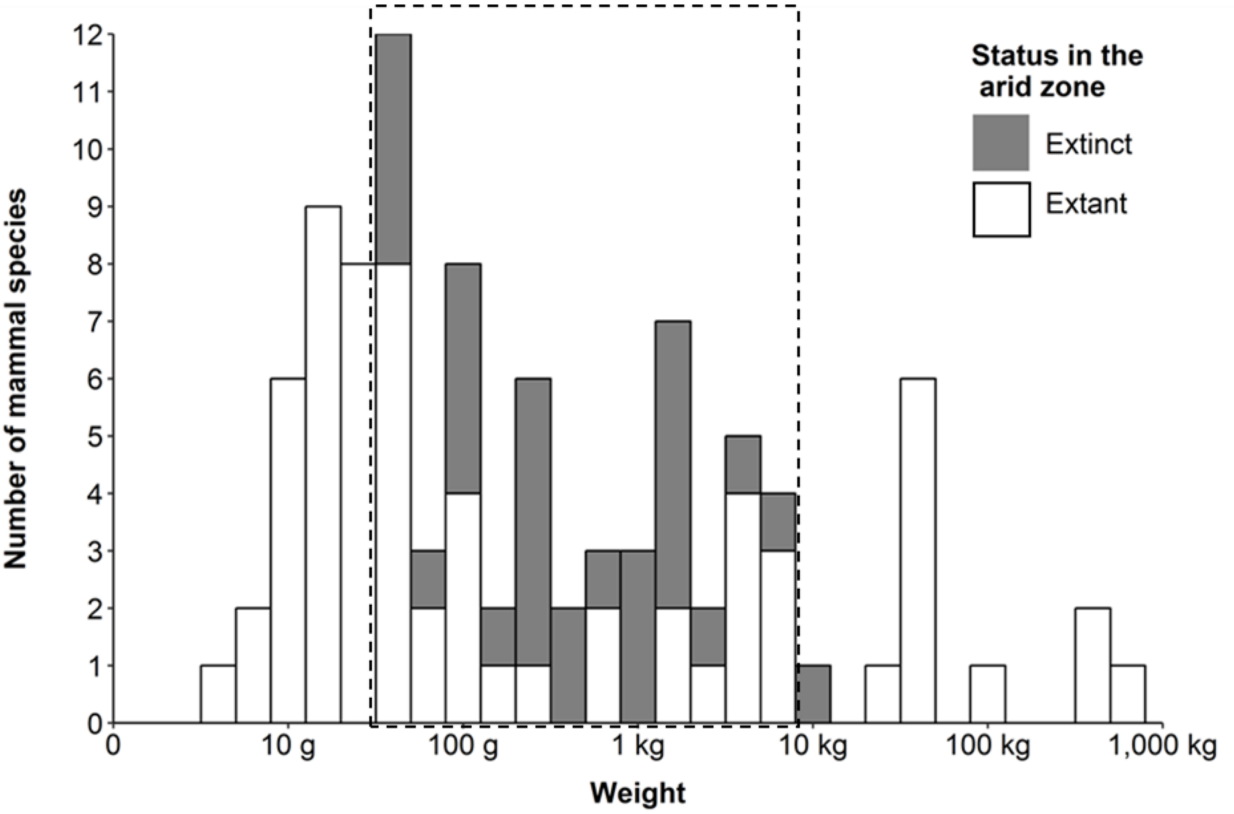

Figure 3.1. The number of extant and extinct mammal species, by mean adult weight, in Australia's arid zone. Extant species refer to those with distributions that overlap the sites in this study (Van Dyck et al., 2013). Arid zone mammals that have suffered range contractions and now only persist outside their former mainland range were included as 'Extinct'. The dashed box corresponds to the critical weight range (35 g – 5500 g). Note the logarithmic scale of the x-axis.

Here, we systematically reviewed the literature and used a meta-analytic approach to analyse the mammalian component of dingo diet quantitatively. Our focus was on the arid zone, where we examined dietary composition, diversity, spatial overlap, and preference for certain species. Specifically, we measured the effects of resource booms and anthropogenic disturbance on diet, and assessed how frequently introduced species were consumed. Based on the literature (reviewed in Doherty et al., 2018), we anticipated a small number of species would emerge as dietary staples, though a broad range of mammals would be consumed. We explored whether the probability of prey species occurring in dingo diet was related to their weight and/or prevailing conditions (boom or non-boom). Finally, we examined the similarities in diet between dingo populations from across the arid zone that were exposed to opposing land uses.

METHODS

Data collection for meta-analysis

Exhaustive searches of the primary scientific literature were conducted in May and June 2018 for studies investigating the diet of dingoes in the arid zone. We searched all databases on ISI's Web of Science using the search terms: (dingo* OR "wild dog*") AND diet AND (dingo* OR arid*). We selected only peer-reviewed studies where the diet of dingoes from the arid zone (as defined by Morton et al., 2011; Fig. 2) was evaluated through morphological analysis of prey remains in scats and/or stomachs. Detection of mammalian prey species in the diet of canids was considered to be equal using either of the two methods. We conducted backwards citation chaining to search for relevant studies not returned in the original search. Only studies that provided the species list of mammals identified in the diet were selected. Separate publications containing data collected from the same study site but from different time periods, were considered independent. Similarly, data from different regions reported in a single publication were treated as independent (if the data reported in the publication allowed it). If dietary samples were collected during the same study period at sites < 50 km apart, they were not considered to be spatially independent and were grouped together (avoiding pseudoreplication).

Major land use at each site was classified as: (1) conservation, which pertained to private or public land managed for conservation at the time of the study (i.e., sites exposed to low anthropogenic impact); or (2) pastoralism, which included cattle and sheep stations, and mining operations (i.e., sites subject to higher anthropogenic impact). For each dataset, we also classified resource availability during the period within which data were collected (boom or non-boom), and the status of each mammal species recorded in the diet (native or introduced). Boom periods were identified based on the occurrence of a La Niña cycle that had a Southern Oscillation Index score ≥ “moderate” and a substantial effect on Australia’s climate (Bureau of Meteorology). Based on Pavey and Nano (2013), we considered dietary samples to be from a boom period if they were collected more than six months following the onset of a La Niña cycle through to six months after the end of the cycle. All other samples were designated as falling within non-boom periods.

We grouped mammals into three weight classes - small (< 35 g), medium (35-5500 g), and large (> 5500 g), based on mean adult weight (sexes were combined) provided in Van Dyck et al. (2013) . The medium size class corresponds to the CWR mammals that have been most impacted by introduced predators in Australia (Burbidge and McKenzie, 1989). To highlight differences in predation pressure for certain species, we included all mammals that occurred at each site, regardless of their presence in dingo diet, based on their distribution in Van Dyck et al. (2013). Species’ range maps are inherently imprecise due largely to gaps in our knowledge of a species’ core distribution, patchiness of their abundance at the fine-scale, and temporal fluctuations in their distribution. Therefore, in order to increase our confidence in which prey species were likely to be available, we used species availability reported in individual studies as well as the Atlas of Living Australia (ALA) resource, which aggregates biodiversity data from various sources (Atlas of Living Australia website at http://www.ala.org.au; Accessed 2 January 2019). We used ALA only to support the presence of species whose distribution may or may not include the study site. Nevertheless, this approach may yield some false positives (i.e., a species recorded as available at a site when it was not). Dingo remains (hairs) are commonly found in their scats, with studies often distinguishing grooming from cannibalism based on an arbitrary number of hairs (e.g., 10) and/or the type of hairs (e.g., guard hairs). We chose to remove any records of dingoes as a dietary item because: (1) it is difficult to distinguish between grooming and cannibalism; and (2) the reporting of dingo hairs within dingo scats has been inconsistent in the literature. Although we acknowledge that dingoes consume a variety of non-mammalian taxa, for simplicity we hereafter use the term 'diet' to refer to the mammalian component only, unless otherwise indicated.

Diet analysis: Kalamurina case study

To add to our database, we quantified the diet of dingoes during a boom and non-boom period at Kalamurina, which is situated between the north shore of Kati Thanda-Lake Eyre and the southern boundary of the Simpson Desert Regional Reserve, South Australia (27°48'S, 137°40'E; Fig. 3.2). Kalamurina is a 667,000 ha sanctuary that has been owned and managed for conservation by the Australian Wildlife Conservancy since 2007. Dingo scats were collected opportunistically along vehicle tracks (c. 100 km), creek lines, sand dunes/swales, around water sources, and from individuals captured as part of a separate study. We followed a similar approach for analysing scats as used in the other studies in this meta-analysis (see Appendix 2 for a detailed methodology).

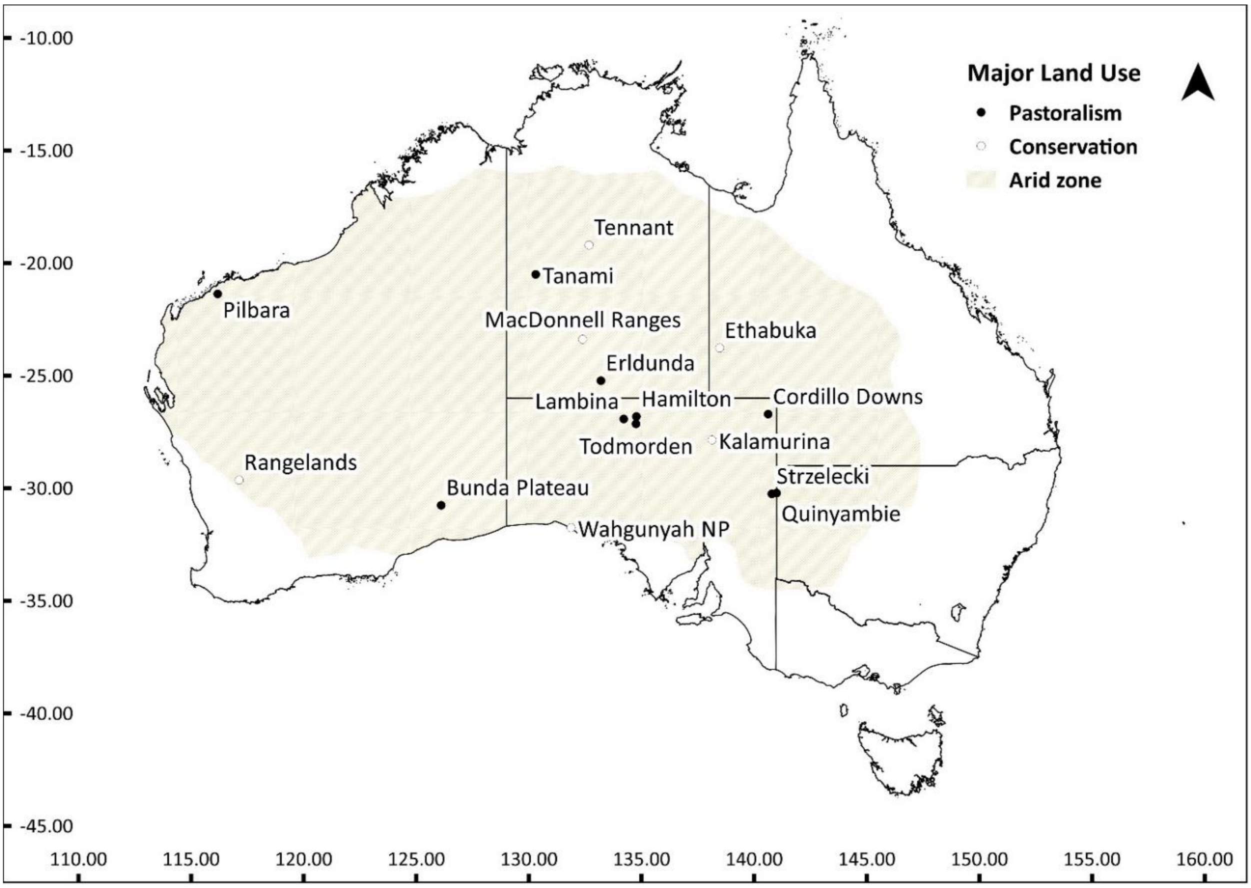

Figure 3.2. Locations that yielded dietary samples that were included in our meta-analysis. Our representation of the arid zone was adapted from Morton et al. (2011) and encompassed both the semi-arid and arid parts of the continent where rainfall/evaporation < 0.4.

Dietary diversity and overlap

All analyses were conducted in the R software environment for statistical and graphical computing (R Core Team, 2017). We converted the data into relative frequency of occurrence (RFO) by dividing the number of detections for each species by the sum of detections for all species, and calculated: (equation 1) the diversity of all species in the diet of dingoes at each site using Shannon's Diversity index (*H*):

$$H = -\sum_{i=1}^{S} p_i \ln p_i \qquad \text{(eqn. 1)}$$

where S is the total number of species recorded in the diet, and p_i is the RFO of species i (i.e. sum of all p_i for a given site equals 1), and (equation 2) the dietary overlap between different sites using Pianka's index (O_{jk}) implemented via the 'EcoSimR' package (Gotelli et al., 2015):

$$O_{jk} = \frac{\sum_i^n p_{ij} p_{ik}}{\sqrt{\left(\sum_i^n {p_{ij}}^2 \sum_i^n {p_{ik}}^2\right)}} \qquad \text{(eqn. 2)}$$

where p_i is the frequency of occurrence (FO) of species i in the diet of dingoes at site j and k (Pianka, 1973). Pianka's index varies between 0 (total separation) and 1 (total overlap).

To consider how sample size affected the dietary diversity, we used resampling to construct diversity rarefaction curves for all sites from which the raw data was available (12 sites representing a total of 5,344 scats). This approach is widely used to estimate the minimum number of dietary samples required to describe the diet adequately, which is indicated by a negligible increase in H above a certain sample size (i.e., when the rarefaction curve reaches an asymptote). We fitted a 4-parameter asymptotic regression model to the resampled data, and defined adequate sampling as that required to reach ≥ 95% of the asymptotic H estimated for each site. We also included estimates of sample size measured from cumulative diversity asymptotes reported in other studies.

Statistical analysis

We tested the effect of major land use on the RFO of individual mammal species using binomial generalised linear models (GLMs). Only the most commonly consumed mammals (i.e., those species consumed at >30% of conservation and pastoral sites) were included in this analysis, to ensure adequate data for this land use comparison.

Using the subset of sites with data for both boom and non-boom periods (n = 7 sites), we tested the effect of period on the per-species probability of occurring in a dietary sample using a binomial mixed effects model. We incorporated the effect of species with a correlated intercepts and slopes term, and also included a fixed effect of weight class (small, medium, or large) and an interaction between class and period. We also used GLMs with a Gaussian error distribution to test the impact of period on dietary diversity (i.e., Shannon's Index), and the impact of land use and inter-site distances on dietary overlap between sites (i.e., Pianka's Index). All mixed effects models were implemented via the 'lme4' package (Bates et al., 2015). Model fit was assessed with residual analysis, plots of fitted values against raw proportions calculated from the data, and evaluation of the deviance explained by a fitted model.

RESULTS

Database

Of the 226 articles returned by our initial search, eleven studies on the diet of dingoes, published between 1987 and 2018, met our criteria and contributed to the meta-analysis (Fig. A2.1). Including data from our own case study, we acquired 25 datasets representing dietary information from eight conservation areas and 17 pastoral properties (Table A2.2 & A2.3). Seven sites reported data from boom and non-boom periods (Table A2.3). One study did not distinguish between two large mammal species and, therefore, this study only contributed to our analysis of weight classes. Dietary samples from the Hamilton site were not spatially independent from Todmorden and were grouped together (hereafter just Todmorden). Overall, we used 8,574 dietary samples (dingo scats and stomachs) to describe the diet of dingoes in Australia's arid zone.

Diet composition and prey occurrence (non-boom periods)

Thirty-one species of non-volant mammal were identified in the diet of dingoes (Fig. 3.3). Dingoes primarily consumed medium-sized (35 – 5500 g) and large (> 5500 g) mammals, indicated by their high proportion and RFO in dietary samples relative to smaller species, regardless of major land use. Of the 66 mammals with distributions that overlapped the study sites, we found those weighing less than 680 g (i.e., below the weight of water rats *Hydromys chrysogaster*) were underrepresented in the diet (Fig. A2.2). We identified a marked disparity in consumption between the two major small mammal clades, with only 18% of insectivorous marsupials (Family: Dasyuridae, 4 – 600 g) ever consumed; compared to 43% of rodent species (Family: Muridae, 10 – 680 g). European rabbits (c. 1.6 kg) were the most frequently occurring dietary item (mean RFO ± se: 0.37 ± 0.07). Remains from rabbit, cattle *Bos taurus*, sheep *Ovis aries*, spectacled hare-wallaby *Lagorchestes conspicillatus*, bilby *Macrotis lagotis*, fawn hopping-mouse *Notomys cervinus*, dusky hopping-mouse *Notomys fuscus*, and common brushtail possum *Trichosurus vulpecula* were found in dingo diet at all sites where they were sympatric (see Fig. A2.2 for lists of species available at each site). Out of all the extant mammals at each site, species in the medium-size class or CWR were consumed at a higher rate, regardless of period.

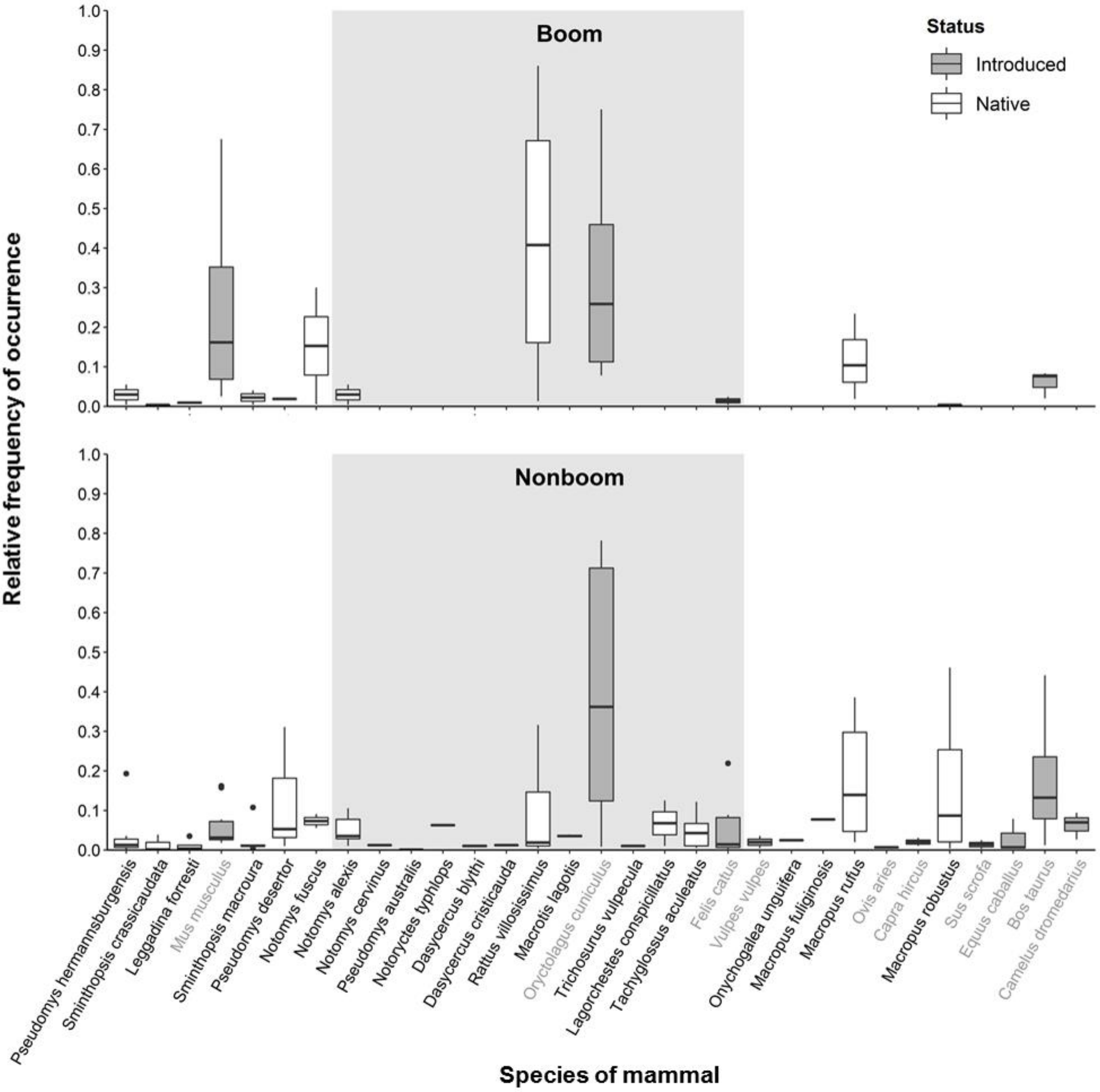

Figure 3.3. The relative frequency of occurrence (RFO) of mammals that were recorded from 8,574 dingo dietary samples from 1968 - 2018. Each boxplot shows the range of RFO measures across sites. Only species that were recorded in the diet are presented. Species are ordered by mean adult weight (low to high), grey labels and boxes represents introduced species and the light grey panel shows mammals in the medium size class. Lower and upper hinges correspond to the first and third quartiles, and the whiskers extend from the hinge to no more than 1.5 x IQR.

Although the breadth of introduced mammal species at each site was generally much lower than native mammals, they occurred with equal frequency in dingo diet. Some evidence of intraguild predation was recorded with feral cats *Felis catus* (c. 4.6 kg) consumed at 12 sites (0.048 ± 0.018) and red foxes (c. 6 kg) at three (0.013 ± 0.002). Major land use had a strong influence on the RFO of the most commonly consumed species in the arid zone (Fig.3.4). Most species, regardless of body size, occurred significantly more frequently in the diet of dingoes from conservation areas. Rabbit, spinifex hopping-mouse *N. alexis* and house mouse *Mus musculus* were the only species to be consumed in equal proportions regardless of major land use (Table A2.4).

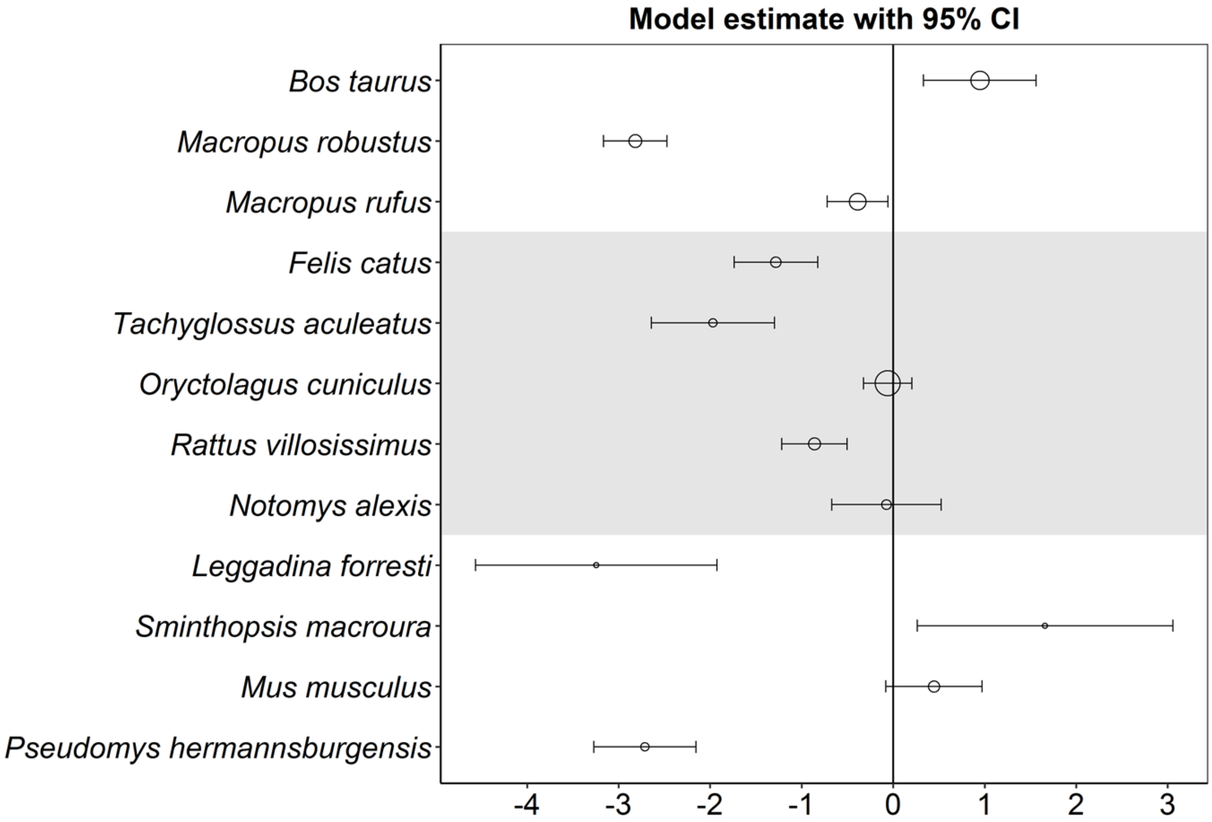

Figure 3.4. Model estimate (± 95% CI) showing the effect of major land use on the relative frequency of occurrence (RFO) of commonly occurring mammal species in the diet of dingoes. Negative estimates indicate the species was recorded more frequently in the diet of dingoes from conservation areas, and positive estimates indicate a higher RFO at pastoral sites. Circles are weighted by their RFO in dingo diet. The grey panel represents mammals in the medium size class

corresponding to critical weight range species, above are larger and below are smaller mammal species. Data from boom periods were not included.

Effect of resource booms

There was an overall negative effect of boom periods on the occurrence of mammals in the diet of dingoes (Table 3.1). Most notably, large mammals showed a significant decrease in their consumption during resource booms ($\beta = -1.83$, $p = 0.01$). In contrast, a few species showed a marked increase in their probability of occurrence during boom periods (Fig. 3.5 & Table A2.6). The probability of a dietary sample containing long-haired rat *Rattus villosissimus* (c. 144 g) was 4.5 times higher during boom periods, making them the most likely mammalian prey item for dingoes at these times. Similarly, house mice (c. 20 g) were 2.5 times more likely to occur in dingo diet samples during resource booms. Further, the breadth of mammal species consumed by dingoes during resource booms was less than half that observed during non-boom periods.

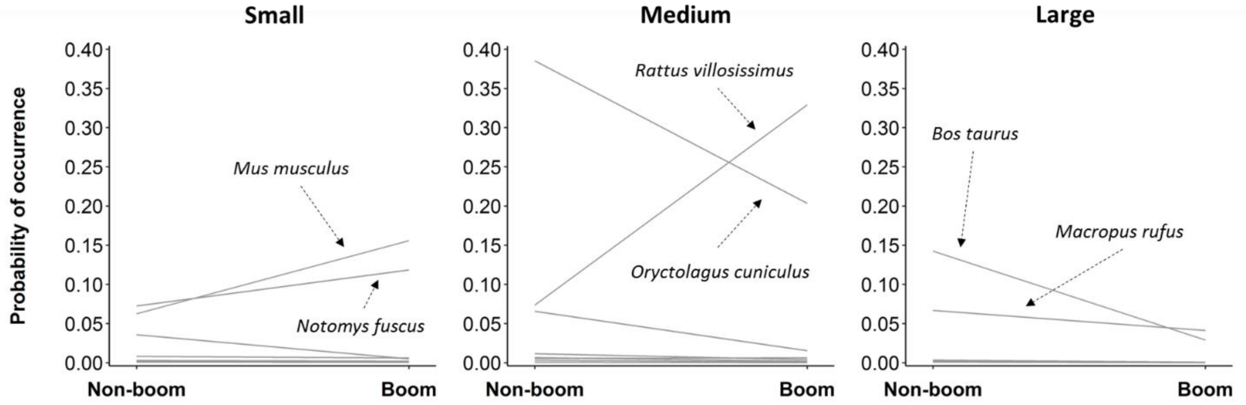

Figure 3.5. The probability of 22 mammal species occurring in the diet of dingoes during non-boom and boom periods. This figure plots model-based estimates for each species derived from the fitted mixed-effects model. Key species are indicated on each graph. See Table A2.6 for species-level probability of presences per sample with associated confidence intervals.

Table 3.1. Model summary for the per-species probability of occurring in a dietary sample. Model estimates, standard errors (SE) and p-values for our correlated intercepts and slopes generalised linear mixed-effects model. Significance is indicated in bold.

Model	Variables	Estimate	SE	*p*-value
P(occurrence) ~ (1 + Period | Species) + Class + Class:Period	(Intercept)	-4.690	0.844	< 0.001
	Medium	-0.090	1.142	0.937
	Large	-0.336	1.248	0.788
	Small:Boom	-0.339	0.555	0.541
	Medium: Boom	-0.709	0.636	0.265
	Large: Boom	**-1.934**	**0.781**	**0.013**

Diversity and overlap

The diversity of mammals in the diet of dingoes varied considerably between sites from H = 0.54 to 2.18 (Table A2.7). For all datasets analysed, the cumulative diversity of prey items in dietary samples exceeded 95% of the asymptote estimated by resampling the data (Fig. 3.6). The mean number of samples needed to describe the overall diet of dingoes in the arid zone adequately was 31 ± 4 (n = 10, non-boom) and 36 ± 3 (n = 6, boom).

The diversity of mammalian prey species in the diet of dingoes was significantly lower during resource booms ($H = 0.96 \pm 0.13$, $t_{12} = -2.25$, $p = 0.04$) than non-boom periods ($H = 1.41 \pm 0.15$). Pairwise comparisons of dingo populations across arid Australia showed a moderate amount of dietary overlap ($O_{jk} = 0.61 \pm 0.01$) and this did not change with increasing distance between sites, despite > 2,500 km separating some populations ($\beta = -1.2\text{x}10^{-6}$, $p = 0.96$; Fig. 3.7). However, there was a significant positive effect of pastoralism on the dietary overlap of dingoes ($\beta = 0.1$, $p = 0.026$) (i.e., dingo diets from pastoral sites were more similar; Table A2.8). Moreover, the dietary overlap between populations was not solely driven by the most commonly occurring species in the diet (i.e., removing rabbits from the dataset did not decrease the amount of overlap).

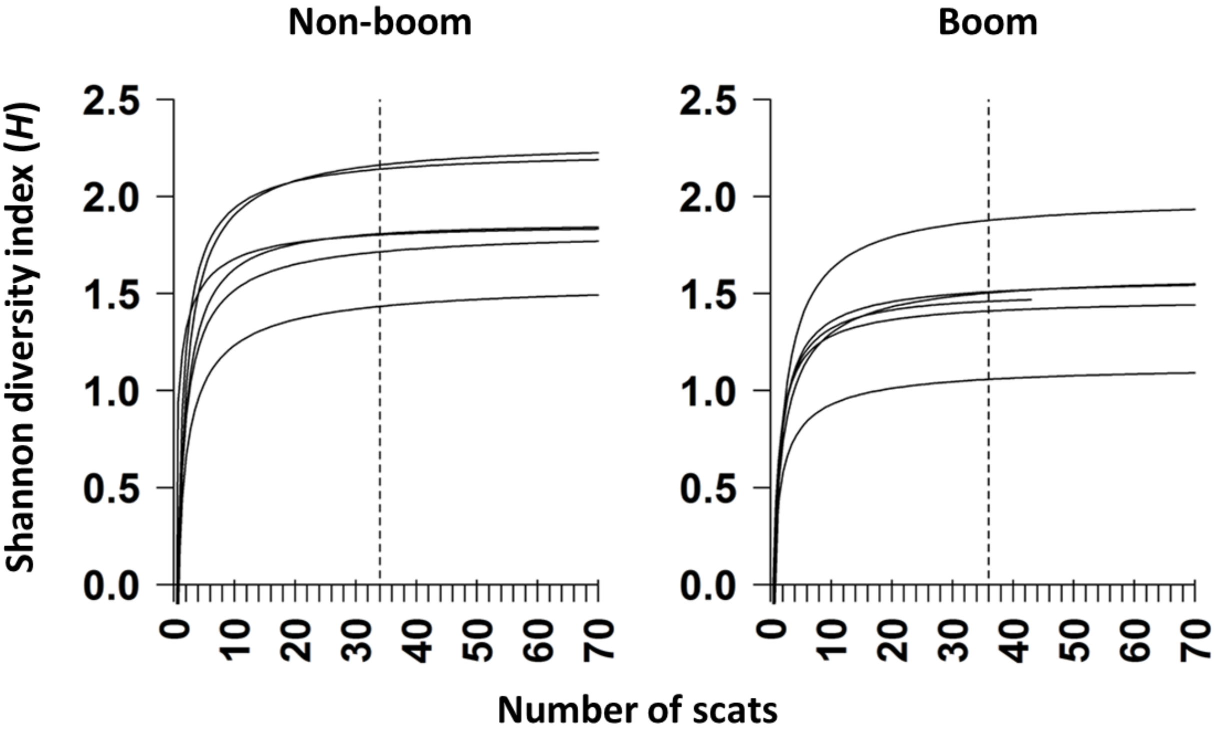

Figure 3.6. Rarefaction curves indicating the number of samples required to describe the overall diet of dingoes in the arid zone during non-boom and boom periods (n = 6 sites). Each solid line represents a site and was fit to the rarefied data using a 4-parameter asymptotic regression model. Minimum sample sizes were determined as that required for H to exceed 95% of the asymptote estimated for each dataset (Table A2.9). Vertical dotted lines indicate the mean number of samples required across all sites. Overall dietary diversity was calculated from datasets where mammals were identified to species and other remains were classified broadly as reptile, bird, invertebrate, and vegetation. For visualisation purposes, x-axes were limited to 70, although the number of dietary samples often exceeded this.

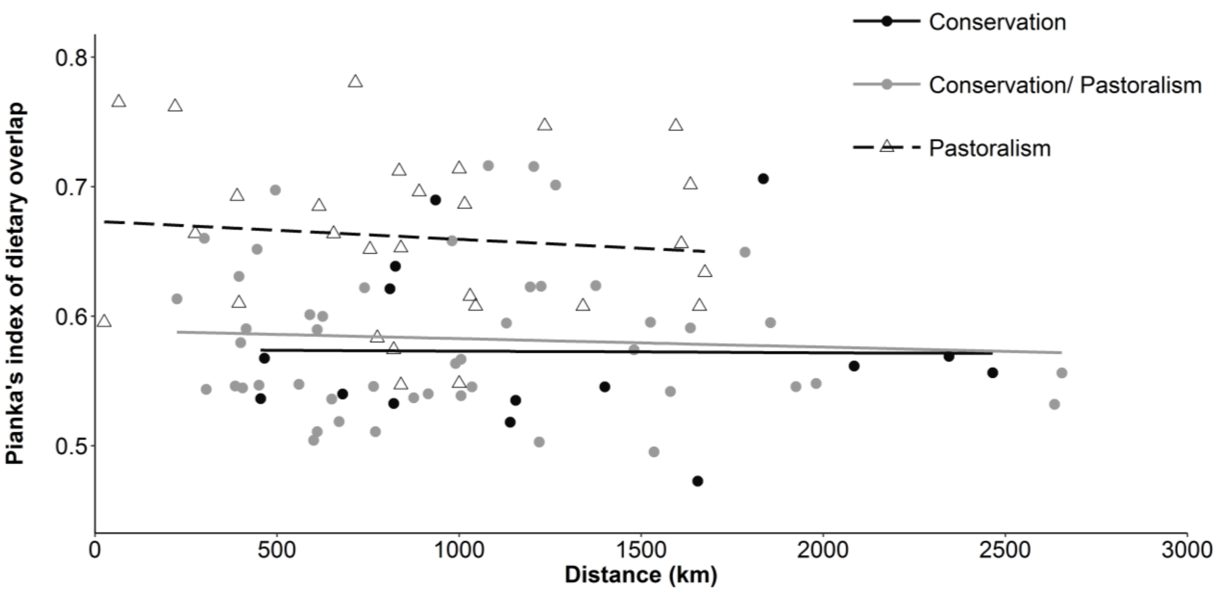

Figure 3.7. The relationship between Pianka's index of dietary overlap and the distance between sites. Each line represents the fitted relationships between dietary overlap and the three groups of pairwise comparisons based on the major land use at each site. Dietary overlap was calculated for the mammalian component of dingo diet only (Table A2.10).

DISCUSSION

We analysed mammal occurrence data from 8,574 dingo dietary samples collected from 12 studies and 15 sites across the arid zone of Australia. Overall, a greater richness and proportion of medium-sized mammal species (relative to the small and large weight classes) were recorded in the diet of dingoes, with introduced European rabbits (c. 1.6 kg) the dominant prey item at most sites where it was present. Resource booms had a clear influence on the diet of dingoes, made especially evident by a major reduction in both the consumption of large mammals and the overall species diversity.

We found most small mammals were consumed infrequently, or not at all (Fig. A2.2). Our results are consistent with a number of studies that have evaluated a hypothesised link between dingo presence and small mammal abundance. A comprehensive desktop study by Smith and Quin (1996) reported that strong, continent-wide patterns of decline in rodent populations were less severe where dingoes were abundant, and a similar relationship has been reported for dasyurids (e.g., Letnic et al., 2009), albeit on a smaller scale (but see Allen, 2011). Australia's arid zone contains an array of small mammal species although they largely fall into the two aforementioned clades. We found dingoes consumed rodents much more readily than dasyurids, although their respective availability (rodents are often more abundant) may have contributed to some of the observed disparity. Different reproductive strategies between the clades and local environmental conditions can facilitate the persistence of rodents at high densities (Yom-Tov, 1985, Krajewski et al., 2000), though comparable densities of dasyurids have also been reported (Letnic et al., 2004). This pattern of predation has been observed in other predators (e.g., feral cats, Doherty et al., 2015a) and might be driven by differences in their respective response to predators (e.g., Cremona et al., 2015) as well as physiological traits (e.g., Geiser and Turbill, 2009). Predation is a major contributing factor behind Australia's decline in small mammals and although a few species of small mammal occurred frequently in the diet of dingoes at some sites (e.g., *Pseudomys desertor*, c. 25 g; RFO = 0.31 at the Tanami site), the bulk of their prey were medium and large species.

Prior to European colonisation, central Australia supported a diverse assemblage of medium sized marsupials (Fig. 3.1) that would have been the primary food source for dingoes (Caughley et al., 1980, Johnson, 2006). Throughout the arid zone, rabbits have effectively replaced the gap in size classes left by a number of extinct or extirpated medium-sized marsupials. In this study, like others, we found rabbits were the most frequently occurring food item in the diet of dingoes and usually comprised a large proportion of the diet wherever or whenever they occurred. The significance of rabbits as a primary food source for dingoes in the arid zone is well documented (e.g., Cupples et al., 2011, Allen and Leung, 2012, Doherty, 2015, Allen et al., 2018), and their occurrence in dingo diet often remains high despite major population fluctuations (Corbett and Newsome, 1987b, Allen et al., 2018). A recent review by Doherty et al.

(2018) found that not only was the frequency of occurrence of rabbit highest in the arid zone, but their occurrence in dingo diet was negatively correlated with other medium-sized mammals. Nevertheless, the frequency at which macropods and cattle were consumed at some sites suggests large mammals were also important food sources. Notably, a large breadth of mammals in the medium size class were consumed. Akin to other similar sized members of the Carnivora, prey species weighing 1–10 kg probably form the dominant basis of dingo diet (Gittleman, 1985, Macdonald and Sillero, 2004). The observed tendency for dingoes in the arid zone to preferentially consume medium-sized or ‘critical weight range’ mammals over other weight classes has important implications for the management of remnant and reintroduced populations.

Introduced mammals were an important prey item for dingoes, which was indicated by their occurrence in c. 50% of all dietary samples despite four times as many native species extant and presumably available across the arid zone. Further, the two most frequently occurring species in dingo diet were both introduced (rabbits and cattle). We also detected an appreciable proportion of feral cats in the diet of dingoes from conservation sites suggesting that in areas with lower anthropogenic impacts, these smaller mesocarnivores form part of the dingo’s prey base. Globally, introduced species are regularly consumed by native predators (Andelt, 1985, Maehr et al., 1990, Branch et al., 1996, Barbar et al., 2016) and this has been well supported by dietary studies on dingoes throughout their continental distribution (Doherty et al., 2018). However, rather than a particular prey preference, their tendency to consume high proportions of non-native mammals is perhaps more indicative of changes in mammalian assemblages that have occurred over the last 200 years, where the most abundant and available prey are often non-native pests and livestock. Similar conclusions have been drawn outside of Australia. For example, Novaro et al. (2000) found that introduced species in Patagonia dominated the diet of native predators as a result of anthropogenic modification to the landscape, concluding that native prey species were functionally extinct.

The dietary overlap between dingoes at pastoral sites was significantly higher than from among conservation areas. Pastoralism can reduce habitat complexity, which tends to reduce biodiversity (Benton et al., 2003, Newbold et al., 2015) and therefore may limit dingoes to a narrower range of prey species. Conversely, conservation areas promote restorative management to increase habitat heterogeneity in order to support a wider range of plants and animals (Singh, 2002). This difference in dietary overlap between areas of opposing land use may indeed become more pronounced if conservation areas continue to reduce the legacy effects of antecedent human disturbance. Surprisingly, dingoes showed considerable dietary similarities throughout the arid zone, despite some sites being separated by a distance equivalent to that between Spain and Russia (Fig. 3.7). This is atypical throughout the Carnivora where marked variation in diet usually occurs between spatially discrete populations of predators due to differences in the distribution of prey species and their abundance (Lake et al., 2003, Lyngdoh et al., 2014).

Resource pulses appear to drive changes in the dietary selection of Australia's largest terrestrial predator. Life in Australia's arid zone is characterised by prolonged periods of limited resources interrupted only by irregular rainfall events that produce short-lived explosions in primary productivity and consequently, mammals (Morton et al., 2011). The dingo's ability to take advantage of prevailing conditions was particularly evident during these resource pulses (boom periods) where the composition of their diet changed markedly to reflect a sudden hyper-abundance of certain prey species. The sudden population explosion and range expansion of native long-haired rats during a boom period in 2011–2012 was exploited by dingoes for over a year at some sites. Further, the increased consumption of a few, presumably hyper-abundant, small and medium-sized mammals during boom periods resulted in significantly fewer occurrences of large mammals in dingo diet (Fig. 3.5). The absolute dominance of a select few species in the diet of dingoes during boom periods has the potential to temporarily benefit other species, particularly those that are strongly affected by top-down forces (e.g., reintroduced CWR mammals). However, arid ecosystems are complex with most small- and medium-sized mammals consumed by several predator species and therefore, temporarily reduced predation from dingoes alone is unlikely to have large impacts on their survival rates.

CONCLUSIONS

Dingo consumption of mammals throughout the arid zone did not vary appreciably except during periods of heightened resource availability where dietary diversity decreased sharply and most species were consumed much less frequently. Medium and large mammals occurred most often and even though some small mammals were regularly consumed, they did not form a major component of dingo diet in the arid zone. The structure of ecological communities throughout Australia's arid zone have changed drastically in the last 200 years, resulting in an alien landscape where the few remaining native mammals are being eaten to extinction. Given the dingo's tendency to consume medium-sized mammals, current approaches to conserving remnant or reintroduced populations may be challenging in their presence.

Statement of Authorship

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Principal Author

Name of Principal Author (Candidate)	Jack Tatler		
Contribution to the Paper	Planned and developed the research, collected the data, developed the models and analysed the data, wrote the manuscript.		
Overall percentage (%)	80%		
Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.		
Signature		Date	18/03/2019

Co-Author Contributions

By signing the Statement of Authorship, each author certifies that:

vii. the candidate's stated contribution to the publication is accurate (as detailed above);

viii. permission is granted for the candidate in include the publication in the thesis; and

ix. the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

Name of Co-Author	Phill Cassey		
Contribution to the Paper	Contributed to the development of the modelling and statistical analysis, revised and edited the manuscript.		
Signature		Date	18/03/2019

Name of Co-Author	Thomas Prowse		
Contribution to the Paper	Contributed to the development of the modelling and statistical analysis, revised and edited the manuscript.		
Signature		Date	18/03/2019

Please cut and paste additional co-author panels here as required.

Chapter 4. High accuracy at low frequency: detailed behavioural classification from accelerometer data

Jack Tatler, Phillip Cassey, and Thomas A. A. Prowse

Publication: Tatler, J., Cassey, P. & Prowse, T. A. A. 2018. High accuracy at low frequency: detailed behavioural classification from accelerometer data. *Journal of Experimental Biology*, 221. 10.1242/jeb.184085

Appendix: Supplementary material accompanying this chapter can be found in Appendix 3 of this thesis.

ABSTRACT

Accelerometers are a valuable tool for studying animal behaviour and physiology where direct observation is unfeasible. However, giving biological meaning to multivariate acceleration data is challenging. Here, we describe a method that reliably classifies a large number of behaviours using tri-axial accelerometer data collected at the low sampling frequency of 1 Hz, using the dingo *Canis dingo* as an example. We used out-of-sample validation to compare the predictive performance of four commonly used classification models (Random Forest, *k*-Nearest Neighbour, Support Vector Machine, and Naïve Bayes). We tested the importance of predictor variable selection and moving window size for the classification of each behaviour and overall model performance. Random Forests produced the highest out-of-sample classification accuracy, with our best performing model predicting 14 behaviours with a mean accuracy of 87%. We also investigated the relationship between overall dynamic body acceleration (ODBA) and the activity level of each behaviour given its increasing use in ecophysiology as a proxy for energy expenditure. ODBA values for our four 'high activity' behaviours were significantly greater than all other behaviours, with an overall positive trend between ODBA and intensity of movement. We show that a Random Forest model of relatively low complexity can mitigate some major challenges associated with establishing meaningful ecological conclusions from acceleration data. Our approach has broad applicability to free-ranging terrestrial quadrupeds of comparable size. Our use of a low sampling frequency shows potential for deploying accelerometers over extended time periods, enabling capture of invaluable behavioural and physiological data across different ontogenies.

INTRODUCTION

The foundation of animal ecology is understanding how individuals interact with their abiotic and biotic environment. These interactions are increasingly being measured with bio-logging techniques, where biological data are recorded remotely from devices attached to animals. This approach has allowed researchers to answer questions on everything from hunting tactics of puma (Williams et al., 2014) to energy expenditure in cormorants (Gómez Laich et al., 2011) and diving behaviour in whales (Ishii et al., 2017). Consequently, the ability to continuously 'observe' free-ranging animals has facilitated the development and exploration of entirely new theories (Wilmers et al., 2015).

Accelerometers are a valuable tool in bio-logging research as they provide quantitative measurements of animal behaviour and physiology, where direct observation is not possible or logistically feasible. The use of accelerometers mitigates some of the major challenges associated with studying the behaviour of wild animals such as extensive time-investment, animal disturbance, and observer bias. Accelerometers measure acceleration (gravitational and inertial) caused by animal movement in different planes, allowing the development of classification models calibrated to predict behavioural states such as resting, walking, swimming, and eating (e.g. Pagano et al., 2017). Further, there is a strong linear relationship between body acceleration and energy expenditure in many taxa, which is of particular interest to ecophysiologists (Wilson et al., 2006, Halsey et al., 2009b, Halsey and White, 2010). Although accelerometry has been used to study animal movement and behaviour for almost two decades (Yoda et al., 1999), recent methodological advancements have increased its accessibility and appeal to a broader scientific community.

Classifying animal behaviours to high-frequency acceleration data presents a suite of new and complex challenges. One approach is unsupervised machine-learning, in which pattern recognition algorithms identify different states directly from the accelerometer signatures.

Unsupervised learning is intrinsically challenging so algorithms are frequently used to 'learn' the relationship between acceleration data and behaviour using a model-training dataset that is acquired from direct observation. The ability of the algorithm to interpret this relationship depends largely on the variables used to characterise the raw acceleration data. Several attempts to simplify or streamline this approach have been made, with varying success. Ladds et al. (2017) introduced a super machine-learning method that identified six behaviours in four species of pinniped with < 78% accuracy. They used a high sampling frequency (25 Hz), large training dataset (~ 90,000 individual data points), and a very large set of input variables (*n* = 147). In contrast, when using fewer input variables and the relatively simple approach (*k*-Nearest Neighbour), McClune et al. (2014) classified four behaviours in Eurasian badgers *Meles meles* with an overall classification accuracy of 89%. In general, it is expected that the classification accuracy of a model will increase when using: a) higher sampling frequencies; b) more training data; and c) broader behaviour categories (i.e., fewer behaviours to be classified). The consequence of following this criteria is not only increased computational time and difficulty, but loss of behavioural diversity and decreased deployment time on free-ranging animals due to memory constraints, i.e., the exact opposite of what researchers are aiming for. Reducing the sampling frequency would greatly increase deployment time (e.g., from days to months) whilst also decreasing computational effort. However, it is challenging to accurately classify a broad range of behaviours using very low sampling rates. If we can create a simple model that overcomes the aforementioned hurdles, we will greatly improve integration with other fields such as movement ecology and physiology.

One major weakness in applying machine-learning algorithms to acceleration data is that for accurate and reliable identification of different behaviours, a period of observation is required to 'train' the algorithm. Therefore, it has only been possible to use this approach on species which can be observed whilst simultaneously recording their acceleration. Campbell *et al.* (2013) made an important step in overcoming this problem by demonstrating the potential of 'surrogacy', whereby a classification model was trained with behavioural observations from one species, and accurately predicted these behaviours in other species that possessed similar morphometrics.

In this study we describe an approach to the classification of behaviours using accelerometer data collected at the very low sampling frequency of 1 Hz. We used the dingo *Canis dingo*, a medium-sized prototypical quadruped, as an example, because it readily exhibits behaviours akin to its wild conspecifics. We used out-of-sample validation to compare the predictive performance of four commonly used classification models (Random Forest, *k*-Nearest Neighbour, Support Vector Machine, and Naïve Bayes). We then tested the importance of predictor variables for the classification of each behaviour as well as overall model performance. We expected behaviours that were functionally similar, such as lateral and sternal recumbency, would produce similar acceleration signatures and thus be more difficult to classify accurately. Given the increasing use of overall dynamic body acceleration (ODBA) as a measure of activity and proxy for energy expenditure (Wilmers et al., 2015), we anticipated ODBA would show a strong, positive relationship with intensity of movement.

METHODS

Data collection

Captive observations were conducted at Cleland Wildlife Park, Adelaide (34.9667˚S, 138.6968˚E) from August 2016 – March 2017 under a University of Adelaide Animal Ethics permit (S-2015-177a). We used three, captive born, adult male dingoes (c. 19 kg) that were kept on permanent display in a 2,500 m^2 outdoor enclosure. We fitted each dingo with a tri-axial accelerometer (LISD2H, ST Microelectronics, USA) built into a custom-made GPS collar (Telemetry Solutions, Concord, CA, USA). The tri-axial accelerometer was programmed to sample changes in acceleration at 1 Hz (one sample per second) and orientated so that the *x*, *y* and *z*-axes recorded acceleration along the sway, heave, and surge planes, respectively (Fig 4.1).

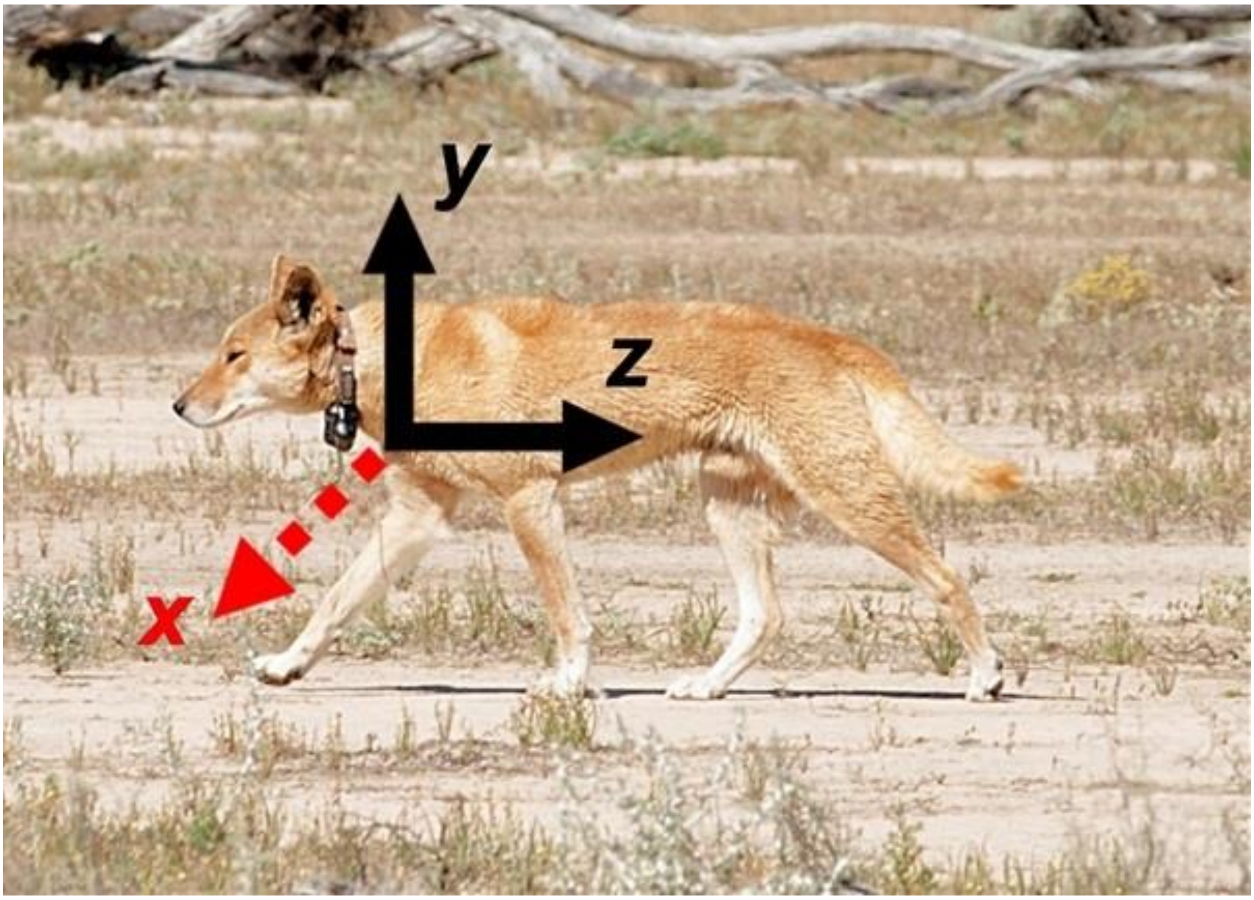

Figure 4.1. Dingo wearing a GPS-accelerometer collar. Arrows indicate axis orientation of the accelerometer (x, sway or side-to side; y, heave or up-and-down; z, surge or back-and-forth). [Photo credit: C. O'Brien]

Dingo movement was recorded continuously with the accelerometer and visually with a camcorder at 30 frames s^{-1} (Sanyo Dual Camera Xacti CG10 HD) for eight, c. 30 minute sessions. Behaviours directly observed from the video footage were manually annotated into a Microsoft Excel spreadsheet by one observer (JT) and matched to the corresponding accelerometer data via concurrent timestamps. We synchronised the accelerometer and camera clocks by setting them using the same laptop computer (internet time server) on the morning of each session.

Prior to manual annotation we consulted the timestamp from auxiliary footage (iPhone 8 also set to the internet time server, 30 frames s^{-1}) to confirm the syncing of our devices. Although a handling keeper was present at all times, the focal animal (only ever one dingo per session) was unrestricted and conducted behaviours largely *ad libitum*. Prior exposure to commercial dog collars ensured the dingoes did not act atypically during the sampling sessions (H. Wells 2017, pers. comm.).

Determining behaviours from acceleration values requires a sampling frequency that is at least twice as fast as the observed behaviour (Nyquist sampling theorem). Thus, our core criteria for what constituted a behaviour was a repeated movement that consistently lasted two or more seconds. We observed 14 such behaviours and annotated them to 9,360 accelerometer data points (equivalent to 156 minutes) on a per-second basis (Table 4.1). Quick transitory movements, between recognised behavioural states, were assigned to either the behaviour (pre- or post-transition) that was mostly common across the 30 frames s^{-1}. We excluded any behaviours that had sample sizes < 20 data points or were clearly observed to be influenced by physical interaction with the keeper. Based on direct observation of dingo movement, each behaviour was broadly assigned to an activity level: low, medium, or high.

Table 4.1. Descriptions of all 14 behaviours that met the selection criteria. Activity classes were assigned post hoc, based on direct observation of behaviours and intensity of movement.

Activity	Behaviour	Description of movement
Low	Lat. lying inactive	Recumbent on flank with head down on the ground
	Stern. lying inactive	Recumbent on sternum with head down on the ground
	Lat. lying alert	Recumbent on flank with head and neck upright
	Stern. lying alert	Recumbent on sternum with head and neck upright
	Sitting	Sedentary, rump on ground, front legs held straight under body
	Standing	Sedentary, with all four legs held straight under the body
Med.	Drinking	Body in standing position, head lowered; rapid jaw movements
	Lat. lying groom	Recumbent on flank with rhythmic head movement
	Searching	Omni-directional movements, head low and focussed on ground
	Walking	Symmetric diagonal gait at a slow pace
	Collar discomfort	Standing/ walking while jerking neck from side to side
High	Trotting	Symmetric diagonal gait; faster than a walk
	Playing	High intensity interactions with conspecifics
	Running	Gallop type movement at a very fast pace

Variable derivation

The ability of classification models to distinguish between behavioural states depends partly on the predictor variables used to characterise the raw acceleration signals. We adopted a comprehensive approach to selecting predictor variables by calculating an extensive list of derived variables (*n* = 66) from the *x*, *y*, and *z* axes. These ranged from simple metrics such as the mean and standard deviation of an axis, to more complex, derived variables such as waveform length and signal magnitude area (Table 4.2). All predictor variables were calculated using a moving window centred on each data point (see detailed description given in 'Model evaluation').

Table 4.2. Descriptions of the predictor variables that were used to fit four different classification algorithms in an attempt to classify dingo behaviours.

	Description
Axes	*x* (side to side), *y* (back and forth), *z* (up and down) axes.
Standard deviation	Measures the spread of the signal for each axis or statistic
Magnitude	Magnitude of acceleration: $\sqrt{x^2 + y^2 + z^2}$
Signal Magnitude Area	A measure of movement intensity within all three axes: $SMA = \frac{1}{N}(\sum_{i=1}^{N}\lvert x_i\rvert + \sum_{i=1}^{N}\lvert y_i\rvert + \sum_{i=1}^{N}\lvert z_i\rvert)$
Waveform Length	The total amount of variance within the signal through the cumulative measure of amplitude, frequency and duration: $WL = \frac{1}{N}(\sum_{i=1}^{N-1}\lvert x_{i+1} - x_i\rvert + \sum_{i=1}^{N}\lvert y_{i+1} - y_i\rvert + \sum_{i=1}^{N}\lvert z_{i+1} - z_i\rvert)$
Kurtosis	Measure of weight of the tails relative to a normal distribution.
Skew	Measure of the lack of symmetry of the distribution.
Correlation	Degree and type of pairwise relationship between the three axes.
Dynamic Body Acceleration	Static acceleration. Calculated by subtracting a running mean from the raw acceleration data from each axis.
Overall Dynamic Body Acceleration	The absolute sum of DBA for each axis: $ODBA = \lvert DBA.x\rvert + \lvert DBA.y\rvert + \lvert DBA.z\rvert$
Vectorial Dynamic Body Acceleration	Vector of the dynamic body acceleration: $VeDBA = \sqrt{DBA.x^2 + DBA.y^2 + DBA.z^2}$
Difference	The difference between successive values on each axis.
Absolute values	Absolute value of the chosen parameters.
Mean	Mean, calculated over a moving window, of the chosen parameters.
Range	Minimum and maximum values calculated over the moving window.

Classification modelling

We used supervised machine-learning techniques to fit classification models that used different combinations of the predictor variables. In supervised learning, an algorithm is employed to learn the relationship between a given set of input and output variables (our predictor variables and manually assigned behaviours, respectively) so that when provided with a new set of input variables, it can predict what the output variables will be. With the goal of finding a reliable method that would be straightforward to implement, we compared four supervised machine-learning algorithms using the R software environment for statistical and graphical computing (R Core Team, 2017). The *k*-Nearest Neighbour (*k*–NN: R library 'class', Venables and Ripley 2002) is a simple algorithm that employs a number of nearest neighbours (defined by the parameter *k*) to contribute to the classification of a sample. The majority of behaviours within *k* observations surrounding the data point being classified, determines the behaviour of that data point (Coomans and Massart, 1982). Naïve Bayes (NB: R library 'e1071', Meyer *et al*. 2015) is a probabilistic classifier that computes the conditional a-posterior probabilities of a categorical class variable given independent predictor variables using Bayes' rule. A Support Vector Machine (SVM: R library 'e1071') constructs an optimal hyperplane to separate patterns, or classes, in the data (Vapnik, 1999). Non-linear classification is achieved using kernel functions (chosen *a priori*), which nonlinearly map the input vectors into a very high-dimensional feature space. A Random Forest (RF: R library 'randomForest', Liaw and Wiener 2002) is an ensemble method for classification in which a set of decision trees are constructed that are then used to classify a new instance according to the majority vote (Breiman, 2001). The number of decision trees needed generally increases with the number of predictor variables used. Each of these modelling approaches are widely used, computationally inexpensive, and represent different degrees of complexity to pattern recognition and classification.

Model evaluation

For each machine-learning algorithm, we evaluated a candidate set of models that ranged in complexity from a 'null' model containing just the *x*, *y*, and *z* axes ($n = 3$ variables) to the most complex model ($n = 69$ variables; Table A3.2). We tested six different moving windows for variable derivation (4, 8, 16, 32, 64, and 128 seconds). We also explored how the predictive ability of our four models was affected when we employed a different number of nearest neighbours (1, 3, 5, 7, and 9; *k*–NN), kernels (linear, radial, and polynomial; SVM), and number of classification trees (500, 1000, 2500, 5000, 7500, and 10000; RF). To measure the predictive performance of each model, we averaged the out-of-sample accuracy (see below) achieved across 10 repeated training-test splits, in each case using a random 90% of the data from each behaviour to train our model and the remaining 10% for testing.

For each test datum, predicted behaviours were labelled as true positive (TP) if they correctly matched the actual behaviour, true negative (TN) if they correctly identified as a different behaviour, false positive (FP) if the behaviour was incorrectly identified, and false negative (FN) if they incorrectly identified as a different behaviour. We evaluated the predictive ability of our models using three measures of accuracy: the True Skill Statistic (*TSS*; equation 1), Matthew's Correlation Coefficient (*MCC*; equation 2), and the *F*-measure (equation 3). The *TSS* was introduced by Allouche et al. (2006) as an improvement to the widely used Kappa, whereby it not only accounts for both omission and commission errors, but is not affected by the sample size of each class.

$$TSS = \frac{\text{TP}}{(\text{TP+FN})} + \frac{\text{TN}}{(\text{TN+FP})} - 1 \qquad \text{eqn.1}$$

Similarly, we chose *MCC* because it is a balanced measure of accuracy when sample sizes are unequal and has been more widely used in bioinformatics than *TSS*.

$$MCC = \frac{\mathrm{TP}\times\mathrm{TN}\text{-}\mathrm{FP}\times\mathrm{FN}}{\sqrt{(\mathrm{TP}+\mathrm{FP})\times(\mathrm{TP}+\mathrm{FN})\times(\mathrm{TN}+\mathrm{FP})\times(\mathrm{TN}+\mathrm{FN})}} \qquad \text{eqn. 2}$$

The *TSS* and *MCC* both return a value between -1 (total disagreement between prediction and observation) and +1 (perfect prediction), with a value of 0 indicating a prediction no better than random chance. We included the *F*-measure, calculated as the harmonic mean of precision and sensitivity, because it is a relatively simple statistic that has been widely used in the literature, thus placing our results in the context of previous studies.

$$F\text{-measure} = \frac{2\times\mathrm{TP}}{(2\times\mathrm{TP})+\mathrm{FP}+\mathrm{FN}} \qquad \text{eqn. 3}$$

We calculated three additional statistics that provide added insight into model performance. These were: precision, denoting the proportion of positive classifications that were correctly identified (equation 4); sensitivity, which is the probability that a behaviour will be correctly classified (equation 5); and specificity, the probability that a behaviour has been correctly classified as a different behaviour (equation 6).

$$\text{Precision} = \frac{\mathrm{TP}}{\mathrm{TP}+\mathrm{FP}} \qquad \text{eqn. 4}$$

$$\text{Sensitivity} = \frac{\mathrm{TP}}{\mathrm{TP}+\mathrm{FN}} \qquad \text{eqn. 5}$$

$$\text{Specificity} = \frac{\mathrm{TN}}{\mathrm{TN}+\mathrm{FP}} \qquad \text{eqn. 6}$$

Classification models produce a corresponding probability to their behavioural predictions, to which we apply a threshold criterion (0.1-0.9) that determines the rate of TP, TN, FP, or FN. The threshold is usually used to fine-tune model parameters such as sensitivity and specificity. Therefore, it is important to choose a threshold based on the research questions and consequences associated with practical application of the model. Given that the intended practical application of this research is to predict behaviours of free-ranging animals, we chose a threshold that would maximise our *TSS* score whilst minimising the amount of unclassified data points.

Overall dynamic body acceleration

Dynamic body acceleration (DBA) was calculated by subtracting a running mean from each acceleration axis to give acceleration values occurring from inertia (i.e. movement). We chose a running mean of four seconds (i.e. four data points) because it was roughly half the length of our most active behaviour (running) and thus, we minimise any loss of resolution for each behaviour. The absolute value for each axis (DBA) was summed to give ODBA, an overall value for dynamic acceleration. To determine whether ODBA differed between the observed behaviours, and if there was a positive relationship between ODBA and activity level, we conducted an ANOVA and Tukey's test for paired comparisons. All analyses were conducted in the R software environment for statistical and graphical computing (R Core Team, 2017).

RESULTS

Across the four machine-learning algorithms we tested, the Random Forest classification models produced superior out-of-sample validation scores (Fig 4.2). The top 50 classification models were all achieved using the Random Forest algorithm. Despite differing considerably in their complexity (Table A3.3), the predictive capacity of these models was similar (Δ mean TSS ≤ 0.04). Our 'best' model, which ranked third overall, was selected due to its low number of predictor variables (26 of a possible 69) and classification trees (1000), in conjunction with returning the lowest range in TSS scores between the 14 behaviours (Table 4.3). This selected Random Forest model predicted all 14 dingo behaviours with high accuracy (mean TSS = 0.87).

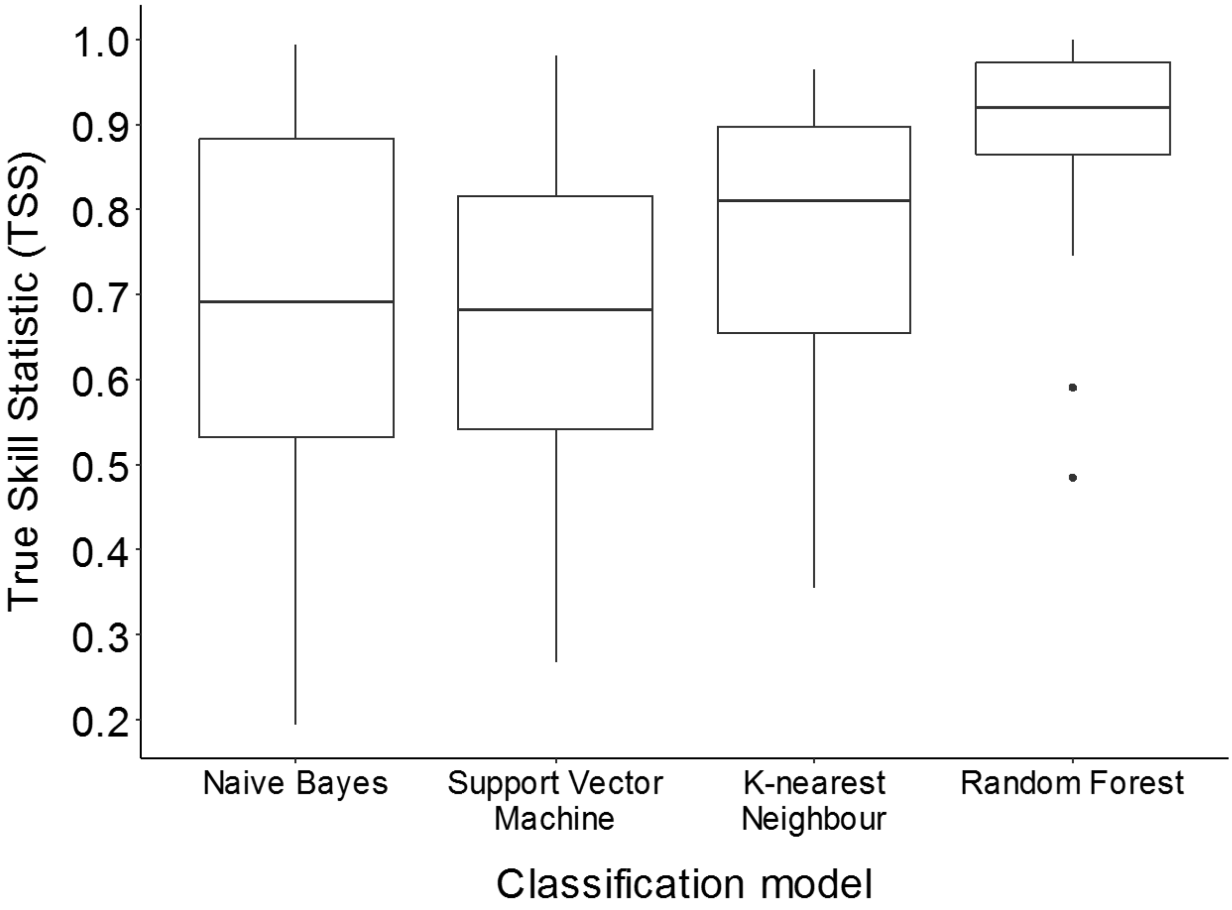

Figure 4.2. The predictive ability (TSS) of the best Naïve Bayes, Support Vector Machine, k-Nearest Neighbour and Random Forest models (no threshold). Each boxplot shows the range of TSS scores from the 14 behaviours classified by each algorithm. Lower and upper hinges correspond to the first and third quartiles, and the whiskers extend from the hinge to no more than 1.5 × IQR. Outliers are represented individually by dots.

Comparisons of different Random Forest models indicated that the predictor variable set used had the strongest influence on the ability of Random Forests to predict dingo behaviours (Fig 4.3). When models were fitted with just the x, y, and z axes (predictor variable set 1) they produced the lowest predictive accuracy. The Random Forest models that were constructed using a moving window of ≥ 16 seconds were substantially better at classifying behaviours, whereas varying the number of classification trees had little effect on model accuracy (Fig 4.3).

The z axis, which measured surge movement, was highly variable between behaviours and therefore, was particularly important for classification (Fig 4.4).

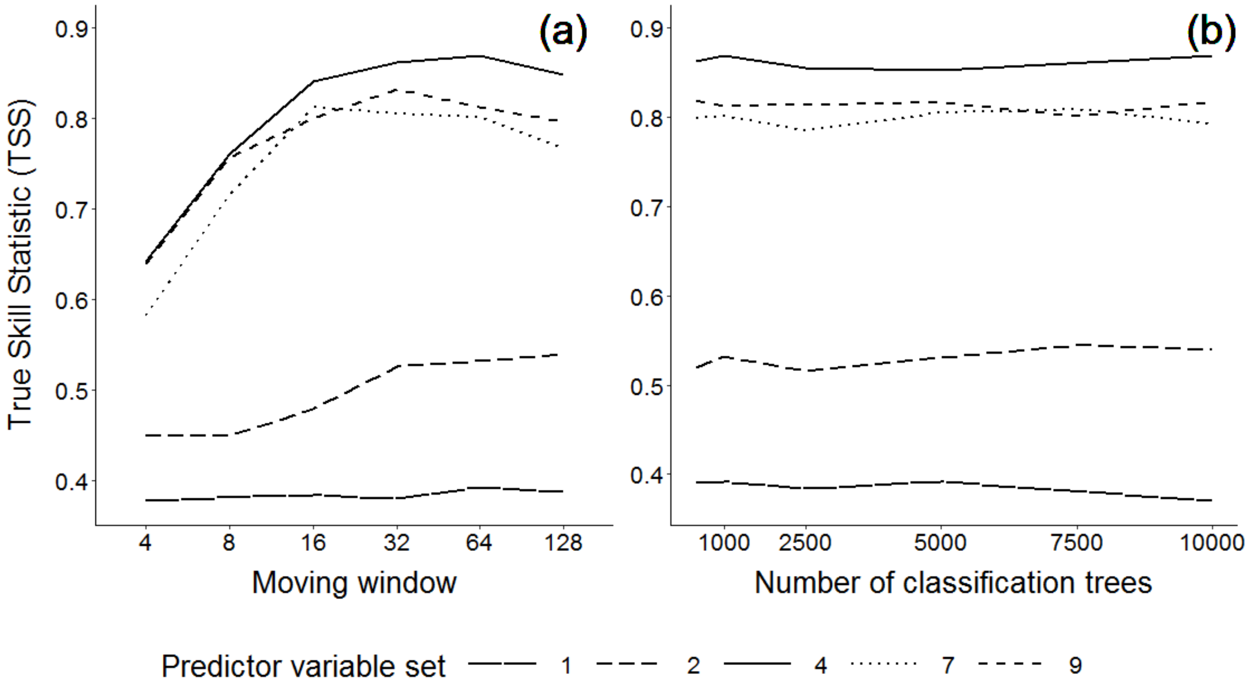

Figure 4.3. The importance of predictor variable set on the predictive ability (mean TSS from ten-fold out-of-sample validation) of Random Forest models when fit with (a) an increasing moving window and fixed number of classification trees (ntree = 1000; as per selected model), and (b) an increasing number of classification trees but a fixed moving window of 64 seconds (as per selected model).

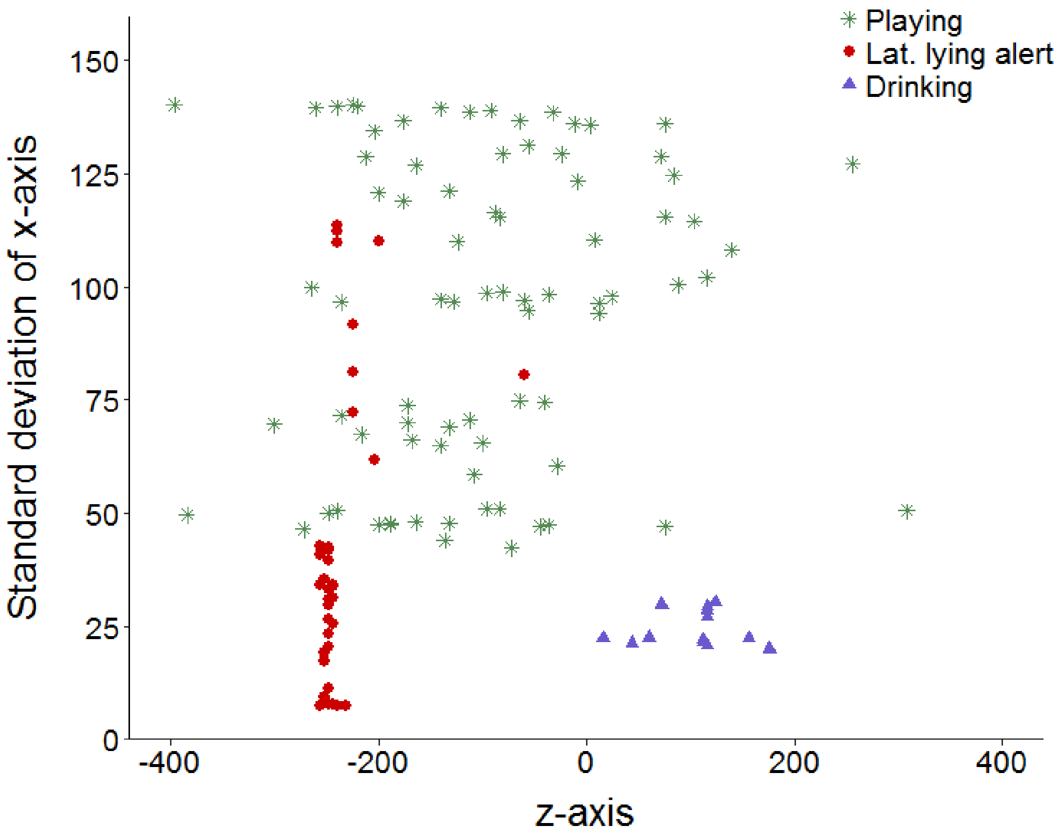

Figure 4.4. Clustering of data points demonstrate the importance of predictor variables for classifying behaviours in our selected random forest model. One behaviour from each activity level was chosen as an example: Lat. lying alert = low activity, Drinking = medium activity, and Playing = high activity.

Further, predictors that described the variation (standard deviation) and characterised the distribution of sway movements proved to be valuable for classifying behaviours (Fig 4.5). We attempted to refine the model further by excluding the variables that contributed least to the model (mean decrease in accuracy ≤ 60%; n = 8) but found a reduction in the ability of the model to identify dingo behaviours (mean values: TSS = 0.85 MCC = 0.87, F-measure = 0.88, precision = 0.91, sensitivity = 0.86, and specificity = 0.99).

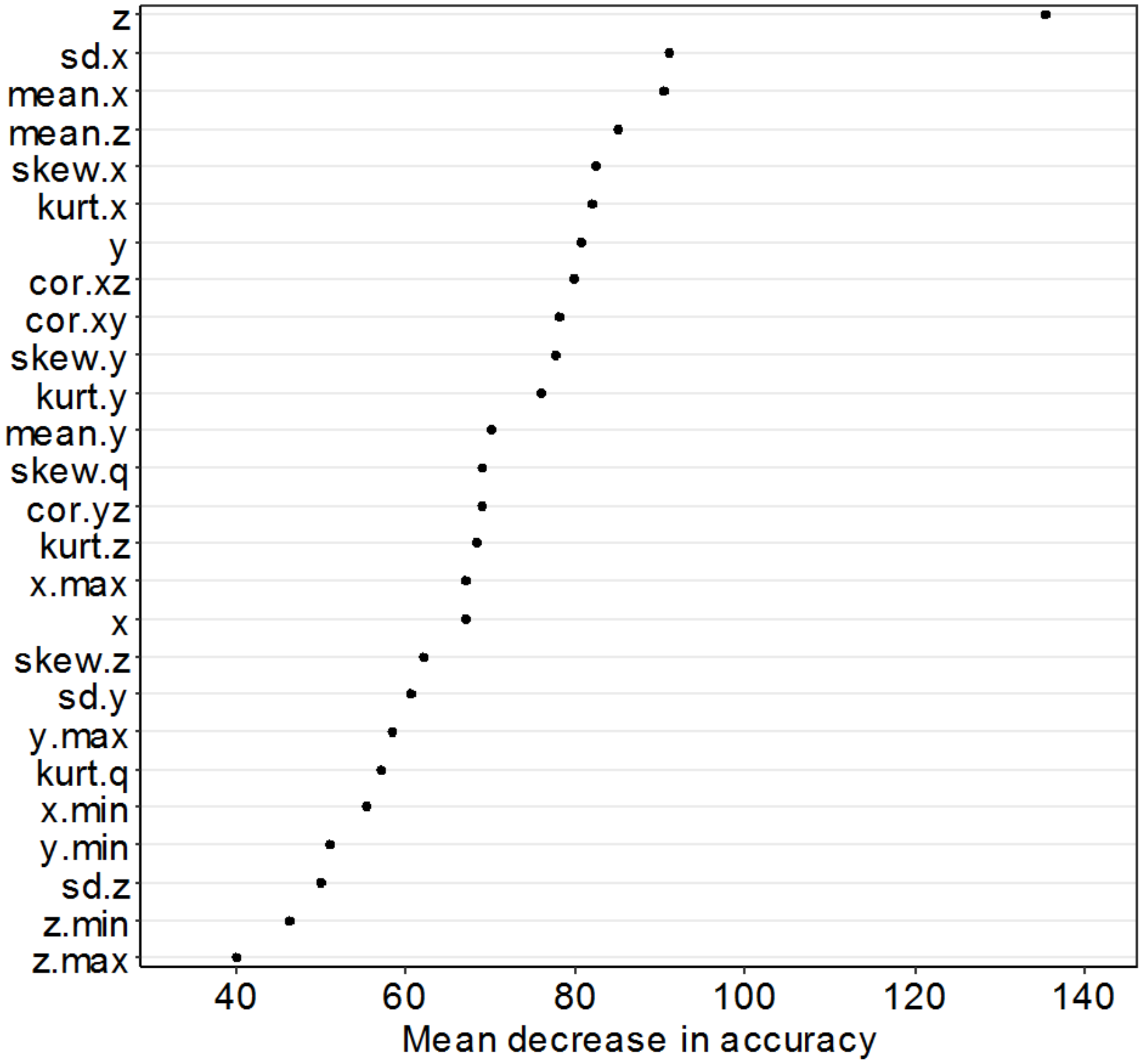

Figure 4.5. Variable importance plot from our selected Random Forest model. The importance plot provides a relative ranking of all 26 predictor variables that were used to fit our selected model, with larger values indicating variables that contributed more to the overall accuracy, or predictive ability, of the model. The mean decrease in accuracy for a variable is the normalised difference of the classification accuracy for the out-of-bag data for a given variable, and the classification accuracy for the out-of-bag data when the values of the given variable have been randomly permuted.

Overall, our selected model performed better at classifying low intensity, stationary behaviours. Specifically, all behaviours where dingoes were lying down were identified with very high accuracy (TSS > 0.90). In contrast, upright and more dynamic movements such as trotting and running were classified less well (TSS = 0.46 and 0.62, respectively). We observed high specificity for each of our behaviours (0.92 – 1.00) and thus our selected model was robust to misclassification. Although the majority of behaviours exhibited a sensitivity above 0.90, low sensitivity for trotting and running indicated the model had difficulty with positive classification of these behaviours (Table 4.3).

Table 4.3. Performance of our selected Random Forest model at predicting 14 different behaviours observed in captive dingoes. We used six widely used techniques for quantitatively assessing the model's predictive ability, at a threshold of 0.3. Our selected model was fit using predictor variable set = #4, a moving window = 64 seconds, and number of classification trees = 1000. 95% confidence intervals are presented in square brackets beneath each metric.

Behaviour	*TSS*	*MCC*	*F*-measure	Precision	Sensitivity	Specificity
Lat. lying inactive	0.99	0.99	0.99	0.99	0.99	1.00*
	[0.98,0.99]	[0.98,0.99]	[0.98,0.99]	[0.98,0.99]	[0.98,0.99]	[1.00,1.00]
Stern. lying inactive	0.90	0.94	0.94	0.99	0.90	1.00*
	[0.88,0.92]	[0.93,0.95]	[0.92,0.95]	[0.98,0.99]	[0.88,0.92]	[1.00,1.00]
Lat. lying alert	0.96	0.98	0.98	0.99	0.96	1.00*
	[0.95,0.97]	[0.97,0.98]	[0.97,0.98]	[0.99,1.00]	[0.95,0.97]	[1.00,1.00]
Stern. lying alert	0.96	0.97	0.97	0.98	0.97	1.00*
	[0.96,0.97]	[0.97,0.97]	[0.97,0.98]	[0.98,0.98]	[0.96,0.97]	[1.00,1.00]
Sitting	0.91	0.95	0.95	1.00*	0.91	1.00*
	[0.89,0.92]	[0.94,0.95]	[0.94,0.95]	[0.99,1.00]	[0.89,0.92]	[1.00,1.00]
Standing	0.85	0.84	0.91	0.88	0.93	0.92
	[0.85,0.85]	[0.84,0.85]	[0.90,0.91]	[0.88,0.89]	[0.93,0.94]	[0.91,0.92]

Drinking	0.97	0.97	0.96	0.96	0.98	1.00*
	[0.96,0.99]	[0.95,0.98]	[0.95,0.98]	[0.94,0.98]	[0.96,0.99]	[1.00,1.00]
Lat. lying groom	0.97	0.97	0.97	0.97	0.97	1.00*
	[0.95,0.98]	[0.96,0.98]	[0.96,0.97]	[0.96,0.98]	[0.95,0.98]	[1.00,1.00]
Searching	0.91	0.90	0.91	0.90	0.92	0.99
	[0.91,0.91]	[0.90,0.90]	[0.91,0.91]	[0.90,0.91]	[0.92,0.93]	[0.99,0.99]
Walking	0.76	0.76	0.81	0.81	0.81	0.95
	[0.76,0.77]	[0.76,0.76]	[0.81,0.81]	[0.80,0.81]	[0.81,0.82]	[0.95,0.95]
Collar discomfort	0.75	0.85	0.83	1.00	0.75	1.00
	[0.70,0.80]	[0.82,0.88]	[0.79,0.87]	[1.00,1.00]	[0.70,0.80]	[1.00,1.00]
Trotting	0.46	0.57	0.57	0.72	0.47	0.99
	[0.44,0.48]	[0.55,0.59]	[0.55,0.59]	[0.70,0.75]	[0.45,0.49]	[0.99,0.99]
Playing	0.88	0.91	0.91	0.95	0.89	1.00*
	[0.88,0.89]	[0.91,0.92]	[0.91,0.92]	[0.94,0.96]	[0.88,0.89]	[1.00,1.00]
Running	0.62	0.66	0.67	0.73	0.62	0.99
	[0.59,0.64]	[0.65,0.68]	[0.65,0.69]	[0.72,0.74]	[0.60,0.65]	[0.99,0.99]

** Denotes values that scored 1.00 after rounding to two decimal places.*

A threshold of 0.3 produced the model with the optimal balance between sensitivity and specificity (*TSS* score), and unclassified data points (Fig A3.1). At this threshold, the overall number of incorrectly classified behaviours was very low, with higher classification errors occurring in the more active behaviours. Misclassifications produced by the model tended to confuse closely related behaviours; for example, 'trotting' most often misclassified as 'walking', and 'running' misclassified as 'trotting' (Table A3.4).

Post-hoc comparisons using Tukey's test indicated that the mean ODBA for each of our highly active behaviours was significantly greater than all behaviours except 'Collar discomfort'

(Table A3.5). When sorted by mean ODBA, all 14 behaviours grouped into their pre-assigned activity level, displaying a positive relationship between ODBA and animal activity (Fig 4.6).

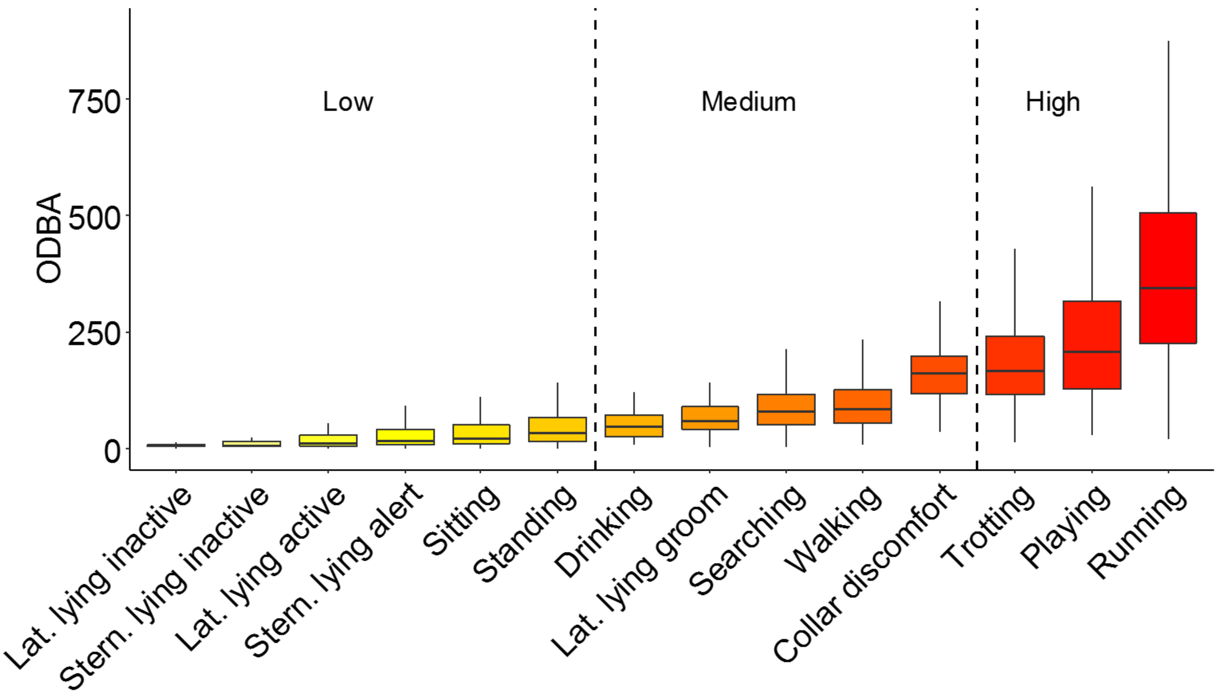

Figure 4.6. Overall dynamic body acceleration values for each behaviour, calculated from a running mean of four seconds and displayed in ascending order of mean ODBA. Lower and upper hinges correspond to the first and third quartiles, and the whiskers extend from the hinge to no more than 1.5 × IQR. Outliers were removed post hoc to better display the differences in the means. Low, Medium and High labels refer to the activity class assigned to the behaviours.

DISCUSSION

Accurate classification across a range of behaviours has been a great challenge for the majority of accelerometry studies. Our study is the first to use accelerometry to accurately classify a broad range of behaviours for an apex predator, at the very low sampling frequency of 1 Hz. Employing a comprehensive, yet strategic approach, to fitting and selecting our best model, allowed us to address a number of challenges associated with translating raw acceleration data into a meaningful and biologically relevant format.

As expected, the choice of predictor variables influenced classification accuracy. Several other studies provide evidence for the importance of predictor variable selection. For example, Alvarenga et al. (2016) achieved and overall model accuracy of ~85% (across five behaviours) when using 44 derived predictor variables whereas Martiskainen et al. (2009) used 28 relatively simple predictor variables and produced a mean accuracy across eight behaviours of ~94%. Although there was only a minor change in overall model accuracy between the larger predictor variable sets, the model's predictive ability for individual behaviours was influenced considerably by choice of predictor variables. Changes in acceleration across each axis depended largely on the type of movement and therefore, a single axis (or predictor variable) may better capture the acceleration signature of one behaviour over another. Graf et al. (2015) reported the heave (up and down) axis to be particularly important for classifying different behaviours in Eurasian beavers *Castor fiber*, while Alvarenga et al. (2016) found that in sheep (*Ovis aries*), the surge (back and forth) axis contributed most to the model. Given some predictor variables will be better suited to assist the classification model in distinguishing certain behaviours, *a priori* selection of predictor variables should be used, where decisions are driven by the behaviours of interest.

Acceleration during movement can change over very short time periods and is therefore commonly measured at infrasecond frequencies (between 8 - 100 Hz). Measuring acceleration at high frequencies increases computational effort for fitting classification models, limits the deployment period of accelerometers due to memory constraints, and may be unnecessary for behavioural classification in many instances. We are the first to show that a large number of distinct behaviours (14) can be classified using tri-axial accelerometer data derived from an unconventionally low sampling frequency of 1 Hz. There are few instances in the literature where an equally low sampling frequency was used, which is surprising given several studies report only minor decreases in classification accuracy when down-sampling, for example, from 64 Hz to 8 Hz (Wang et al., 2015), or 25 Hz to 10 Hz (Alvarenga et al., 2016). However, there is a lower limit to sampling frequency that can be used to classify certain behaviours. In our study, the classification accuracy for our most active behaviours was not high. Given the more active behaviours like running and playing are swift movements performed over short time periods, our sampling frequency may not have allowed enough of the acceleration signature to be captured in order to adequately train the model. This issue is highlighted in small species, owing to their tendency for rapid movements of short duration (Hammond et al., 2016). Hammond et al. (2016) attached accelerometers to chipmunks (bodyweight c. 50g) and found the lowest sampling frequency that resulted in negligible decreases in model accuracy to be 20 Hz. Our study provides evidence that a very low sampling frequency can be used to classify a range of behaviours with high accuracy, in a medium-sized animal.

In our study, the expectation that functionally similar behaviours would most often misclassify as each other was only realised for the highly active behaviours. This is best explained by high intra-behaviour variation and inter-behaviour overlap within the axes. If classifying high intensity behaviours with high accuracy is crucial, it may be necessary to increase the resolution of the acceleration signature by using a higher sampling frequency, but at a cost to deployment time. Our selected model performed extremely well (low misclassification rate) at classifying low intensity, functionally similar behaviours like different resting postures. In studies where misclassification is particularly undesirable, it is common to group behaviours into broader classes like ‘active’ and ‘inactive’, which has the benefit of increasing classification accuracy but at the cost of behavioural diversity (e.g. Shamoun-Baranes et al., 2012). We chose a model that would identify a range of highly active behaviours, despite relatively low classification accuracy. We then managed our misclassification errors (model sensitivity) by choosing a threshold that would balance the number of unclassified and misclassified samples whilst retaining high overall model accuracy. If we were to apply our selected model to accelerometer data from free ranging dingoes, we propose increasing the threshold from 0.3 to 0.5 for three reasons. Firstly, at 0.5 our overall model accuracy remains high at over 80%, secondly, our data will not be swamped by errors of omission and lastly, we are not overly concerned with a minor increase in misclassifications because the majority of behaviours will be misclassified to a functionally similar movement with comparable ODBA values. Overall, our methodological approach and resulting classification model is robust, and can readily be adapted to answer questions about different study systems.

Since Wilson et al. (2006) first presented evidence to suggest a positive correlation between ODBA and activity in cormorants, the use of accelerometry as a tool to remotely measure physiological traits like energy expenditure and energy-time budgets has exploded. We also found a positive relationship between animal activity level and ODBA. Highly active behaviours exhibited significantly higher mean ODBA values than all low and medium behaviours. However, our results suggest some caution should be taken when using ODBA as a proxy for energy expenditure. One of our highest ODBA scores came from the behaviour ‘collar discomfort’, which was typified by low overall body movement but acute movement of the accelerometer device due to quick side-to-side actions of the head. The result was ODBA values indistinguishable from ‘trotting’, an energetically demanding and ecologically important behaviour (Reilly et al., 2007). Energy and time budgets are of paramount importance for our understanding of how animals interact with their environment, especially for apex predators given their critical role in maintaining the structure of ecological communities (Fretwell, 1987). A recent study by Wang et al. (2015) used accelerometry to understand how an apex predator modulated their energy budget by examining foraging strategies (akin to ‘searching’ in our study), and in doing so they highlighted the potential benefits for conservation initiatives and human-wildlife conflict resolution. We extend the potential of future research by showing that classifying ecologically relevant behaviours whilst maintaining their aforementioned relationship with ODBA is possible even with acceleration data sampled at a very low frequency. The implication is that we can deploy accelerometers over much longer time periods to capture invaluable behavioural and physiological data across different life history stages of free-ranging animals.

Accelerometry is an exciting tool that is transforming the study of animal behaviour and physiology. The use of accelerometers to remotely classify behaviours of free-ranging animals has appreciable potential. However, prevailing methods limit our ability to establish meaningful ecological conclusions due to the challenge of classifying a diversity of behaviours over a significant period of time. Our approach addresses these constraints and has applicability to free-ranging terrestrial quadrupeds of comparable size. We propose that our approach using the Random Forest model can be directly applied to accelerometer data from other members of the family Canidae, given their shared body type and consistent style of locomotion (Flynn et al., 1988). Canids are a diverse lineage whose members are ecologically and economically important the world over, for example red wolves *Canis rufus* are threatened with extinction (Kelly et al., 2008), gray wolves *Canis lupus* are keystone predators (Estes et al., 2011), and red foxes *Vulpes vulpes* are invasive pests that cause millions of dollars of damage each year in Australia alone (McLeod, 2004). Through building a classification model that exhibits high predictive performance at low frequency and across a large number of ecologically relevant behaviours, we increase the accessibility of accelerometer-based behavioural research and support much needed integration with the fields of animal physiology and movement ecology.

Statement of Authorship

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Principal Author

Name of Principal Author (Candidate)	Jack Tatler		
Contribution to the Paper	Planned and developed the research, collected the data, developed the models and analysed the data, wrote the manuscript.		
Overall percentage (%)	80%		
Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.		
Signature		Date	18/03/2019

Co-Author Contributions

By signing the Statement of Authorship, each author certifies that:

x. the candidate's stated contribution to the publication is accurate (as detailed above);

xi. permission is granted for the candidate in include the publication in the thesis; and

xii. the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

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Contribution to the Paper	Planned and developed the research, contributed to the development of the modelling and statistical analysis, revised and edited the manuscript.		
Signature		Date	18/03/2019

Chapter 5. Extreme individual variation in resource selection of an apex predator

Jack Tatler, Phillip Cassey, Manuela Fischer, David Roshier, and Thomas A. A. Prowse

Appendix: Supplementary material accompanying this chapter can be found in Appendix 4 of this thesis.

ABSTRACT

Resource selection occurs when an animal uses a resource in excess of its availability in the landscape; reflecting the mechanistic link between animal behaviour and location in space. We investigated resource selection and movement ecology of the dingo *Canis dingo*. We obtained 150,798 GPS locations from 18 dingoes (13 female, 5 male) from April 2016 – May 2018. We fitted separate resource selection models for each dingo to capture individual variation in resource use, and used a meta-analytic approach to identify population-level responses. We found extreme individual variation in space use by dingoes that was significantly affected by season. At the population level, dingoes strongly selected watercourses and shelters, avoiding salt lakes. Given survival of canids in desert ecosystems necessitates access to food, refuge, and free water it was not surprising that dingoes preferred sand dunes (food sources), desert woodlands (refuges), and watercourses (free water). However, this was not sufficient to explain patterns of habitat-use through time, with behaviour/social dynamics also affecting how dingoes moved, e.g., females may have deliberately avoided males during the pup-rearing and whelping months by shifting their activity from a crepuscular to diurnal pattern. We highlighted the importance of individual-level resource selection modelling for an apex predator.

INTRODUCTION

Understanding and predicting animal movement and resource selection is complex because it is influenced by interactions between an individual's life history, behaviour, physiology, and habitat (Boyce et al., 2002). Wildlife management is increasingly reliant on resource selection studies because such studies identify areas or resources of importance, and can predict how a species will move to access those resources following changes in abundance or distribution due to seasonal changes, or disturbances such as fire, drought or climate change (e.g., Boyce and McDonald, 1999, Martin, 2001, Klop et al., 2007, Chetkiewicz and Boyce, 2009). In addition to the selection of physical resources, complex human-wildlife relationships such as avoidance of humans, increased mortality risk, and habitat fragmentation can be explored using resource selection functions (RSFs; Boyce and McDonald, 1999, Johnson et al., 2005, Sinclair and Byrom, 2006). Also, interactions between species can be inferred using RSFs, which have been particularly effective at demonstrating different predator-prey relationships; including risk avoidance, which is linked to energetic costs (Abrahams and Dill, 1989), trophic disruption (Schmitz, 1998), and modified habitat selection (Gilliam and Fraser, 1987).

The Australian continent has experienced widespread and rapid recent human-induced disturbance that has resulted in a globally-unrivalled rate of mammal extinctions (Woinarski et al., 2015). Habitat modification and introduced predators are often reported as the major causes for these extinctions and ongoing population declines (Woinarski et al., 2015). However, declines in the distribution and abundance of Australia's largest terrestrial predator – the dingo *Canis dingo* - has been suggested as another strong causal agent for the widespread ecosystem disruption (Johnson et al., 2007). Substantial human-wildlife conflict, which accompanied the spread of pastoralism in the 19th century, in conjunction with widespread hybridisation with domestic dogs *Canis familiaris*, has severely reduced the abundance and distribution of dingo populations (Fleming et al., 2001).

Dingoes, akin to other top predators, are difficult to study due to their cryptic nature, generally low population densities, and inter- and intra-individual behavioural variation. They are highly adaptive generalists that occupy sub-tropical islands, urban areas, alpine habitats, rainforest and arid deserts (Fleming et al., 2001). As a result, their diet (reviewed in Doherty et al., 2018 and Tatler et al., 2019), social organisation (Fleming et al., 2001), and breeding strategies (e.g., *Chapter 2*) are highly flexible. Dingoes are medium-sized eutherian carnivores with a high metabolic rate that need regular access to free water, drinking daily if possible (Allen, 2012). Despite this, more intact dingo populations persist in arid central Australia (Stephens et al., 2015), where extremes in climate drive temporal differences in their ecology (e.g., diet; *Chapter 3*). Only two studies have explored dingo habitat selection using GPS technology and they both present information from populations that were severely impacted by human landscape modification (Robley et al., 2010, Newsome et al., 2013b). In some landscapes, the habitats occupied by undisturbed dingo populations are also the habitats of remnant populations of critically endangered and threatened small to medium mammals. In these landscapes where dingoes maintain their natural behaviours there is a need to understand their movement patterns and resource selection.

Here, we investigated the movement ecology and resource selection of a population of dingoes in arid central Australia that are largely free from the impacts of anthropogenic disturbance, hybridisation with domestic dogs, habitat modification, and lethal control for livestock protection (see Tatler et al. 2019). Dingoes in arid Australia persist in a patchy, resource-limited landscape that is characterised by irregular rainfall and high temperatures. The first aim of this study was to quantify the selection for different resources (hereafter ‘landscape features’) by dingoes. We expected that individuals would prefer high-value resources such as watercourses and desert woodlands, and that their selection preferences would be influenced by reproductive season. Consequently, we expected that the majority of home range overlaps would also occur in these landscape features. We anticipated that dingoes would habitually return to discrete locations in their home range (e.g., dens or shelter sites), and that these locations would be situated in the sand dunes or on the flats (i.e., areas more secluded from conspecifics).

Dingoes are a highly mobile species that balance the need to traverse over large areas, to meet daily energetic requirements, with the maintenance of social ties and territorial boundaries. As a result, the decision to move is biologically important and likely to vary at fine (e.g., daily) and broad (e.g., seasonal) temporal scales, as well as spatially. Our second aim was to determine how the movement patterns of dingoes varied as a function of time (daily and seasonal) and space (landscape feature). Overall, we expected dingo movement to peak during twilight hours and although we did not expect to see an effect of sex on the pattern of movement, we predicted that males would move further than females. Finally, given the tendency for dingoes to use tracks as movement corridors (Fleming et al., 2001, Raiter et al., 2018), we expected they would show increased rates of movement when on a track relative to other landscape features.

METHODS

Study area and species

Our study was conducted at Kalamurina Sanctuary (hereafter ‘Kalamurina’), a 6,670 km^2 conservation area owned and managed by Australian Wildlife Conservancy, and located at the intersection of three of Australia’s central deserts: the Simpson, Tirari, and Sturt’s Stony Desert (27°48'S, 137°40'E; Fig. 5.1). Kalamurina adjoins protected areas to the north and south to create a 64,064 km^2 contiguous area that is managed for conservation. Neighbouring properties to the east and west operated as cattle stations during the study. It is located in the Simpson-Strzelecki Dunes Bioregion and the dominant landform is sand dunes (< 18 m), with scattered floodplains, claypans and salt lakes. The dune crests and flanks are dominated by sandhill canegrass *Zygochloa paradoxa* with an overstorey of scattered shrubs including species of *Acacia* and *Hakea.* The dune swales are characterised by chenopod shrubland where the main vegetation is species of *Acacia*, *Eremophila*, and *Atriplex*. Extensive coolabah *Eucalyptus coolabah* woodlands exist along the banks and floodplains of the larger watercourses.

The dingoes at Kalamurina exhibit high levels of dingo ancestry (*Chapter 2*), making this study the first known assessment of resource selection in a population of pure dingoes. Although space use by dingoes can be influenced by human-induced perturbation (e.g., anthropogenic resource subsidies; Newsome et al., 2013b), the population at Kalamurina is largely free from human impacts. Kalamurina has experienced only a brief history as a pastoral property and the original vegetation and landscape features are largely intact. The primary legacy of human-impacts is the presence of European rabbits *Oryctolagus cuniculus.* This introduced species comprises the bulk of dingo diets in this landscape, but they also consume reptiles, birds, invertebrates and vegetation depending on the time of year (*Chapter 3*).

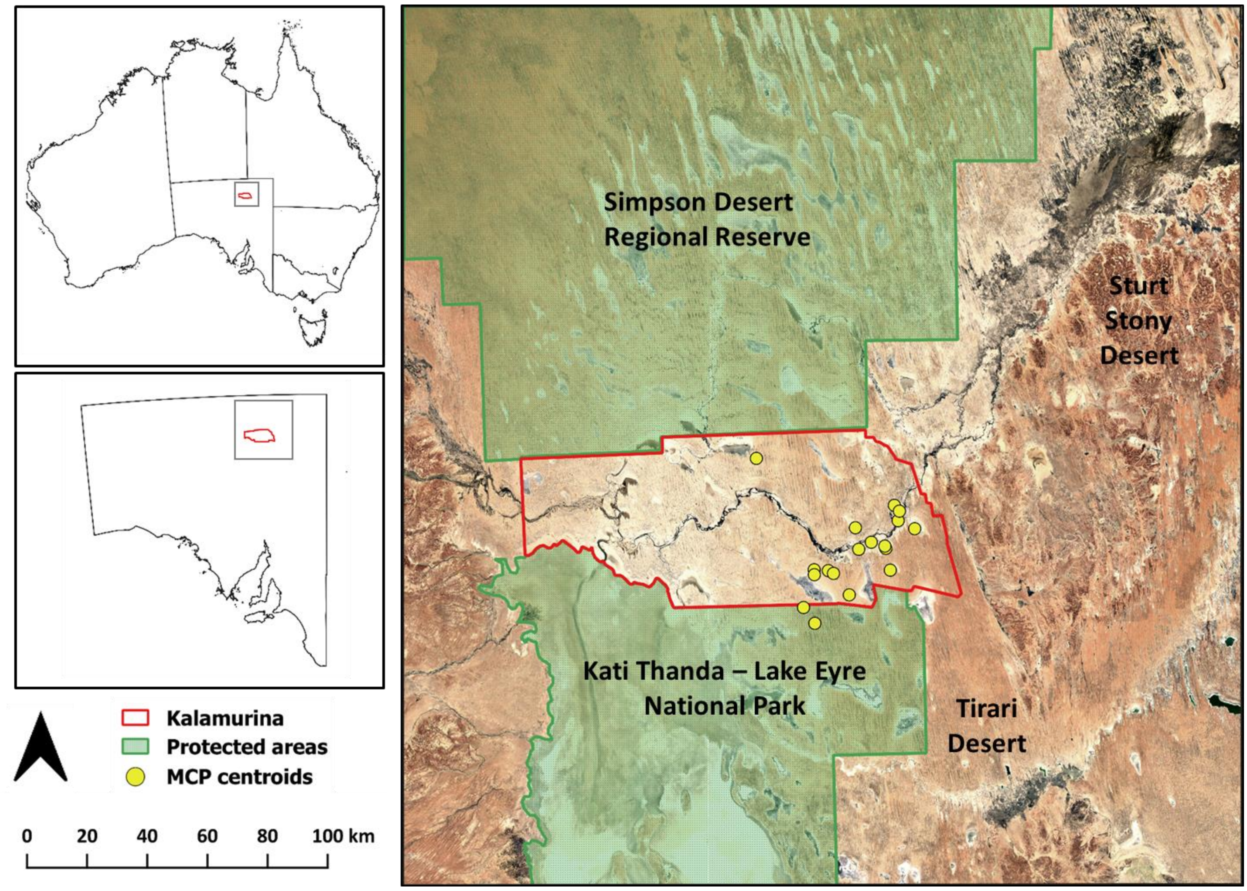

Figure 5.1. Location of MCP centroids for dingoes tracked in central Australia using satellite transmitters, from 2016 – 2018 (n = 18). The black box around Kalamurina represents the area from which 'available' locations were calculated for dingoes in this study. The boundary of Kalamurina is shown by the red line.

Data collection, cleaning and processing

From April 2016 to May 2018 we obtained location information for 18 individual dingoes, 13 females and five males. Dingoes were captured following the procedure described in *Chapter 2*. We used Telemetry Solutions Iridium-GPS collars that were set to record a location every 15 minutes on a duty cycle of two-days on, two-days off. To discount abnormal behaviour that might occur immediately following capture and collaring, we discarded the first 24 hours of location fixes. Location data were also discarded if they had a horizontal dilution of precision (HDOP) ≥ 9 (a measure of GPS accuracy) or occurred after the collar had dropped-off. In total we discarded

10,178 fixes (c. 6% of all fixes). All data manipulation and analyses were conducted in the R software environment for statistical and graphical computing (version 3.5.1; R Core Team, 2017).

Environmental covariates

Landscape covariates. We compiled spatial data on the major landscape features in the study area using vegetation data from NatureMaps (Department of Environment and Water; downloaded 27/03/2018), and the location of tracks and permanent water sources on Kalamurina (Australian Wildlife Conservancy; updated 27/03/2018). In total we classified seven landscape features; watercourses; desert woodland; low shrubland; tracks; salt lakes; sand dunes; and flats. Each landscape layer was rasterized to the same resolution (25 m) and extent (56366, 6798279; 339166, 7094179; UTM Zone 54S) using the R package 'raster' (Hijmans, 2017). Additional raster layers were generated from the landscape rasters by calculating the shortest distance from every cell to each landscape feature. Prior to statistical analysis, all such 'distance to landscape feature' variables were standardised (x – mean(x) / standard deviation(x)) and pairwise correlations (Pearson's *r*) were calculated. Distance to flats was removed from the analyses because it was highly correlated with distance to sand dunes ($r = 0.84$). All other pairwise correlations were low ($|r| < 0.7$).

Climatic covariates. We annotated environmental data (temperature, wind speed, precipitation, and NDVI) to each GPS location using the Env-DATA system on Movebank (Wikelski and Kays, 2018), which sourced the information from the European Centre for Medium-Range Weather Forecasts (Dee et al., 2011) and NASA Land Processes Distributed Active Archive Center (Didan, 2015).

Temporal covariates. Dingoes exhibit seasonal patterns of behaviour that are driven by their reproductive cycle (Thomson, 1992a). Therefore, we grouped our location data into four 'seasons'; non-breeding (Dec-Feb), breeding (Mar-May), whelping (Jun-Aug), and rearing (Sep-

Nov). We also determined the astronomical time of day for each GPS location (dawn, day, dusk, night) using the R package ‘maptools’ (Bivand and Lewin-Koh, 2018).

Home range calculation and overlap

Spatial data were curated and analysed using the R software environment for statistical and graphical computing in combination with QGIS version 3.4.0 (QGIS, 2018). We used dynamic Brownian Bridge Movement Models (dBBMM), implemented in the ‘move’ package (Kranstauber et al., 2018), to determine the 95% utilisation distribution (95% reduces bias from outlying data points, hereafter ‘home range’) for each dingo. Due to the gaps in our trajectories from the sampling regime, we calculated our dBBMMs by first subsampling the data into 15 minute ‘bursts’ (i.e., distances between fixes that were recorded more than 15 minutes apart were not used for fitting the dBBMM). This meant our home range estimates were not inflated by the relatively larger distances that result from fixes that were several hours apart. We used an estimated location error of 10 m and grid cell size of 25 m (larger than twice the location error to increase the probability of occurrence in each cell).

We determined the location in the landscape where dingo home ranges overlapped by calculating the number of home ranges that crossed each 25m^2 grid cell. The resulting raster recorded discrete cell values ranging from one to eight, where, for example, a score of one represented cells in the home range of a single dingo and eight represented cells within the home range of eight dingoes.

We assessed whether the degree of home range overlap was related to landscape feature by constructing a GLM with a Poisson distribution. We used the number of home range overlaps per cell (1-8) as our response variable (count) and included landscape feature as a fixed effect.

Identification and location of 'shelters'

Dingoes repeatedly use specific areas (hereafter referred to as 'shelters') for resting, rearing offspring, or socialising. The selection of these shelters in the landscape is not only biologically informative, but may be an important predictor of space use. We used the R package 'recurse' (Bracis et al., 2018) to identify shelters for each dingo by using a combination of (1) recursion to an area, and (2) the average amount of time spent in that area. Shelters were defined individually for each dingo by an average residence time per visit of ≥ 30 minutes and a rate of recursion in the 95th percentile of their total recursions (Table 5.1). We included shelters as a landscape feature and calculated a 'distance to shelters' variable for each location fix.

We assessed whether dingoes selectively positioned their shelter sites within their home range by using a binomial generalised linear mixed effect model (GLMM) in the R package 'lme4' (Bates et al., 2015). We used GPS fixes at shelters ('site presences') and GPS fixes not at shelter sites ('site absences') as our binary response variable. We fitted the interaction between landscape feature and season as a fixed effect and included a random effect of individual dingo (ID).

Movement analysis

To determine the daily movement patterns (i.e., whether dingoes at Kalamurina were nocturnal, diurnal or crepuscular), and how this varied throughout the year, we calculated movement distances between GPS fixes for each dingo, which we analysed using generalised additive models (GAMs) with the R package 'mgcv' (Wood, 2011). Although the success rate of fix attempts was high (> 99%), movement distances were only calculated between fixes that were c. 15 minutes apart (> 97% of all fixes) to ensure our distance measures were as accurate as our data allowed (R package 'adehabitatLT'; Calenge, 2006). Given the likely differences in movement behaviour of the sexes through the seasons, we modelled movement distance as a function of sex, season, the interaction between hour-of-day and sex, and the interaction between hour-of-day and season. Both interaction terms were fitted with a cyclic cubic regression spline and 20 knots. We also assessed whether the rate of movement was influenced by landscape feature by fitting a generalised linear model (GLM; Bates et al., 2015) with distance as the response variable and all possible interactions between habitat, sex, season, and hour-of-day.

Resource selection

We developed a resource selection function to compare the habitat used (GPS locations) by each dingo to what was theoretically available in the landscape (Manly et al., 1993). We sampled the available habitat using correlated random walks (CRW), which apply the step lengths and turning angles of the dingo's movement path to simulate random trajectories with a sampling frequency identical to that of the actual GPS data (Bovet and Benhamou, 1988). To ensure that CRWs lay within the available area of individual dingoes they were constrained within a buffer around the 100% minimum convex polygon (MCP) of the original data. Buffer zones were calculated as twice the square root of the 100% MCP, which created an area of available habitat that was appropriate for each dingo. All CRWs started at the same start location as the focal dingo's original GPS trajectory. Within each individual's unique area of available habitat we simulated 75 CRWs per trajectory using the R package 'adehabitatHR' (Calenge, 2006).

Resource selection analysis

Dingoes may exhibit different functional responses in resource selection. Mixed models with random slopes and intercepts may accommodate non-independence within groups (i.e., individual dingoes) but it is challenging to account for functional responses to different habitat types simultaneously. Therefore, we chose to analyse the resource selection of each dingo separately so that individual preferences in habitat selection could be clearly identified.

We used observed GPS locations (presences) and CRWs (pseudo-absences) as our binary response variable. Based on our aims and *a priori* assumptions of dingo resource selection, we built a candidate set of models (n = 20) and used Akaike's Information Criterion and R^2 as support for the model that performed best across all dingoes (Table A4.1). Our selected model included landscape feature (sand dunes, flats, watercourses, desert woodland, tracks, low shrubland, and salt lakes), shelters, season (non-breeding, breeding, whelping, and rearing), and the distance to six landscape features (watercourses, desert woodland, tracks, low shrubland, salt lakes, and shelters). One individual (JT07) had limited location data, and only for one month, so we removed it from our resource selection analyses.

To identify population-level habitat selection patterns, we performed a meta-analysis (using individual dingo resource selection models) to generate global parameter estimates across all individual dingoes, using a linear model performed on the estimates produced for each individual. For the meta-analysis, we weighted the estimates from the individual models by the inverse of each estimate's standard error, to account for variation in the number of locations we recorded per dingo.

RESULTS

We obtained 150,798 useable GPS locations from 18 dingoes (13 female, 5 male; Table 5.1) across the 26 month study period (April 2016 – May 2018). Data were collected for up to 358 days and, on average, yielded 8,378 successful fixes per individual. The CRWs yielded 11,460,648 locations from which we sampled the available habitat of dingoes in our study. For animals with more than 30 days of tracking data (estimated amount of time to reach all areas of their home-range; n=16), estimates of home range size varied from 14.2 km^2 to 100.0 km^2 (mean = 42.9 km^2).

Each home range overlapped with at least one other dingo, with some areas visited by eight individuals during the course of the study. We identified between 1 and 14 shelters for each dingo (mean = 4).

Table 5.1. Attributes of the 18 dingoes tracked at Kalamurina from 2016 – 2018. Dynamic Brownian Bridge Utilisation Distribution (dBBUD) were used to indicate the size of each dingo's home range (95%) and core area (50%). The maximum number of recursions to shelters are presented as well as the mean length of time (mins) each dingo spent at that shelter site during each visit.

Dingo ID	Sex	Weight (kg)	Age class	Collection period (duration in days)	Usable GPS fixes	dBBUD (km^2) 95%	50%	Shelter sites	Max. Recursions	Residence time (mins)
01	M	20.5	Adult	14 Apr - 9 Oct 16 (178)	5965	32.10	0.43	1	117	75
JT02	F	16.0	Adult	10 Apr - 10 Nov 16 (214)	8569	24.25	1.09	5	32	105
JT03	F	16.0	Older adult	17 Apr - 1 Aug 16 (106)	5093	25.96	0.44	5	20	122
JT04	F	16.0	Adult	10 Apr - 31 Aug 16 (143)	4047	17.91	0.20	14	18	269
JT05	F	16.5	Older adult	11 Apr 16 - 1 Jan 17 (265)	12135	26.60	0.50	3	60	78
JT06	F	18.0	Older adult	17 Apr - 16 May 16 (29)	1110	7.26	0.14	3	9	90
JT07	M	20.5	Older Adult	12 Apr - 28 Apr 16 (16)	466	1.77	0.04	1	18	65
JT08	M	25.0	Adult	15 Apr - 8 Jun 16 (54)	2271	14.16	0.32	1	12	47
JT09	F	16.0	Adult	11 Apr - 1 Dec 16 (234)	11030	22.57	0.27	2	127	101
JT31	F	14.0	Young adult	19 May 17 - 13 Feb 18 (270)	12211	39.33	1.87	5	36	89
JT32	F	23.5	Adult	20 May - 15 Dec 17 (209)	9626	26.23	0.33	1	181	140
JT33	F	20.5	Adult	23 May 17 - 26 Jan 18 (248)	11298	73.36	1.26	4	37	197
JT34	F	17.5	Older adult	19 May 17 - 30 Jan 18 (256)	11890	38.11	0.32	2	106	299
JT35	F	15.5	Older adult	19 May 17 - 30 Jan 18 (256)	11259	79.79	1.26	1	92	251
JT36	F	15.5	Adult	23 May 17 - 16 May 18 (358)	17420	67.36	1.88	1	60	448

JT37	M	17.0	Adult	19 May 17 - 07 Feb 18 (264)	12538	99.95	2.38	4	48	65
JT38	M	21.5	Older adult	23 May 17 - 03 Jan 18 (225)	10807	70.93	1.24	8	25	65
JT39	F	16.0	Older adult	23 May - 24 Jul 17 (62)	3066	27.85	0.07	4	6	78

Movement patterns

Mean (± se) daily distance moved by male dingoes (11.6 km ± 0.4 km) was significantly greater than that moved by females (9.9 km ± 0.2 km); *p* = 0.002). Dingoes showed marked differences in their daily movement patterns that was influenced by the hour-of-day, season, and sex, and revealed by our GAM analyses (Fig. 5.2). Males and females were active at different times of the day during the rearing and whelping season, though their daily pattern of movement during the breeding season was nearly identical. Regardless of season, the movement patterns of male dingoes indicated peaks during twilight hours, which was particularly pronounced during the non-breeding and breeding seasons (coinciding with the warmer months). Although females exhibited similar crepuscular behaviour during the first half of the year, their movement patterns during the whelping and rearing seasons showed they were most active during the day. Movement distance varied significantly between the sexes depending on what landscape feature they occupied, though both males and females moved the greatest distances when on tracks and salt lakes (Table A4.2). Similarly, both sexes moved least when residing at their shelter sites.

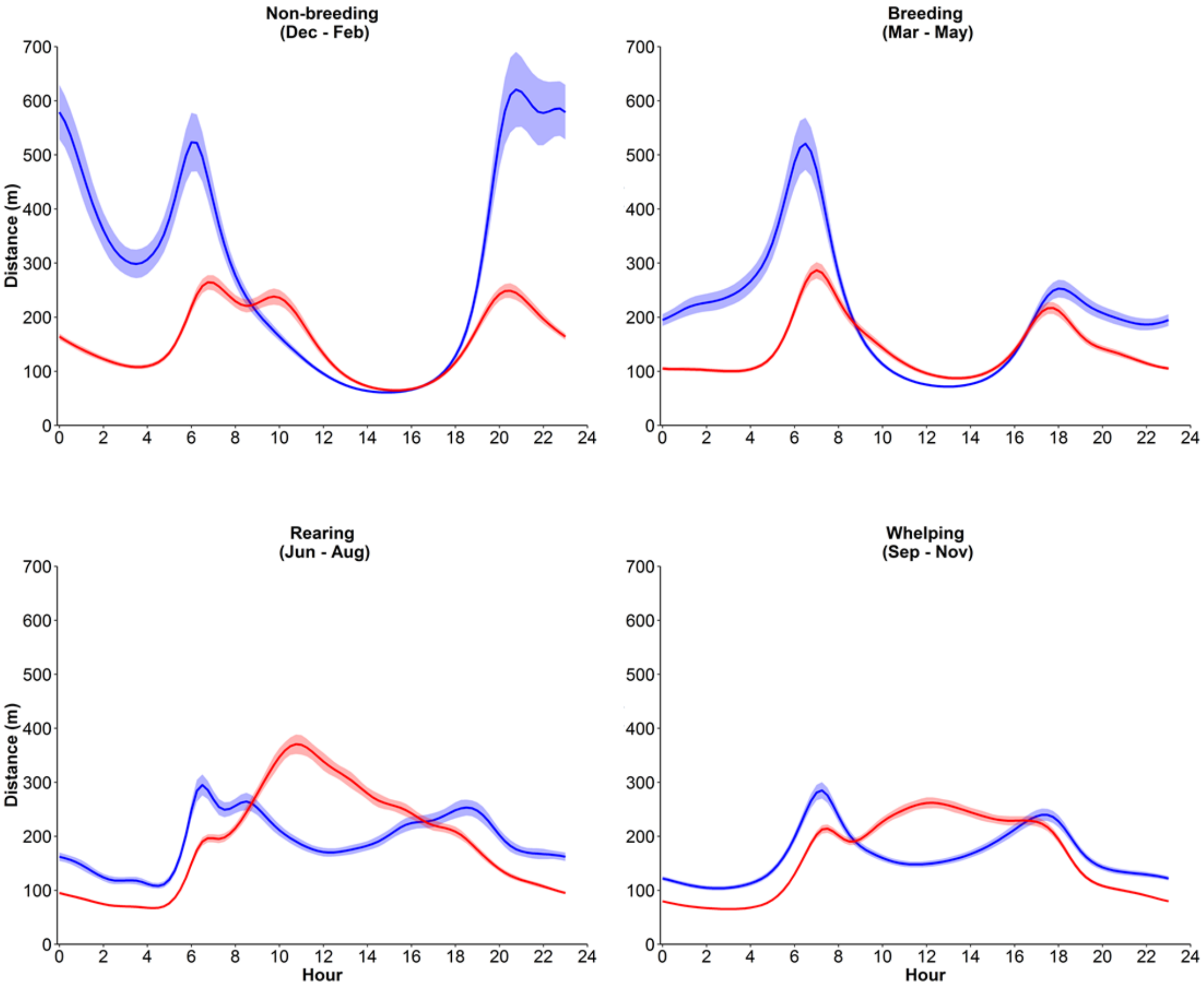

Figure 5.2. Estimated movement distances travelled by dingoes (per 15-minute location cycle) as a function of hour of day, split by season and sex. These results are derived from generalised additive models using GPS locations for 18 dingoes tracked between 2016 and 2018 at Kalamurina in central Australia. Red lines represent female dingoes and blue lines represent males, shading represents 95% confidence intervals.

Home ranges overlapped significantly more on tracks than any other landscape feature (Table 5.3). Conversely, we found dingoes were least likely to co-occur in the sand dunes. Season had a significant effect on the likelihood of home ranges overlapping, with most overlap occurring during the breeding season and the least during the pup-rearing season. Dingoes preferred to locate their shelters along watercourses and in the desert woodlands (Table 5.4). Shelters were least likely to be located on salt lakes and although dingoes may have socialised and traversed along tracks (based on their movement patterns), they were not used as shelters. On average, shelters made up less than 0.01% of each dingo's home range area.

Table 5.3. Model summary showing the locations in the landscape where dingo home ranges were more or less likely to overlap, as well as the effect of season on the amount of home range overlap, relative to desert woodlands and whelping. Model estimates, standard errors (SE) and p-values for our generalised linear mixed model are presented.

Model	Variables	Estimate	SE	*p*-value
Landscape features	(Intercept)	0.5568	0.0078	< 0.0001
	Salt lakes	0.1656	0.0261	< 0.0001
	Sand dunes	-0.0559	0.0083	< 0.0001
	Flats	-0.0260	0.0079	0.001
	Low shrubland	-0.0162	0.0114	0.1556
	Tracks	0.3497	0.0149	< 0.0001
	Watercourses	0.2101	0.0093	< 0.0001
Season	Breeding	0.0704	0.0055	< 0.0001
	Non-breeding	0.0201	0.0060	0.0007
	Rearing	-0.0604	0.0048	< 0.0001

Table 5.4. Model summary showing the preference for dingo shelters occurring in each landscape feature relative to desert woodlands. Model estimates, standard errors (SE) and p-values for our generalised linear mixed model are presented.

Model	Variables	Estimate	SE	*p*-value
Landscape features	(Intercept)	-1.9619	0.1081	< 0.0001
	Salt lakes	-21.0577	0.7725	< 0.0001
	Sand dunes	-0.9325	0.0369	< 0.0001
	Flats	-0.3454	0.0320	< 0.0001
	Low shrubland	-0.9533	0.0561	< 0.0001
	Tracks	-3.6932	0.1707	< 0.0001
	Watercourses	0.6893	0.0341	< 0.0001

Resource selection for individual dingoes

There was substantial variation in habitat selection between individual dingoes (Fig. 5.3). For example, two females (JT35 and JT36) occupied adjacent and overlapping home ranges but preferred different habitats. Dingo JT35 showed strong selection for desert woodlands and low shrubland, whereas JT36 avoided these areas. Only one dingo (JT04, female) significantly avoided watercourses, preferring desert woodlands and sand dunes. Although close in space, there was little home range overlap between the male dingoes and they showed different preferences for certain landscape features (sand dunes, desert woodland, tracks, watercourses), relative to the nearest (adjacent) male dingo. Dingoes also showed considerable inter-individual variation in their selection for different habitats depending on the season, though there was no discernible pattern (e.g., sex differences; Fig. A4.1). There was large variation between each dingo’s response to their proximity to water.

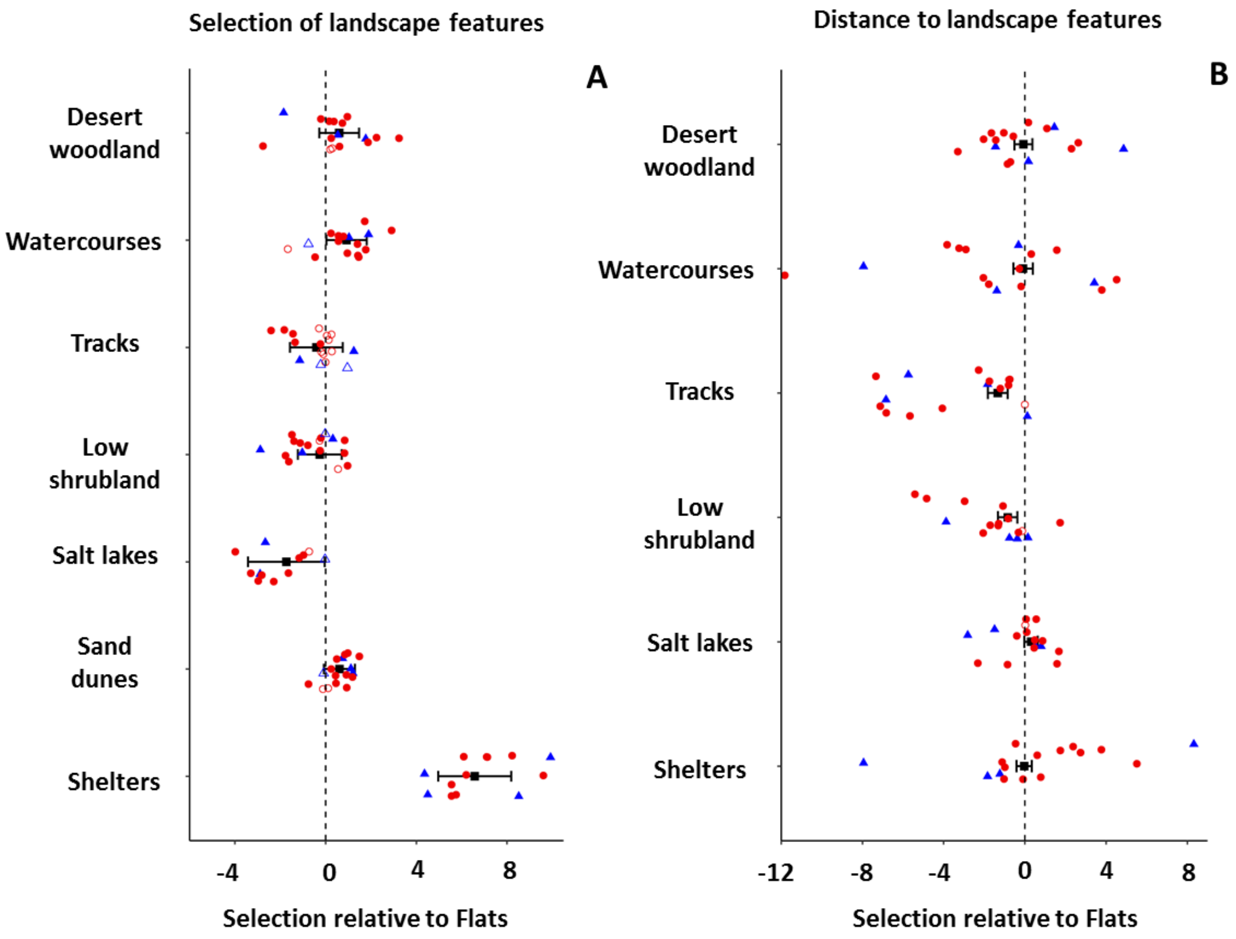

Figure 5.3. Estimates from our individual resource selection models showing (A) selection of landscape features and (B) effect of increasing distance from landscape features on the probability of occurrence, relative to flats. Circles (red) represent females (n= 13) and triangles (blue) represent males (n = 4); filled symbols indicate significance (p-value < 0.05). Squares (black) represent the estimates (± 95% CI) from our population level model that tested for common resource selection across all dingoes. In (A), negative estimates indicate selection against a given landscape feature whereas positive estimates indicate selection for a given landscape feature. In (B), negative estimates indicate the dingo was less likely to occur with increasing distance from the landscape feature, and a positive estimate indicates the dingo was more likely to occur at greater distances from the landscape feature. Outlying, non-significant effects were removed before plotting.

Meta-analysis of individual-level resource selection models

At the population level, dingoes strongly preferred shelters and watercourses over other landscape features. They also used sand dunes and desert woodlands more than they were available, although this was not significant, and avoided salt lakes (Fig. 5.3A). Season had little effect on selection for different landscape features although females tended to avoid watercourse and desert woodlands during the pup whelping season (Fig. A4.1). Distance to certain landscape features was a strong predictor for dingo occurrence, with dingoes preferring to stay closer to tracks and low shrubland and further from salt lakes (Fig 5.3B). There was no population level effect of the distance to desert woodland, watercourses, and shelter sites.

DISCUSSION

We found substantial individual variation in resource selection within and between dingoes in an undisturbed, intact population in arid central Australia. For many species, survival in the resource limited deserts of central Australia necessitates access to food and free water, and shelter from solar radiation (Letnic and Dickman, 2010, Rymer et al., 2016, Pavey et al., 2017). At our study site, the three most preferred landscape features used by dingoes were watercourses (free water), desert woodlands (which offer a reprieve from harsh climatic conditions), and sand dunes (provision of prey sources). Since the spread of pastoralism in Australia, artificial water points are common throughout the arid zone, serving as anthropogenic resource subsidies that sustain or inflate populations of native and introduced species (Fleming et al., 2001). Free water at our study site was limited to irregular local rainfall and downstream river flows although there is one artificial water point (on Kalamurina) and it exists adjacent to the major watercourse. One male’s home range was located almost entirely in the sand dunes with seemingly no access to free water, suggesting sporadic and short duration traverses to the major watercourse or an unknown natural source of water in the dunes. In a landscape dominated by exposed sand dunes and swales (flats), desert woodlands not only offer considerable protection from the elements but they are often associated with watercourses and paleo-drainage lines, making this landscape feature a valuable refuge for many arid zone species (Morton et al., 2011). A preference for sand dunes may be driven by the presence of European rabbits in this habitat (Myers, 1965), which are the primary food source for dingoes in arid Australia (Tatler et al. 2019). Also, at an elevation of c. 15 m, sand dunes are often the highest point in the landscape and may offer a superior vantage point for sighting conspecifics and detecting prey.

Although dingoes used watercourses and desert woodlands more than was expected from their availability, not all preferred to remain in close proximity. The resource dispersion hypothesis states that the social and spatial arrangement of a population is driven by resource availability, which in turn affects territoriality and avoidance behaviours (Macdonald, 1983). Newsome et al. (2013a) showed that the dispersion of resources in the Tanami Desert exerted strong effects on the home range size and location, activity patterns, and group size of a population of dingoes. The location of home-ranges for some dingoes in our study support the conceptual model of territoriality presented in Newsome et al. (2013a), where a resource is shared by multiple individuals though it forms the core territory of only one individual. At our study site, dingoes primarily consumed medium-sized species (between 0.1 and 1.6 kg; Tatler et al. 2019) so their social organisation is unlikely to be driven by the need for cooperative hunting; however, these dingoes likely need to defend other important (and limited) resources such as water and dense vegetative refuges. Dingoes are territorial and exhibit aggression towards unfamiliar conspecifics, which is likely to have a strong effect on how these limited, but preferred, resources were shared (Thomson, 1992c, Robley et al., 2010, Newsome et al., 2013a). Dominant individuals will maintain territories that overlap valuable resources (e.g., watercourses and desert woodlands) and although subordinate individuals may require regular access to these areas (e.g., access to water), they avoid potentially fatal confrontations by reducing the time spent in the vicinity of these resources.

Numerous behavioural and ecological factors affect the movement patterns of animals including the acquisition of food, ambient temperature, and predation risk (Nathan et al., 2008). Mammalian predators often exhibit nocturnal- or crepuscular-dominated movement patterns that reflect the activity times of their prey (Monterroso et al., 2013). Dingoes are generally considered to be crepuscular or nocturnal, particularly in the arid zone (Thomson, 1992a, Fleming et al., 2001). We found clear crepuscular activity patterns for both sexes during the non-breeding and breeding seasons, which coincided with the warmer months. Movement at higher ambient temperatures is more energetically costly and increases water loss (Fuller et al., 2014), therefore dingoes are likely to reduce their movement during the hottest part of the day as a behavioural adaptation to arid conditions. Females shifted to a primarily diurnal pattern during the pup whelping and rearing seasons, resulting in opposing activity schedules between the sexes. This behavioural change in female dingoes suggests they may avoid male conspecifics whilst pregnant or lactating, despite the physiological stressors associated with diurnal activity in the arid zone.

Roads or vehicle tracks can act as movement pathways for wild animals and are widely used by predators to increase landscape permeability, or improve hunting and travel (Avgar et al., 2013, DeGregorio et al., 2014, Doherty et al., 2015b). The dingoes in our study revealed increased rates of movement when on tracks, which is consistent with directional traversing behaviour (e.g., travel routes). Raiter et al. (2018) also found dingo activity was strongly biased towards tracks, and that even unmaintained tracks concentrated predator activity. Like other predators, dingoes mark their territory by depositing visual and olfactory cues (e.g., faeces and urine) in conspicuous places to maximise their detection by conspecifics. At Kalamurina, tracks are distinct landscape features used for travel and therefore may be used to demarcate territorial boundaries and convey messages to other pack members. At the population level, dingoes did not use tracks preferentially to other landscape features however, they were more likely to occur closer to tracks. The largely open and flat landscape at Kalamurina may support more off-track movements than populations in densely vegetated areas, or some individuals (e.g., subordinate, young, or loners) may limit their time on tracks to avoid conflict with resident dingoes. There is evidence that species that use olfactory communication trade off the social benefits of receiving cues with the perceived risk of predation (Hughes et al., 2009). However, the majority of tracks were located close to watercourses and woodland habitat, which are preferred by dingoes and thus may have inflated the strength of the estimated relationship between dingo occurrence and distance to tracks in our study.

Many mammals use discrete areas in their home range for sleeping or resting (Kushata et al., 2018), food caches (Juhasz et al., 2018), socialising (Anderson, 1998), and denning (Kowalczyk et al., 2004). Proximity of these shelter sites to favourable resources can have important fitness consequences for individuals or group living mammals through decreased predation risk and reduced energetic costs associated with distance to food and water (Jackson et al., 2014). We found dingoes preferred to locate their shelters along watercourses and in desert woodlands, which offers easy access to resources that are crucial for survival in arid Australia. Dingo shelters were rarely, if ever, located in salt lakes and tracks, which were two landscape features where dingoes were likely to come into contact with conspecifics. Shelters are essential for the survival and reproduction, and although their area (km^2) was miniscule relative to each dingo’s home range, they explained a large amount of variance in dingo resource selection. However, shelters are not regularly incorporated into resource selection studies and thus a major factor driving how animals use their environment may have previously gone unnoticed.

CONCLUSIONS

Our findings largely support previous research on the habitat selection and movement patterns of dingoes. However, we discovered marked variation in resource selection between individuals within the same population and during the same study period. We also found that female dingoes alter their daily movement patterns from crepuscular to diurnal during the cooler months when they are likely to have dependant offspring. Moreover, we foreground the importance of incorporating high-use areas (i.e., shelters) in resource selection studies given they explain much of the mechanistic link between an animal’s behaviour and its location in space.

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Principal Author

Name of Principal Author (Candidate)	Jack Tatler		
Contribution to the Paper	Planned and developed the research, collected the data, developed the models and analysed the data, wrote the manuscript.		
Overall percentage (%)	75%		
Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.		
Signature		Date	18/03/2019

Co-Author Contributions

By signing the Statement of Authorship, each author certifies that:

xiii. the candidate's stated contribution to the publication is accurate (as detailed above);

xiv. permission is granted for the candidate in include the publication in the thesis; and

xv. the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

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Chapter 6. Accelerometer informed time-energy budgets reveal the importance of temperature to the activity of a wild, arid zone canid

Jack Tatler, Shannon E. Currie, Phillip Cassey, Anne K. Scharf, David A. Roshier, and Thomas A. A. Prowse

Appendix: Supplementary material accompanying this chapter can be found in Appendix 5 of this thesis.

ABSTRACT

Movement is the major contributor to energy expenditure in most vertebrates and it is regularly characterised by body acceleration that can be captured by animal-attached accelerometers (ACC). Overall dynamic body acceleration (ODBA) is a metric derived from ACC data, which can be used as a proxy for energy expenditure over fine time scales. Here, we used ACC and GPS data collected from free-ranging dingoes in central Australia to investigate their activity-specific energetics, and activity patterns through time and space. We classified dingo activity into stationary, walking, and running behaviours, and estimated daily energy expenditure via activity-specific time-energy budgets. We tested whether dingoes behaviourally thermoregulate by modelling ODBA as a function of ambient temperature during the day and night. We used traditional distance measurements (GPS) as well as fine-scale activity (ODBA) data to assess their daily movement patterns. We retrieved ACC and GPS data from seven dingoes. Their mass-specific daily energy expenditure was significantly lower in summer (288 kJ kg^{-1} day^{-1}) than winter (495 kJ kg^{-1} day^{-1}; $p = 0.03$). Overall, dingoes were much less active during summer when 91% of their day was spent stationary in contrast to just 46% during winter. There was a sharp decrease in ODBA with increasing ambient temperature (T_a) during the day ($R^2 = 0.59$), whereas ODBA increased with increasing T_a at night ($R^2 = 0.39$). Distance and ODBA were positively correlated ($R = 0.65$) and produced similar crepuscular patterns of activity. Our results indicated solar radiation and ambient temperature drove the location and behaviour of dingoes. Seasonal differences of DEE in free-ranging eutherian mammals have been reported in several species, although this was the first time it has been observed in a wild canid. The negative relationship between dingo activity (ODBA) and T_a during the day implies that high heat gain from solar radiation is a factor limiting diurnal dingo activity in an arid environment.

INTRODUCTION

In order to improve individual fitness, an animal must maximise its acquisition of required resources whilst minimising exposure to unfavourable conditions (Leake, 1961, Southwood, 1977, Stephens et al., 2007). Driving these decisions is the need to balance energy acquisition and expenditure, which ultimately dictates an animal's behaviour and location in the landscape (Harding et al., 2005, Nathan et al., 2008, Wilson et al., 2012). Given that animals tend not to position themselves randomly (e.g., Wolf et al., 2005, Nathan et al., 2008, Revilla and Wiegand, 2008, Wilson, 2010), non-random movements and use of space provides insight into the ecophysiology and ecology of mobile taxa. How wild animals balance their energetics through time and space is increasingly being studied by integrating movement data with activity-specific time-energy budgets (Halsey et al., 2011).

Movement is the primary contributor to energy expenditure in most vertebrates (e.g., Schmidt-Nielsen, 1972, Tatner, 1986, Karasov, 2015). Animals move for various reasons (e.g., foraging, predator avoidance, to find mates) and variation in the landscape such as substrate, vegetation type, and elevation is responsible for varying movement costs (Rubenson et al., 2006, Wall et al., 2006). The relationship between an individual's energy expenditure and its use of space can be described as its energetic landscape, i.e., an environmentally dependent reflection of the cost of movement that may vary in space and time (Wilson et al., 2012).

Animal movement can be reliably captured by animal-attached accelerometers (ACC). These are lightweight devices that measure changes in acceleration in up to three axes (Gleiss et al., 2011). Ecologists and physiologists now regularly use ACC to capture fine-scale measurements of animal movement that can then be translated into distinct behaviours (e.g., lying, walking, running; Tatler et al., 2018). As energy expenditure is a function of activity, these behaviours can then be linked to activity specific measures of energy expenditure to produce robust time-energy budgets in free-ranging animals. Time-energy budgets, the categorisation of energy cost per activity integrated over the time spent performing that activity, can provide a reliable measure of daily energy expenditure but have proved difficult to apply to free-ranging animals where continuous monitoring of activity is often unavailable. The most commonly used measure of field energy expenditure for large vertebrates, doubly labelled water (DLW), only provides a broad measure of overall energy expenditure over the period of study. Doubly labelled water measures the turnover of oxygen (^{18}O) and hydrogen (^{2}H) isotopes injected into the body water pool as a direct proxy for metabolic rate via CO_2 production and water loss. Yet DLW is an expensive and invasive method requiring blood sampling and animal recapture, which is especially challenging for agile or cryptic species like eutherian carnivores. Overall dynamic body acceleration (ODBA), a metric derived from tri-axial accelerometer data, has proved to be a useful proxy for energy expenditure over fine time scales in a number of species (e.g., cormorants; Wilson et al., 2006, and chickens, geese, skunks, penguins; Halsey et al., 2009b). It is based on the idea that dynamic acceleration (tri-axial acceleration with the gravitational component removed) is a function of an animal's movement and thus is proportional to the amount of energy consumed during muscular contraction (Wilson et al., 2006, Gleiss et al., 2011).

Although ACC-derived estimates of energy expenditure require captive calibration studies correlating respirometric calculations of O_2 consumption ($\dot{V}O_2$) and/or CO_2 production ($\dot{V}CO_2$) to ODBA measurements during different activities, it generates a more comprehensive set of measurements whilst imposing less disturbance to wild animals than the DLW method. The relationship between ODBA and energy expenditure is well supported for terrestrial animals (Halsey et al., 2009b), although incorporating activity-specific energy budgets through time can greatly improve the accuracy of ODBA as a predictor of daily energy expenditure (Jeanniard-du-Dot et al., 2017). Free-ranging animals perform a variety of activities that incur different energetic costs. Although animal activity is readily measured in controlled settings (i.e., captivity), the same degree of precision could not be obtained from wild animals until recently, due to a lack of resolution in their daily behaviours. Accelerometry now enables accurate estimates of animal activity in the wild without direct observation, and thus activity-specific time-energy budgets can now be calculated for free-ranging individuals.

Most medium and large carnivores are highly interactive across trophic levels, and whose presence in the landscape propagates changes through ecosystems (Ritchie and Johnson, 2009, Estes et al., 2011). Quantifying the behaviour and resulting energy demands of free-ranging carnivores is therefore essential for predicting their resource requirements and subsequent selection of patchily distributed resources across the landscape. Australia's largest terrestrial predator, the dingo *Canis dingo*, is a medium-sized eutherian carnivore that persists across a wide range of environments (Fleming et al., 2001). Dingoes have been shown to acclimate physiologically to both extreme heat and cold by shifting or extending their thermoneutral zone (TNZ) and altering thermal conductance, effectively minimizing their basal metabolic rate (BMR) and energy expenditure (Shield 1972). For populations in the harsh, resource-limited deserts of central Australia, survival depends on making daily choices that minimise behavioural energetic expenditure (and evaporative water loss) whilst optimising the acquisition of beneficial resources (e.g., food, shelter, water).

Measuring energetic costs for free-ranging and highly active predators like dingoes is challenging and, to date, we have a limited understanding of how physiological capacities and environmental variables affect their movement and use of space. Here, we used ACC and GPS data collected from free-ranging dingoes in central Australia to investigate their behaviour-specific energetics and activity patterns through time and space. We classified broad classes of behaviour from ACC data and used it to estimate daily energy expenditure via activity-specific time-energy budgets. We explored the dingo's ability to behaviourally thermoregulate at different times of the day and year and examined daily patterns in activity. Finally, we constructed an energetic landscape to investigate how dingoes partition their energy in relation to landscape features.

METHODS

Study area and species

Our study took place from April 2016 to May 2018 at Kalamurina Wildlife Sanctuary (hereafter ‘Kalamurina’), a 6,670 km^2 conservation area owned and managed by Australian Wildlife Conservancy, and located at the intersection of three of Australia’s central deserts: the Simpson, Tirari, and Sturt’s Stony Desert (27°48'S, 137°40'E, UTM Zone 54S; Fig. 1). The site adjoins protected areas to the north and south to create a 64,064 km^2 contiguous area that is managed for conservation.

The dingoes at Kalamurina possess high levels of dingo ancestry (*Chapter 2*), making this study the first assessment of energetics in a wild population of pure dingoes. European rabbits *Oryctolagus cuniculus*, c. 1.6 kg comprise the bulk of their diet, but they also consume reptiles, birds, invertebrates and vegetation (*Chapter 3*).

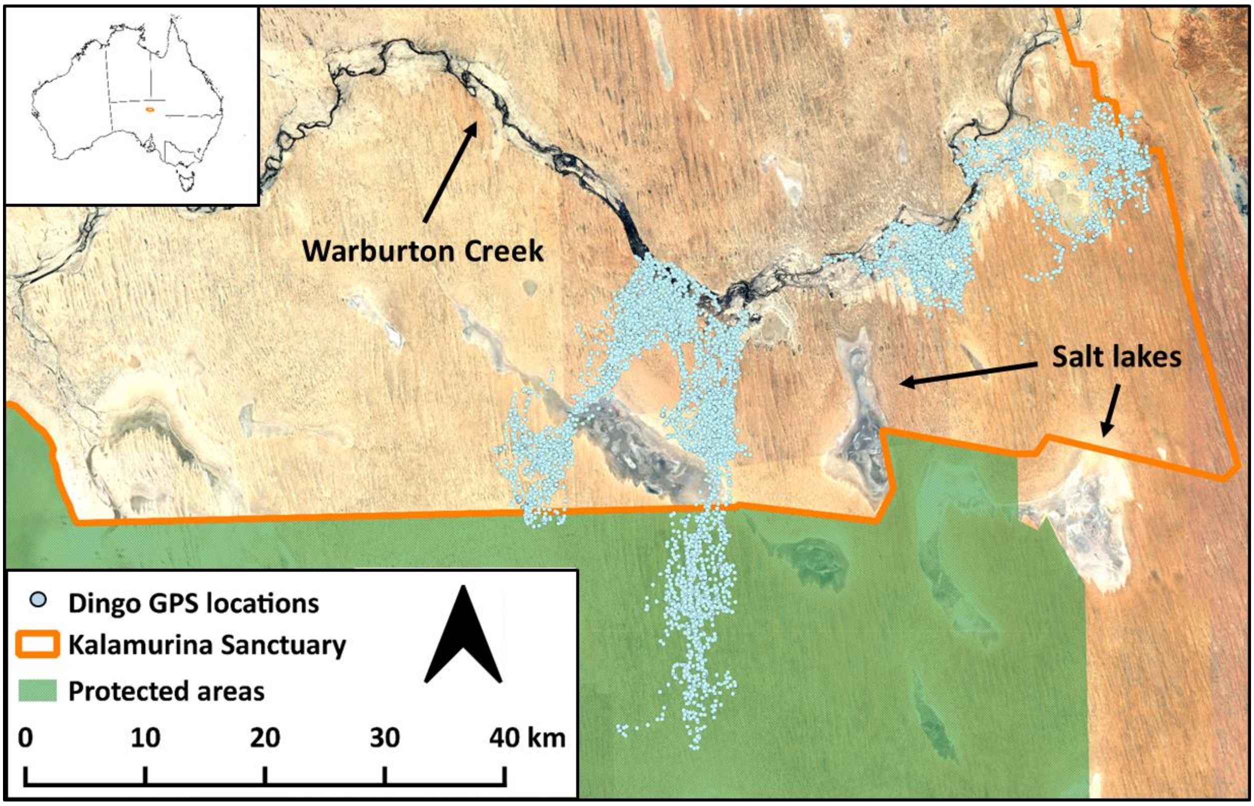

Figure 6.1. Tracking data from seven dingoes at Kalamurina Sanctuary. Inset displays the location of Kalamurina in central Australia. The Warburton Creek is the only major watercourse on the eastern side of the study site, and it is bordered by shrubland and desert woodland along its length. The majority of Kalamurina consists of sand dunes and flats.

Data collection, cleaning, and processing

We fitted 19 dingoes with ACC-GPS collars (Telemetry Solutions, Concord, CA, USA) that were equipped with tri-axial accelerometers (LISD2H, ST Microelectronics, USA) programmed to sample changes in acceleration at 1 Hz (one sample per second) and orientated so that the x, y and z-axes recorded acceleration along the sway, heave, and surge planes, respectively. To increase the temporal window of data collection, accelerometers were scheduled to record on a one-day on, three-days off sampling regime. We programmed the GPS to record a location every 15 minutes on the days the ACC was active. We were able to retrieve ACC and GPS data from seven dingoes (Table 6.1). Three individuals were tracked during Austral winter (April – August) and four during summer (October – January).

Table 6.1. Attributes of the seven dingoes equipped with ACC-GPS collars at Kalamurina Wildlife Sanctuary, including the number of shelters, the mean (± se) daily distance travelled (km d^{-1}) and daily energy expenditure (kJ kg^{-1} d^{-1}).

ID	Sex	Weight (kg)	ACC collection period (days)	Total ACC fixes	Shelters	Daily energy expenditure	Distance travelled
JT04	F	16.0	12 Apr – 7 Aug 16 (44)	2,737,402	10	521 ± 1	6.9 ± 0.7
JT05	F	16.5	16 Apr – 3 Aug 16 (63)	2,652,399	3	611 ± 1	10.7 ± 0.6
JT07	M	20.5	12 Apr – 27 Apr 16 (4)	427,560	1	353 ± 1	3.9 ± 1.4
JT32	F	23.5	28 Oct – 11 Dec (25)	1,067,736	2	226 ± 3	11.2 ± 1.0
JT34	F	17.5	28 Oct – 24 Jan (46)	2,040,072	4	278 ± 4	9.1 ± 0.6
JT36	F	15.5	28 Oct – 24 Jan (64)	2,720,096	1	337 ± 4	12.8 ± 0.9
JT37	M	17.0	28 Oct – 24 Jan (46)	2,257,778	4	311 ± 4	15.5 ± 1.2

To limit the effect of abnormal behaviour that might occur as a result of capture and collaring, we discarded any GPS and ACC data recorded during the 24 hours immediately following release. Data were also discarded if they had a horizontal dilution of precision ≥ 9 (a measure of GPS accuracy) or occurred after the collar had dropped-off. All data manipulation and analyses were conducted in the R software environment for statistical and graphical computing (version 3.5.1; R Core Team, 2017).

Dingo behaviour, ODBA, and energetic expenditure

We classified wild dingo behaviours from the ACC data using the Random Forest model described in Tatler et al. (2018). This model was found to accurately classify 14 dingo behaviours using 1 Hz ACC data. However, for the purposes of this chapter, we were only interested in general movement patterns that would influence daily energy expenditure. Therefore, we trained a new Random Forest model (with the same set of parameters as Tatler et al. 2018) to identify five classes of movement: lying down, sitting, standing, walking, and running (Table 6.2). Initially, we combined all stationary behaviours (lying down, sitting, and standing) but the acceleration signatures of sitting and standing were too different and resulted in a combined classification accuracy that was lower than if they were classified separately. Grouping the higher intensity behaviours improved the accuracy at which our model classified more energetically costly movements such as walking, trotting, and running (Table 6.1). Following the classification of our five grouped behaviours to our wild dingo ACC data, WE pooled Lying, Standing, and Sitting into 'Stationary' due to 1) low sample size of Standing and Sitting behaviours, and 2) similar energetic costs.

Table 6.2. Performance of the Random Forest model from Tatler et al. (2018) at predicting 14 different behaviours versus grouped behaviours. We combined similar behaviours to create three broad movement classes. The True Skill Statistic was used as our measure of classification accuracy, and the 95% confidence intervals are presented in square brackets next to each metric.

Behaviours	Classification accuracy	Grouped behaviours	Classification accuracy	
Lying inactive (laterally)	0.99 [0.98,0.99]	Lying	0.97 [0.97, 0.98]	Stationary
Lying inactive (sternally)	0.90 [0.88,0.92]			
Lying alert (laterally)	0.96 [0.95,0.97]			
Lying alert (sternally)	0.96 [0.96,0.97]			
Grooming (lying down)	0.91 [0.89,0.92]			
Drinking	0.85 [0.85,0.85]			
Standing	0.97 [0.95,0.98]			
Sitting	0.91 [0.91,0.91]			
Searching	0.76 [0.76,0.77]	Walking	0.81 [0.80, 0.81]	
Walking	0.75 [0.70,0.80]			
Trotting	0.46 [0.44,0.48]			
Playing	0.88 [0.88,0.89]	Running	0.76 [0.75, 0.77]	
Running	0.62 [0.59,0.64]			

The total acceleration recorded by accelerometers is the result of both static (gravitational) and dynamic (animal movement) components. Overall dynamic body acceleration uses the dynamic component and thus acceleration due to gravity must be removed. We calculated dynamic body acceleration (DBA) by subtracting a running mean (five seconds) from each acceleration axis (x, y, and z) to give acceleration values occurring from movement. The absolute value of DBA for each axis was then summed to give a per-second value of ODBA.

Time-energy budgets have been shown to be an effective estimate of DEE when compared to DLW in previous trials (Weathers et al., 1984) and more recently VeDBA (akin to

ODBA) was shown to accurately predict energy expenditure when activity-specific (Jeanniard-du-Dot et al., 2017). We calculated DEE using time-energy budgets calculated from our ACC derived behaviours and equations derived from the literature. For resting metabolic rate (applied to all stationary behaviours) We used oxygen consumption data from dingoes collected by Shield (1972) and derived the following equation (equation 1) for $\dot{V}O_2$ against T_a.

$$\dot{V}O_2\ \left(\text{ml kg}^{-1}\text{min}^{-1}\right) = 0.007 \times T_a^2 - 0.298 \times T_a + 9.968 \qquad \text{(eqn. 1)}$$

Where T_a was calculated per second using the Env-DATA system on Movebank (see 'Environmental covariates' section below). Shield (1972) calculated $\dot{V}O2$ using flow through respirometry from dingoes of a similar size to those in our study (mean ± se = 18.8 ± 0.2 kg vs 18.1 ± 0.4 kg) and over a similar temperature range to that experienced by the dingoes at Kalamurina. We selected $\dot{V}O_2$ data from the control group in Shield (1972) as they were kept in an average ambient temperature of 23˚C over the course of the study, which was not distinctly different from the average ambient temperature at Kalamurina over the study period (26 ± 0.1˚C). For the purpose of this study it was assumed that the rate of energy expenditure when sleeping is the same as when stationary. For our walking and running behaviours we calculated energy expenditure using the following equation (equation 2) from Bryce and Williams (2017) for 'northern breeds' assuming an average speed of 1.985 m s^{-1} for walking and 4.96 m s^{-1} for running.

$$\dot{V}O_2\ \left(\text{ml kg}^{-1}\text{min}^{-1}\right) = 7.5 + 6.16 \times \mathit{speed} \qquad \text{(eqn. 2)}$$

Total DEE was calculated per day for each individual by summing the cost of each activity multiplied by the time (in hours) each activity was undertaken. This was then converted to kJ kg^{-1} day^{-1} by multiplying by a factor of 20.1 (Schmidt-Nielsen, 1997).

Environmental covariates

We created a map of the major landscape features in the study area using vegetation data from NatureMaps (Department of Environment and Water; downloaded 27/03/2018) and a spatial layer representing tracks and permanent water sources on Kalamurina (Australian Wildlife Conservancy; updated 27/03/2018). We classified seven landscape features; watercourses; desert woodland; low shrubland; tracks; salt lakes; sand dunes; and flats. A detailed description of how we derived these landscape covariates can be found in *Chapter 5*. We used the Env-DATA system on Movebank to annotate environmental data (temperature, NDVI, rainfall, and wind speed) to each GPS location, with information sourced from the European Centre for Medium-Range Weather Forecasts (Dee et al., 2011) and NASA Land Processes Distributed Active Archive Center (Didan, 2015). We collected data in two different field seasons, 'winter': April - August 2016, and 'summer' Oct 2017 – Jan 2018, and used the R library 'Maptools' (Bivand and Lewin-Koh, 2018) to calculate astronomical time of day (day, night, dawn, and dusk). We then grouped dawn and dusk together as 'twilight'. We extracted hour and Julian day from our dataset as additional temporal covariates.

Identification of high-use 'shelters'

Dingoes repeatedly shelter in discrete areas for resting, rearing offspring, and/or socialising (hereafter referred to as 'shelters') and thus they may be an important predictor of energy use (see *Chapter 5*). We used the R package 'recurse' (Bracis et al., 2018) to identify shelters for each dingo by using a combination of (1) recursion to the same location (25 m radius), and (2) the average amount of time spent in that area. Shelters were defined individually for each dingo by an average residence time per visit of ≥ 60 minutes and a rate of recursion in the 90th percentile of all recursions (Table 6.2).

Statistical analysis

Behaviour in space and time: Dingoes may exhibit different behavioural responses depending on their location in the landscape. So that individual differences in behaviour through space and time could be clearly identified, we chose to analyse the relationship between behaviour and landscape features for each dingo separately, using a multinomial logistic regression in the R package ‘MDM’ (De'ath, 2013). Our dependent variable was the proportion of time a dingo was engaged in each behaviour (stationary, walking, and running) in the 900 seconds (i.e., 15 minutes) prior to the GPS fix, with landscape feature as our predictor variable. To investigate population-level seasonal differences in dingo behaviour, we performed a meta-analysis to generate global parameter estimates across dingoes tracked during winter (JT04, JT05, and JT07) and summer (JT32, JT34, JT36, and JT37). We weighted the estimates from the individual models by the inverse of each estimate’s standard error, to account for variation in the sample size.

Daily activity: To investigate daily activity patterns of dingoes at Kalamurina we constructed two generalised additive models (GAMs) using the R package ‘mgcv’ (Wood, 2011). Our first activity model assessed movement distance (between successive 15 minute GPS locations) as a function of hour of day (0 – 23). Similarly, the second activity model assessed ODBA (averaged across the same, preceding 15 minute period as the distance measure) as a function of hour. Prior to statistical analysis, both response variables were standardised ($x -$ mean(x) / standard deviation(x)). GAMs were fitted with a cyclic cubic regression spline and 20 knots. We also ran a Pearson's correlation to test the strength and direction of the correlation between the response variables.

To assess whether dingoes exhibited behavioural thermoregulation by adjusting their activity levels as a result of ambient temperature, we used a generalised linear model (GLM) with ODBA (standardised) as our response variable, and ambient temperature (standardised) and time of day (day or night) as our predictors. We included dingo 'ID' and 'Julian day' as random effects.

Energetic landscape: We used linear mixed effect models in the R package 'lme4' (Bates et al., 2015) to explore the relationship between (log transformed) ODBA and our environmental/temporal covariates. Based on our aims and observations of dingo activity, we built a candidate set of models (n = 25) and used Akaike's Information Criterion corrected for small sample sizes (AICc) and conditional R^2 (R package 'MuMin'; Barton, 2018) to rank the models (Table A5.1). All candidate models included dingo ID as a random effect to account for individual variation. The model with the lowest AICc and highest R^2 (0.57) nested behaviour within ID, included Julian day as a random effect, and landscape feature, time of day, and the interaction between time of day and period as fixed effects.

RESULTS

Dingoes were much less active during summer where 91 ± 0.02% (mean ± se) of their day (24 hours) was spent stationary versus only 46 ± 0.05% during winter (Table A5.2). Season had the most profound effect on dingo behaviour (Fig. 6.2). In summer, dingoes were much more likely to remain stationary regardless of the habitat they occupied. In contrast, there was a similar probability of dingoes being stationary, walking, or running during winter.

Distance and ODBA were positively correlated with each other (r = 0.65, $p < 0.001$), and both these variable indicated crepuscular patterns of activity (Fig. 6.3). Dingoes were most active at dawn and into the early hours of the morning and least active just before dawn and in the middle of the afternoon.

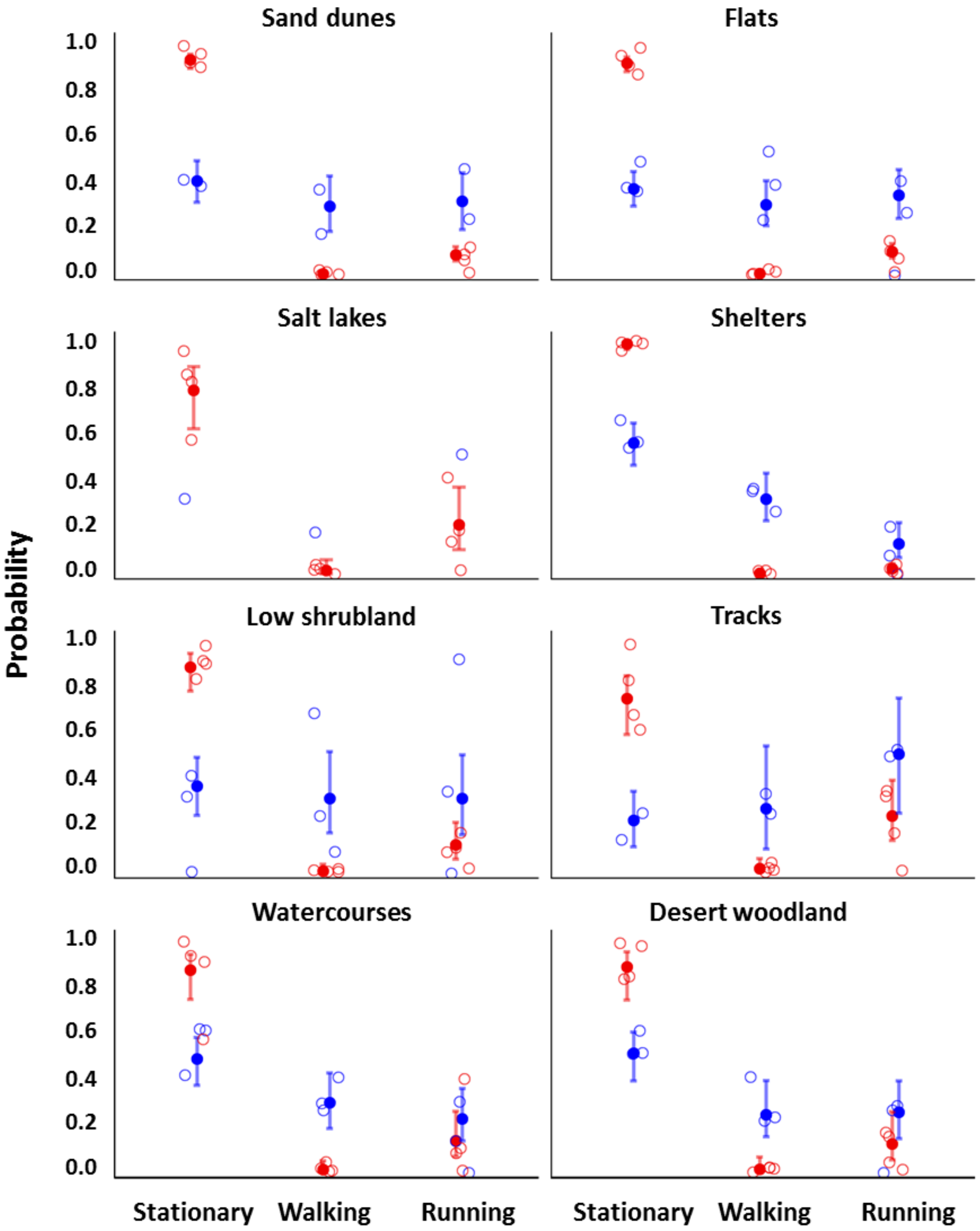

Figure 6.2. Predicted probabilities of being stationary, walking, or running in each habitat. Blue represents dingoes tracked during winter (n = 3), and red represents dingoes tracked during summer (n = 4). Hollow circles indicate probabilities for individual dingoes and solid circles represent global estimates (± 95% confidence intervals) from our meta-analysis of the multinomial model estimates for each individual. In winter, only one dingo occurred on salt lakes, so no global statistic was calculated.

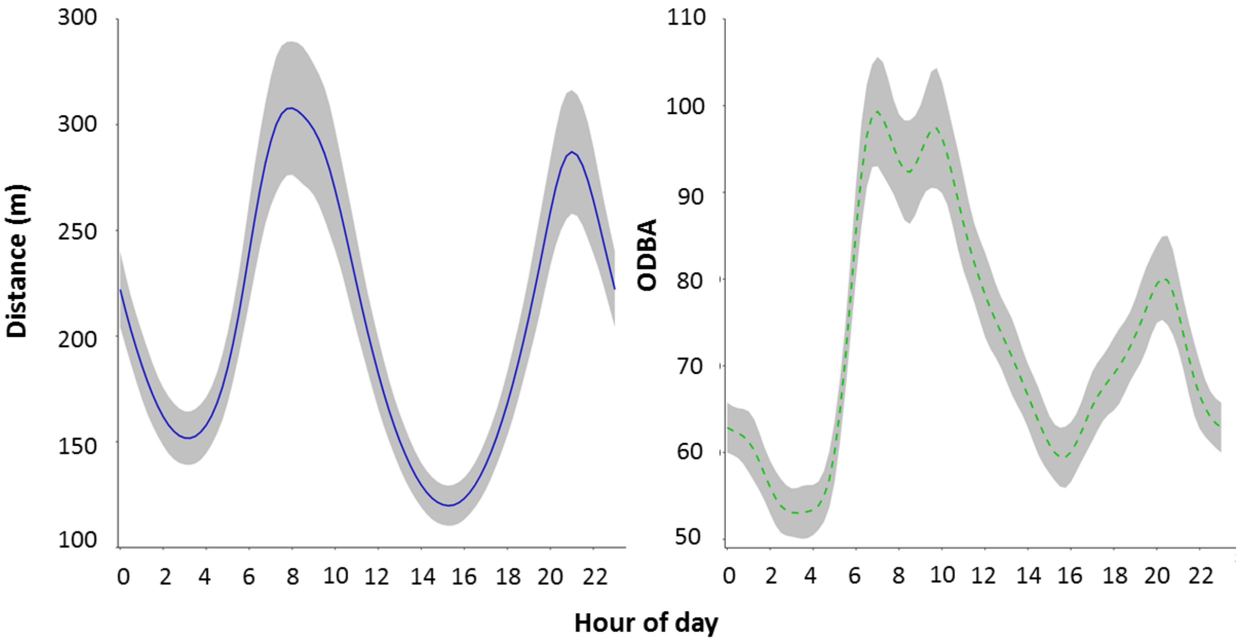

Figure 6.3. Daily activity patterns of dingoes (n = 7) at Kalamurina. The solid blue line (left panel) represents the predicted distance moved between successive 15 minute GPS location, and the dotted green line (right panel) represents the predicted, mean ODBA value across 900 seconds (i.e., 15 minutes), as a function of hour of day. Both models were fitted using > 13,200 data points. The 95% confidence intervals are represented by grey shading.

We found a contrasting relationship between ODBA and T_a that was driven by the time of day (day or night; Fig. 6.4). There was a sharp decrease in ODBA with increasing T_a during the day ($R^2 = 0.59$), whereas ODBA increased with increasing T_a at night ($R^2 = 0.39$). Estimates of mean daily energy expenditure are shown in Table 6.1. The mean energy expenditure of dingoes was significantly higher in winter (495 kJ kg^{-1} day^{-1}) than summer (288 kJ kg^{-1} day^{-1}; $p = 0.03$).

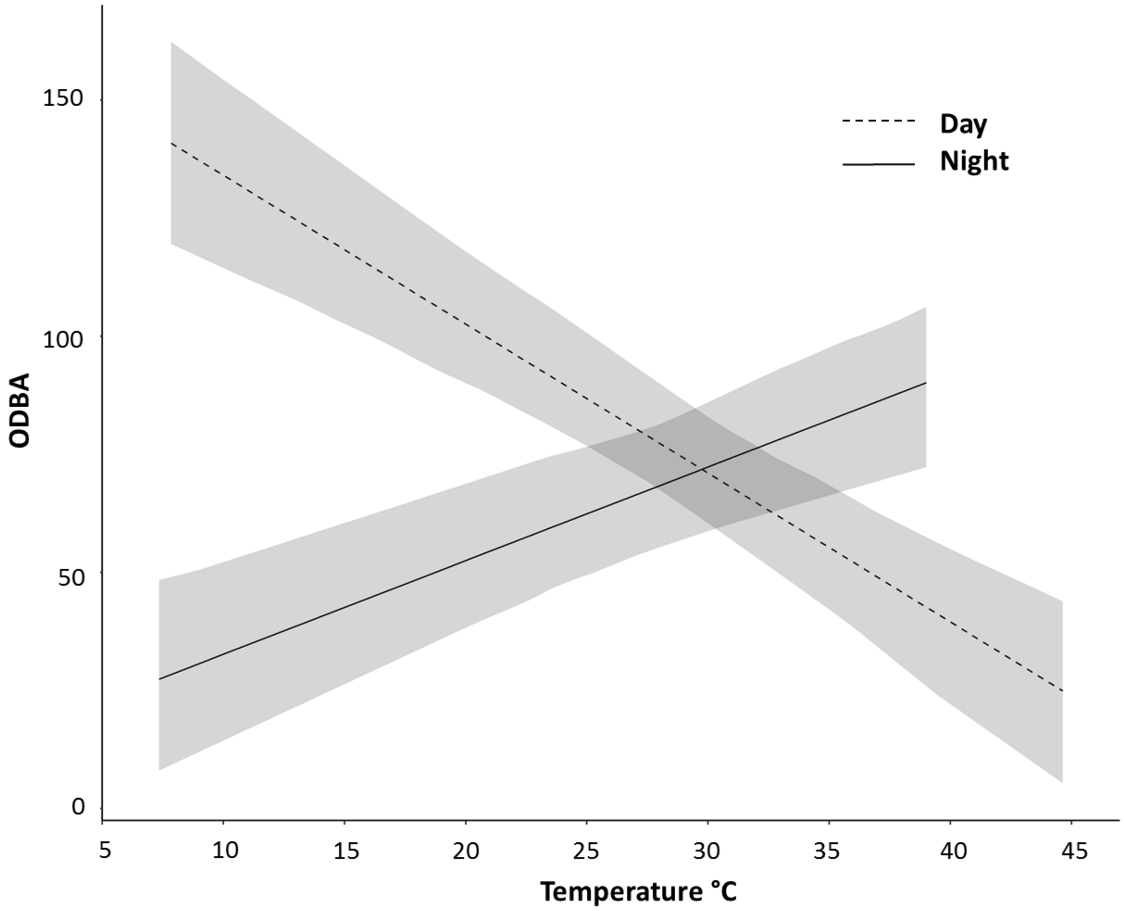

Figure 6.4. Predicted ODBA values (activity) by ambient temperature for dingoes (n = 7) at Kalamurina. The 95% confidence intervals are represented by grey shading.

There was a significant effect of landscape feature on the activity levels (ODBA) of dingoes at Kalamurina (Fig. 6.5). Dingoes were most active on salt lakes, tracks, and flats, and least active when at their shelters (Table A5.3). Dingo activity was influenced by period, with dingoes in winter significantly less active during twilight but more active at night than dingoes in summer. The activity level of dingoes during the day was not significantly different between summer and winter. The time of day had a significant effect on how active dingoes were in each landscape feature during summer but not in winter (Fig. 6.5). Overall, dingoes exhibited a moderate - low level of activity in most landscape features.

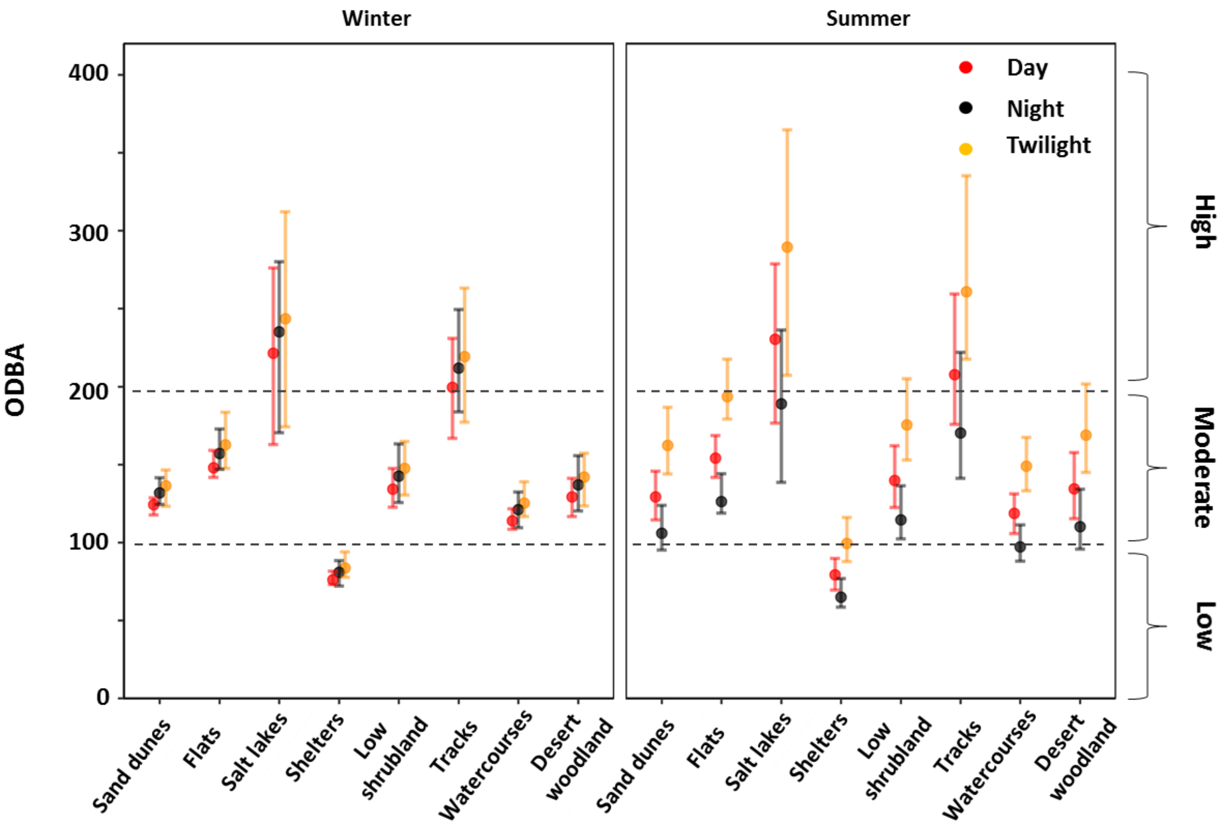

Figure 6.5. Predicted ODBA values from our selected generalised linear mixed-effect model for dingoes (n = 7) in eight landscape features during the day, night, and twilight. Approximate activity levels (low, moderate, and high) were adapted from the relationship between ODBA and behaviour reported in Tatler et al. (2018) and broadly represent our three grouped behaviour classes (stationary, walking, and running), respectively. Error bars represent 95% confidence intervals.

DISCUSSION

Patterns and processes of all life in the arid zone are shaped by extremes in temperature and water availability. Kalamurina is one of the hottest and driest places in Australia with a long term median annual rainfall < 135 mm and maximum temperatures regularly exceeding 40 °C throughout summer. In our study the activity of arid zone dingoes, as measured by ODBA, was primarily driven by ambient temperature. Specifically, we found that this was reflected in activity patterns across time of day, season, and even landscape features.

Movement is energetically costly and evaporative water loss is highest during energetically demanding activities at high ambient temperatures (Schmidt-Nielsen, 1972, McNab, 2002). Dingoes in this study were crepuscular and exhibited moderate to low activity levels year round. Akin to other animals, the movement ecology of dingoes is influenced by seasonally-variable intrinsic and extrinsic factors, with either primarily diurnal or primarily nocturnal activity patterns reported in other studies (Allen et al., 2013, *Chapter 5*). Activity patterns of predators usually coincide with those of their major food source, which are also linked to ambient temperature (e.g., Jenny, 2005, Harmsen et al., 2011). Rabbits comprise the bulk of dingo diet in the arid zone (Tatler et al., 2019) and they are most active in the early evening and throughout the night (Myers 1965). Moreover, as a vagile species, constraining high activity movements (or reducing them altogether) to the less climatically extreme times of the day is likely an adaptation to mitigate thermal stressors associated with desert life (Nathan et al., 2008, Aublet et al., 2009, Norris and Kunz, 2012).

Seasonally driven activity constraints have been reported for other species (e.g., northern flying squirrels *Glaucomys sabrinus* Cotton and Parker, 2000, and desert woodrats *Neotoma lepida* Murray and Smith, 2012) and suggests a trade-off between remaining in areas which offer thermal respite versus obtaining essential resources. Seasonal differences of DEE in free-ranging eutherian mammals have been found in several species, although this is the first time it has been observed in a wild canid. It has been shown that dingoes are capable of acclimating physiologically to extreme temperatures (-41°C to +45°C) over the course of a few months by shifting their TNZ and altering their BMR (Shield 1972). This was observed in concert with a change in thermal conductance brought about by altered coat composition (Shield, 1972). It is reasonable to assume that these physiological changes contribute dramatically to seasonal changes in DEE, however behavioural thermoregulation via altered activity patterns remains an important facet of energy balancing exhibited by dingoes. As for daily patterns of activity, during extended periods of high ambient temperatures (e.g., summer) dingoes would benefit from remaining inactive in order to reduce hyperthermia and evaporative water loss (Terrien et al., 2011). We found that dingoes were stationary for approximately 22 hours a day during summer compared to only 12 hours during winter. Winter also coincided with the breeding and whelping seasons and thus dingoes were more likely to be active during this time (e.g., searching for mates). The DEE of the two female dingoes tracked in winter was considerably higher than the male's, which could be a consequence of increased metabolic demands associated with lactation. Activity levels of lactating females rise in response to increased foraging effort due to additional energetic demands and fluid requirements for milk production, which can be twice those of basal needs (Pond, 1977).

The mean estimated DEE of dingoes (6620 kJ day^{-1}) was comparable to a highly active domestic dog (6,700 kJ day^{-1}) but less than half that of the similar sized African wild-dog *Lycaon pictus* (15,300 kJ day^{-1}; Gorman et al. 1998). African wild-dogs incur high energetic costs due to endurance hunting of large ungulates whereas dingoes in arid Australia primarily target much smaller prey (1-2 kg) that can subdued relatively quickly. There is some evidence that dingoes in the arid zone may consume more large prey (e.g., kangaroos; c. 40 kg) during winter (Paltridge, 2002) when energetic costs of sustained high intensity movement are lower as a result of lower T_a.

Many species alter their behaviour in response to solar radiation, usually to reduce thermal stress associated with hyperthermia and the difficult task of dumping excess heat (Walsberg, 2000, Terrien et al., 2011). Regardless of season, we found evidence that dingoes behaviourally thermoregulate by decreasing their activity levels with increasing ambient temperature during the day. Conversely, the positive relationship between activity and temperature at night implies that dingoes could be compensating for low daily activity by partially shifting foraging or movement to nocturnal periods, where radiative heat gain is no longer an issue.

Dingoes displayed the highest activity levels on salt lakes and tracks, which was expected given they are primarily used for commuting (*Chapter 5*). The very low activity levels observed when dingoes were in their shelters was probably indicative of stationary behaviours such as resting or sleeping. Returning to discrete areas for shelter and/or denning is common amongst mammalian carnivores and can increase individual fitness by providing thermoregulatory benefits (Weber, 1989), reducing predation rates (Ruggiero et al., 1998), and increasing offspring survival rates (Baker et al., 1998). Further, microclimate selection (i.e., location of shelters in the landscape) is an important thermal defence employed by animals to buffer changes in ambient temperature. Data collected in *Chapter 5* on the same dingo population found that shelters were significantly more likely to be located in the densely vegetated desert woodlands and along watercourses than in exposed habitats like salt lakes.

The daily activity patterns of animals are usually described by the distance moved between successive GPS locations, and can vary widely depending on the sampling rate (Mills et al., 2006, Marcus Rowcliffe et al., 2012). The distance between two points cannot account for animal activity that is not related to movement distance such as playing and fighting. Therefore, studies using relocation data to describe animal activity could potentially overlook much of an animal's true activity pattern (Marcus Rowcliffe et al., 2012). However, we found a strong positive correlation between fine-scale activity measurements (ODBA) and much broader scale distance calculations (GPS; Fig. 6.3). In addition, the daily patterns of activity (distance or ODBA) were nearly identical and suggests both methods are appropriate for describing general daily fluctuations in animal activity.

Chapter 7. Final Discussion

Dingoes are ecologically important apex predators, yet they are severely persecuted by humans and heavily impacted by recent anthropogenic activity, particularly hybridisation with domestic dogs. Human-facilitated hybridisation is a major threatening process for many species, and given hybrid animals often exhibit different functional traits, identifying the lineage of animals prior to ecological studies is critical for making accurate conclusions. Indeed, until now, evidence of hybridisation has been found in every dingo population studied; thus, disentangling the considerable effects of this on their fundamental ecology is problematic at best. Our research revealed a lack of hybridisation in the population of dingoes at Kalamurina, and this distinctive 'pure' status was a core underpinning of my thesis that provided a unique perspective on their natural ecology.

Contemporary methods can be used to challenge our understanding of an animal's ecology

Using molecular tools, I provided empirical evidence for the existence of multiple mating strategies in a wild population of dingoes. Similar results have been reported for other species that were once believed to be monogamous, using molecular-based methods (Amos et al., 1993, Hughes, 1998). There is considerable value in adding molecular techniques to ecological studies, particularly for identifying genetic mating systems and discerning the genetic make-up of populations threatened with hybridisation.

Population level variation in animal ecology is well documented (e.g., Harden, 1985, Fleming et al., 2001, Allen et al., 2013, Newsome et al., 2013b), yet we found substantial individual variation in how dingoes interacted with their surroundings. The importance of assessing individual differences in behaviour and habitat selection has been shown in other species, e.g., the use of urban versus forest areas by red foxes (Hradsky et al., 2017) and the effect of season on habitat avoidance in moose (Gillingham and Parker, 2008), although it is still overlooked in many animal movement and resource selection studies. Investigating individual variation may be particularly important for other generalist predators such as badgers (Robertson et al., 2014), feral cats (Dickman and Newsome, 2015), and coyotes (Newsome et al., 2015), which exhibit individual foraging strategies that can threaten the persistence of some prey species. Together with previous research, my thesis supports the utility of considering individual-level responses, and therefore I advocate for its inclusion in future ecological studies; particularly for other generalist predators.

As top order predators with a generalist diet, dingoes regularly prey on a range of taxa (Doherty et al., 2018). However, their general preference for mammals (see *Chapter 3*) could pose a risk to vulnerable or endangered mammal populations. Our research was a timely addition to the review by Doherty et al. (2018), which broadly investigated dingo diet in relation to major ecosystems across Australia. I was able to build on this study by focussing on the effect of temporary resource pulses and anthropogenic disturbance on the probability of occurrence and diversity of mammal species in dingo diet. Previous dietary studies did not have the temporal and geographic resolution, nor sample size, to rigorously evaluate the diet of arid zone dingoes in great detail. Moving forward, the use of meta-analytic techniques is a valuable approach for teasing out population level dietary preferences of generalist predators.

Bang for the buck: Biologging tools and the value of integrating complimentary techniques

The diversity of contemporary biologging methods has afforded new insights into the lives of many species. However, logging fine-scale animal movement using accelerometers has only recently been applied to answer ecological questions effectively. Previously hindered by memory constraints stemming from an ideology that mandated high frequency sampling, our results demonstrated that numerous behaviours can be accurately classified using ACC data collected at very low sampling frequencies. There is increasing support for the use of sampling frequencies as low as 1 Hz, even for small-bodied species (Studd et al., 2019). Indeed, the increased popularity of accelerometry has stimulated the development of new software that automates behavioural classification, and provides useful summaries and metrics (Walker et al., 2015, Song and Cox, 2016). As such, the use of ACC loggers over different seasons and even ontogenies is now possible, with potentially enormous consequences for our understanding of animal behaviour and survival under natural conditions.

The scope at which biologging can be used to explore ecological phenomena is dramatically enhanced if we integrate complimentary techniques such as ACC and GPS. Several studies have successfully linked ACC and GPS data from wild animals to answer questions at the interface of behaviour and ecology (e.g., Nathan et al., 2012, Abrahms et al., 2016, Scharf et al., 2016). Yet, the scheduling of both ACC and GPS fixes has significant ramifications for statistical analysis and ecological inference. The limited memory (< 30 days) of the ACC units used in this thesis hindered the detection of behavioural responses to landscape features and additional behavioural thermoregulation strategies. Nevertheless, recent advances in the memory capacity of ACC units now permit continuous data to be recorded over longer time periods, which is a boon for future ACC based studies.

Finally, as well as integrating dingo activity and resource selection, I linked energetic data to corresponding behaviours and created energy budgets. This is an innovative approach that could be broadly applied to increase our understanding of the ecophysiology of wild animals. The integration of physiology into the study of predator ecology should be a priority for future research, because an animal’s energy budget ultimately drives how they interact with their surroundings.

Future research directions

There is an ever increasing arsenal of biologging tools that are furthering our ability to understand the natural world. Alongside these new tools are technical and methodological developments that have improved our capacity to capture and analyse biologging data. Continued progress in the study of animal movement and behavioural ecology requires the implementation of emerging approaches to monitoring wild animals in combination with appropriate statistical methodologies. Specifically, fine time scale GPS and ACC data are a necessity for future studies on the movement and resource selection of wild carnivores. In addition, programming ultra-fine time scale GPS fixes (e.g., several fixes a minute) during bouts of high activity (measured by ODBA) would allow the calculation of exact velocities and in turn, increase the accuracy of activity-specific time energy budgets. Additional loggers, like iButtons, could be easily attached to tracking devices (e.g., collars) and would enable direct physiological data (e.g., skin temperature) to be collected. This will extend the scope of questions that can be addressed in ecological studies, with only minor additional investment.

The research in this thesis promotes the use of: (i) genetics for inferring ecology; (ii) meta-analytic approaches; (iii) resource selection research; (iv) the integration of biologging techniques; and (v) the application of contemporary statistical analyses. Tools for the remote monitoring of wild animals have never been so accessible, and thus the integration of multiple approaches has never been so achievable. Indeed, to effectively advance our understanding of the natural world it is imperative we move to a more holistic and integrative strategy for data collection and statistical analysis.

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APPENDIX 1. Supplementary material to Chapter 2

Table A1.1. Capture details for dingoes trapped at Kalamurina from 2016 – 2018.

Dingo ID	Coat colour	Age class	Sex	Weight (kg)	Body condition (1 – 5)	Purity (%)
JT01	White	Adult	Male	20.5	4	91
JT02	Sandy	Adult	Female	16	4	88
JT03	Sandy	Older adult	Female	16	4	96
JT04	Black and tan	Adult	Female	16	4	88
JT05	Sandy	Older adult	Female	16.5	4	90
JT06	Sandy	Older adult	Female	18	4	90
JT07	Sandy	Older adult	Male	20.5	4	89
JT08	Sandy	Adult	Male	25	5	89
JT09	Sandy	Adult	Female	16	4	92
JT10	Sandy	Adult	Male	19	4	100
JT31	Sandy	Young adult	Female	14	3	86
JT32	Sandy	Adult	Female	23.5	5	88
JT33	Sandy	Adult	Female	20.5	4	91
JT34	Sandy	Older adult	Female	17.5	4	91
JT35	Sandy	Older adult	Female	15.5	4	88
JT36	Sandy	Adult	Female	15.5	3	75
JT37	Sandy	Adult	Male	17	4	98
JT38	Sandy	Older adult	Male	21.5	4	85
JT39	Black and tan	Older adult	Female	16	3	93
JT50	Sandy	Adult	Male	17	4	96
JT51	Sandy	Adult	Male	15	4	86
JT52	Sandy	Older adult	Female	14.5	3	89
JT53	Sandy	Adult	Male	19	4	88
JT54	Sable	Older adult	Male	23	4	97
JT55	White	Adult	Male	16.25	4	87
JT100	Black and tan	Sub adult	Female	10.5	3	100
JT101	Black and tan	Sub adult	Male	14	3	100
JT103	White	Adult	Female	16.5	4	87
JT104	Sandy	Sub adult	Male	9.5	1	90
JT106	Black and tan	Young adult	Male	15	4	84
JT107	Sandy	Young adult	Male	14	3	91
JT108	Black and tan	Young adult	Male	13	2	92
JT109	Sandy	Young adult	Male	17	4	96
JT110	Black and tan	Young adult	Female	12	2	83
JT111	Sandy	Young adult	Female	10	2	86
JT201	Sandy	Sub adult	Female	9	2	99
JT202	Sandy	Sub adult	Male	9.5	2	98
JT203	Sandy	Young adult	Female	10.5	3	91
JT204	Sable	Young adult	Female	10.25	3	90
JT205	Sandy	Young adult	Male	15	3	89
JT206	Black and tan	Sub adult	Male	10	3	94

JT207	Sandy	Sub adult	Female	9	2	92
JT208	Sable	Young adult	Male	13	3	89
JT209	Sandy	Young adult	Female	12	3	94
JT211	Sandy	Young adult	Female	11.5	3	94
JT212	Black and tan	Young adult	Male	15.5	4	87
JT213	Sandy	Young adult	Male	17	4	96
JT214	Sable	Young adult	Female	13	3	96
JT215	Sandy	Adult	Male	19	4	97
JT217	Sandy	Young adult	Male	14	3	89
JT218	Sandy	Sub adult	Male	16	3	94
JT219	Sable	Young adult	Male	17.5	4	94
JT220	Sandy	Sub adult	Male	14	3	86
JT221	Sandy	Young adult	Male	16.5	3	92
JT222	Sandy	Young adult	Male	17	3	93
JT223	Sandy	Sub adult	Female	12	3	89
JT224	Sandy	Young adult	Male	17.5	4	85
JT225	Sable	Sub adult	Male	15	3	84
JT226	Sable	Sub adult	Male	15	3	100
JT227	Sandy	Young adult	Male	16	3	83
JT228	Sandy	Sub adult	Female	13	4	84
JT229	Sandy	Young adult	Male	16	3	87
JT230	Sandy	Sub adult	Female	10.5	3	97
JT231	Sandy	Sub adult	Male	13.5	3	98
JT301	Sandy	Sub adult	Female	13	4	95
JT302	Sandy	Sub adult	Female	12.5	4	91
JT303	Sandy	Sub adult	Male	12	4	83
JT304	Sandy	Young adult	Male	12.5	2	98
JT305	Sandy	Older adult	Male	13	1	97
JT306	Sandy	Sub adult	Female	8	3	94
JT307	Sandy	Sub adult	Female	10	3	93
JT308	Sandy	Older adult	Male	18	4	92
JT309	Sandy	Young adult	Male	13.5	3	86
JT310	Sandy	Sub adult	Female	11	2	93
JT311	Sandy	Young adult	Male	19	4	89
JT312	Sandy	Adult	Male	19.5	4	87
JT313	Sandy	Sub adult	Female	12.5	4	99
JT314	Sable	Sub adult	Female	10	2	85
JT315	Black and tan	Adult	Male	15	3	94
JT316	Sandy	Older adult	Female	13	3	89
JT317	White	Adult	Male	21	4	99
JT318	Sandy	Older adult	Male	15.5	2	90
JT319	Sandy	Adult	Female	17	4	100
JT320	Sable	Older adult	Female	13	3	89

Table A1.2. Model summary for the effect of age class, coat colour, and sex on body condition of dingoes at Kalamurina. Model estimates, standard errors (SE), and p values are presented for our generalised linear model.

Model	Variables	Estimate	SE	*p* value
Body condition ~	(Intercept)	1.331	0.224	< 0.001
Age class +	Older adults	-0.164	0.191	0.391
Coat colour +	Sub adults	-0.315	0.178	0.076
Sex	Young adults	-0.248	0.171	0.148
	Sable coats	0.050	0.263	0.848
	Sandy coats	0.059	0.194	0.761
	White coats	0.051	0.328	0.878
	Males	0.007	0.124	0.956

Table A1.3. Model summary for the effect of coat colour, sex, age class, and weight on body the purity (amount of dingo ancestry) of dingoes at Kalamurina. Model estimates, standard errors (SE), and p values are presented for our generalised linear model.

Model	Variables	Estimate	SE	*p* value
Purity ~	(Intercept)	2.432	0.590	< 0.001
Coat colour +	Sable coats	0.024	0.316	0.940
Sex +	Sandy coats	-0.038	0.234	0.872
Age class +	White coats	-0.067	0.422	0.873
Weight	Males	0.157	0.173	0.366
	Older adults	-0.001	0.243	0.997
	Sub adults	0.213	0.305	0.488
	Young adults	-0.191	0.253	0.453
	Weight	-0.009	0.033	0.785

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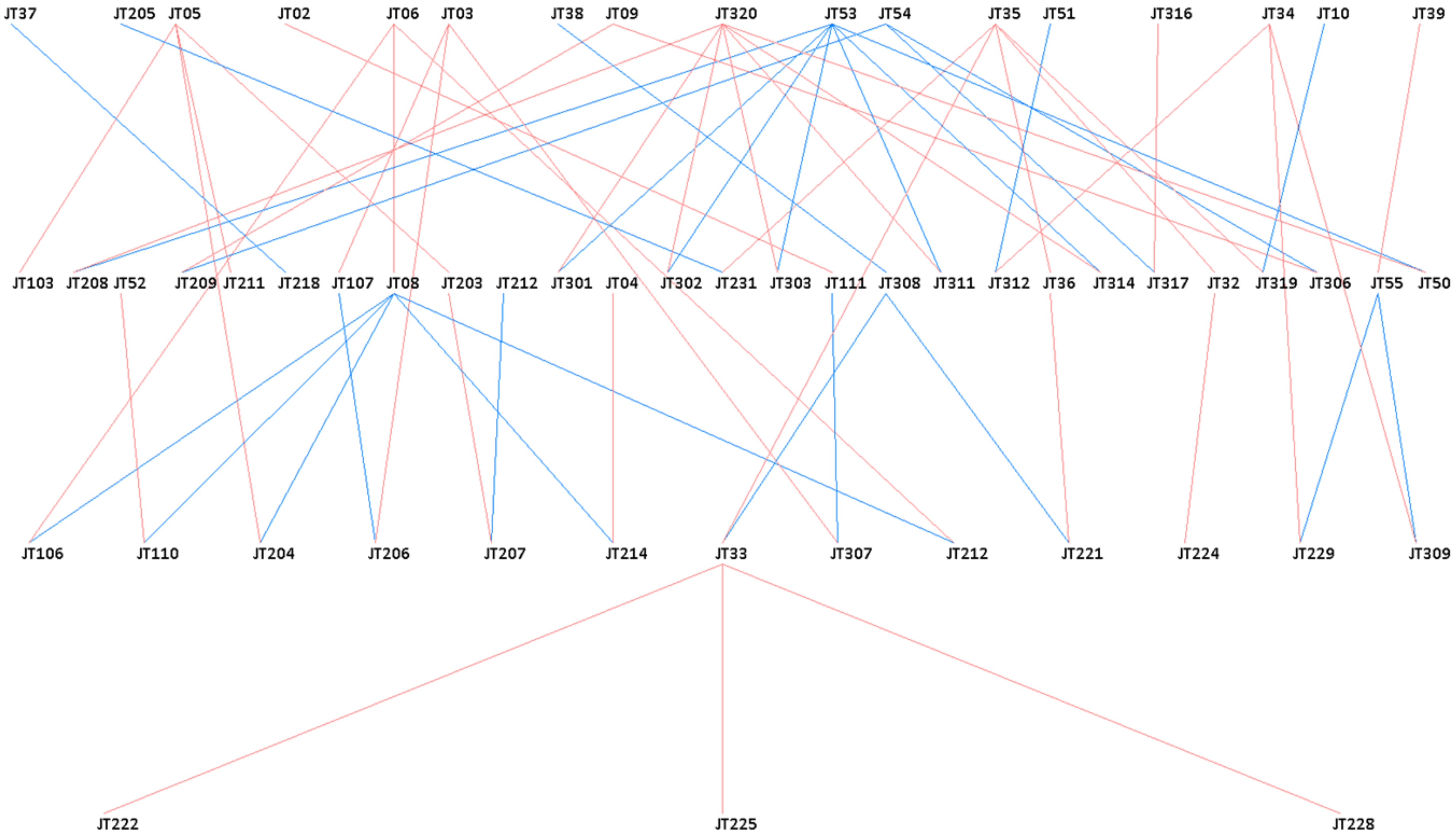

Figure A1.1. Pedigree analysis revealing parentage of 60 dingoes at Kalamurina. Blue lines indicate sires and red lines indicate dams. Different levels are used to represent different generations.

APPENDIX 2. Supplementary material to Chapter 3

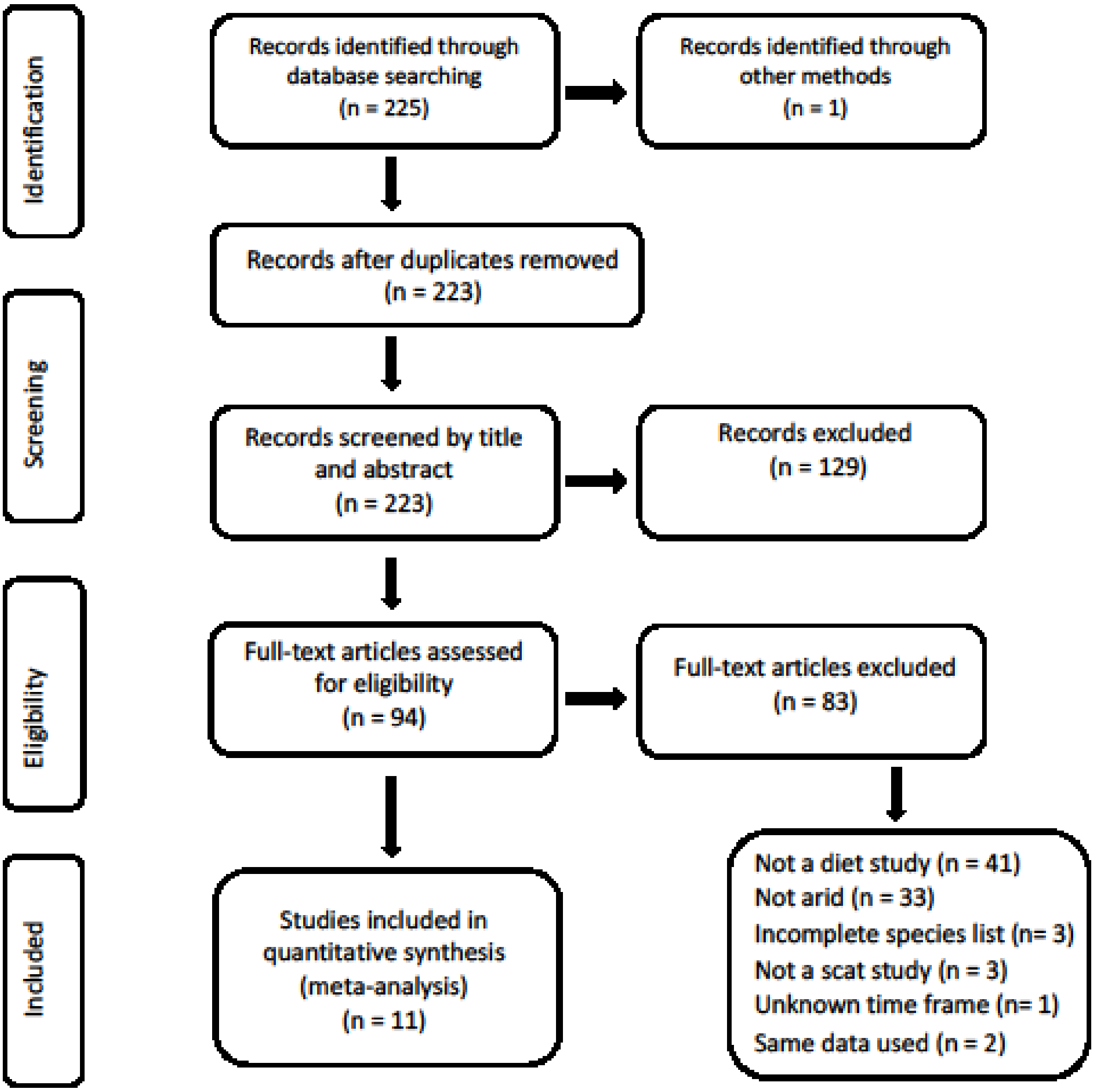

Figure A2.1. PRISMA flow chart illustrating the results of the search strategy.

Table A2.1. The number of dietary samples (scats and stomachs) that contained remains from a given mammal species during non-boom periods at each site. Mean adult weight for each of the 66 species (sexes were combined) extant at the study sites was calculated from values given in Aitken et al. (2013). Mammals were classed as small (< 35g), medium (light grey shading; 35 – 5500g), and large (> 5500g). Records marked with a single asterisk (*) denote a species that is extant at the site but not recorded in dingo diet. Records in bold indicate conservation sites.

Species	Weight	Corbett & Newsome (1987)	Marsack & Campbell (1990)	Thomson (1992) – Site 1	Thomson (1992) – Site 2	Thomson (1992) – Site 3	**Paltridge (2002)**	Cupples *et al*. (2011) – Strzel.	**Cupples *et al*. (2011) – Nullar.**	Allen & Leung (2012) – Cor. D.	Allen & Leung (2012) – Ham.	Allen & Leung (2012) – Lamb.	Allen & Leung (2012) – Tod.	Newsome *et al*. (2014)	Allen & Leung (2014) – Quin.	**Doherty (2015)**	**Spencer, Newsome & Dickman (2017)**	**McDonald *et al*. (2018)**	**Current study**
Planigale ingrami	4g						*****			*									
Ningaui timealeyi	5.6g			*	*	*													
Planigale tenuirostris	6.1g	*						*		*	*	*	*		*		*****		*****
Ningaui ridei	8.5g	*					*****			*	*	*	*		*		*****	*****	*****
Planigale gilesi	9.2g							*		*									*****
Sminthopsis youngsoni	10g	*		*	*	*											*****	*****	
Pseudomys delicatulus	10.5g			*	*	*	*****												
Sminthopsis ooldea	11g	*					*****				*	*	*					*****	
Pseudomys hermannsburgensis	12g	11		*	*	*	*****	*		1	*	*	*	13	1	*****	**22**	**2**	**1**
Pseudomys chapmani	12.5g			*	*	*													

Cercartuetus concinnus	13.5g								*										
Pseudomys bolami	13g		*					*											
Pseudomys johnsoni	13.5g						*												
Sminthopsis crassicaudata	15g	*	*					*	**1**	1	*	*	*		2	*	*	*	*
Sminthopsis hirtipes	15g	*																*	*
Sminthopsis dolichura	15.5g															*			
Leggadina lakedownensis	17.5g			*	*	*													
Sminthopsis longicaudata	18g																	*	
Sminthopsis gilberti	19.5g															*			
Leggadina forresti	20g	1						*		1	*	*	*	2	*		**4**	*	**1**
Sminthopsis macroura	20g	*		*	*	*	*	*		142	1	*	1		23		*	**1**	**1**
Mus musculus	20g	22	*	*	*	*	**1**	4	**2**	199	*	10	12	25	40	*	**3**	**7**	**2**
Pseudantechinus roryi	23.5g			*	*	*													
Antechinomys laniger	25g	*						*		*	*	*	*		*	*	*	*	*
Pseudomys desertor	25g	*		*	*	*	*			*	*	*	*	318			**6**	**1**	*
Pseudomys albocinereus	28.25g															*			
Dasykaluta rosamondae	28.75g			*	*	*													
Notomys fuscus	32g														203				
Pseudantechinus macdonnellensis	33g	*					*				*	*	*				*	*	
Notomys alexis	35g	28		*	*	*	*			74	*	2	16	29		*	**12**	**1**	*
Notomys cervinus	35g																		**1**
Zyzomys argurus	36g			*	*	*													
Pseudomys nanus	37.63g						*												
Pseudomys australis	40g										*	*	*		1				*
Pseudantechinus woolleyae	40g			*	*	*													
Notomys mitchelli	52g		*						*							*			

Notoryctes typhlops	55g	*					**2**				*	*	*					*	*
Dasycercus blythi	84g	*												11			**1**	*	
Zyzomys pedunculatus	110g																	*	
Dasyuroides byrnei	117.5g									*									
Dasycercus cristicauda	120g										*	*							*
Rattus villosissimus	144g	4					*			183			*	10	9		**36**	*	**2**
Rattus rattus	280g			*	*	*										*			
Dasyurus hallucatus	597.5g			*	*	*													
Hydromys chrysogaster	680.5g									*							*		*
Macrotis lagotis	1350g						**1**							40					
Oryctolagus cuniculus	1600g	150	83					104	**20**	273	4	9	35	8	**1750**	**8**		**59**	**62**
Trichosurus vulpecula	2625g																	**1**	
Lagorchestes conspicillatus	3175g						**4**							10					
Petrogale lateralis	4125g																	*	
Tachyglossus aculeatus	4500g	*	*	7	1	1	**2**	1	*	*	*	*	2	23	*	**4**	*	**7**	*
Felis catus	4600g	3	2	*	2	*	**7**	2	**1**	5	*	*	1	80	4	*	*	**9**	**7**
Petrogale rothschildi	5150g			1	*	*													
Vulpes vulpes	6kg	*	5	*	*	1	*	*	*	*	*	*	*	4	*	*	*	*	*
Onychogalea unguifera	6.6kg						*							25					
Lasiorhinus latifrons	27kg								*										
Macropus fuliginosis	36kg		*					*	**2**						*				
Macropus rufus	40kg	43	42	223	65	45	**12**	21	*	50	2	16	150	42	43	**10**	**15**	**5**	*
Ovis aries	40kg			2	*	31		1											
Macropus giganteus	40kg							*							*				
Macropus robustus	44kg	1		**	**	**	*	*		*	*	*	2	69	*	**10**	**12**	**47**	
Capra hircus	44kg							*	*						*	**1**		**1**	

Sus scrofa	86kg	*					*	*		3					*		*		**2**
Equus asinus	325kg	*									*	*	*					*	*
Equus caballus	400kg	2									*	*	*	4				**8**	*
Bos taurus	700kg	47	10	18	28	1		17		311	8	30	164	240	163			**10**	**1**
Camelus dromedarius	800kg	*	*				**3**		*	*	*	*	*	71	*	*	**3**	*	*
Total samples		275	131	248	92	73	**77**	146	**34**	**1303**	18	79	424	1907	**2261**	**37**	**145**	**98**	**82**

*** did not distinguish between Macropus rufus and M. robustus in the sample.*

Table A2.2. The number of dietary samples (scats and stomachs) that contained remains from a given mammal species during boom periods at each site. Mean adult weight for each species (sexes were combined) was calculated from values given in Aitken et al. (2013). Mammals were classed as small (< 35g), medium (light grey shading; 35 – 5500g), and large (> 5500g). Records marked with a single asterisk (*) denote a species that is extant at the site but not recorded in dingo diet. Records in bold indicate conservation sites.

Species	Weight	Corbett & Newsome (1987)	Allen & Leung (2012) – Cor. D.	Allen & Leung (2012) – Lamb.	Allen & Leung (2012) – Tod.	Allen & Leung (2014) – Quin.	**Spencer, Newsome & Dickman (2017)**	**Current study**
Planigale ingrami	4g		*					
Ningaui timealeyi	5.6g							
Planigale tenuirostris	6.1g	*	*	*	*	*	*	*
Ningaui ridei	8.5g	*	*	*	*	*	*	*
Planigale gilesi	9.2g		*					*
Sminthopsis youngsoni	10g	*					*	
Sminthopsis ooldea	11g	*		*	*	*		
Pseudomys hermannsburgensis	12g	*	*	*	*	1	**6**	*
Sminthopsis crassicaudata	15g	*	*	*	1	*	*	*
Sminthopsis hirtipes	15g	*						*
Sminthopsis longicaudata	18g	*						
Leggadina forresti	20g	*	*	*	*	*	**1**	*
Sminthopsis macroura	20g	*	*	*	*	1	*	**3**
Mus musculus	20g	2	10	52	120	11	**17**	*
Antechinomys laniger	25g	*	*	*	*	*	*	*
Pseudomys desertor	25g	*	*	*	*		**2**	*
Notomys fuscus	32g		2			84		
Pseudantechinus macdonnellensis	33g	*		*	*		*	
Notomys alexis	35g	*	*	*	1		**6**	*
Notomys cervinus	35g							*
Pseudomys australis	40g			*	*	*		*

Notoryctes typhlops	55g	*		*	*			*
Dasycercus blythi	84g	*					*	
Dasyuroides byrnei	117.5g		*					
Dasycercus cristicauda	120g			*				*
Rattus villosissimus	144g	*	344	1	56	42	**75**	**46**
Hydromys chrysogaster	680.5g		*				*	*
Oryctolagus cuniculus	1600g	9	36	6	52	140		**25**
Tachyglossus aculeatus	4500g	*	*	*	*	*	*	*
Felis catus	4600g	*	*	*	7	1	*	*
Vulpes vulpes	6kg	*	*	*	*	*	*	*
Macropus fuliginosis	36kg					*		
Macropus rufus	40kg	*	*	18	30	*	**2**	*
Macropus giganteus	40kg					*		
Macropus robustus	44kg	*	*	*	1	*	*	
Capra hircus	44kg					*		
Sus scrofa	86kg	*	*			*	*	*
Equus asinus	325kg	*		*	*			*
Equus caballus	400kg	*		*	*			*
Bos taurus	700kg	1	8	*	22	*		*
Camelus dromedarius	800kg	*	*	*	*	*	*	*
Total samples		10	377	76	279	259	**91**	**52**

Table A2.3. Studies used in the meta-analysis of dingo diet in the arid zone. The period indicates whether the dietary data were collected during resource booms or non-booms, and major land use at each site was classified as: (1) conservation, which pertained to private or public land managed for conservation at the time of the study; or (2) pastoralism, which included cattle and sheep stations, and mining operations (i.e., sites subject to high anthropogenic impact). Dietary data were collected from scats and stomach and the sample size reflects the total number of dietary samples collected.

Reference	Site	Period	Major land use	Method	Sample size
Corbett & Newsome 1987	Erldunda	Non-boom	Past.	Stomach	275
Corbett & Newsome 1987	Erldunda	Boom	Past.	Stomach	10
Marsack & Campbell 1990	Bunda Plateau	Non-boom	Past.	Scat/ stom.	131
Thomson 1992	Pilbara	Non-boom	Past.	Scat/ stom.	413
Paltridge 2002	Tennant	Non-boom	Cons.	Scat	77
Cupples *et al*. 2011	Strzelecki	Non-boom	Past.	Scat	146
Cupples *et al*. 2011	Wahgunyah NP	Non-boom	Cons.	Scat	34
Allen & Leung 2012	Hamilton	Non-boom	Past.	Scat	18
Allen & Leung 2012	Lambina	Boom	Past.	Scat	76
Allen & Leung 2012	Lambina	Non-boom	Past.	Scat	79
Allen & Leung 2012	Todmorden	Boom	Past.	Scat	279
Allen & Leung 2012	Todmorden	Non-boom	Past.	Scat	424
Allen & Leung 2012	Cordillo Downs	Boom	Past.	Scat	377
Allen & Leung 2012	Cordillo Downs	Non-boom	Past.	Scat	1303
Newsome *et al*. 2014	Tanami	Non-boom	Past.	Scat	1907
Allen & Leung 2014	Quinyambie	Boom	Past.	Scat	259

Allen & Leung 2014	Quinyambie	Non-boom	Past.	Scat	2261
Doherty 2015	Rangelands	Non-boom	Cons.	Scat	37
Spencer *et al*. 2017	Ethabuka	Boom	Cons.	Scat	91
Spencer *et al.* 2017	Ethabuka	Non-boom	Cons.	Scat	145
McDonald *et al*. 2018	MacDonnell R.	Non-boom	Cons.	Scat	98
Current study	Kalamurina	Boom	Cons.	Scat	52
Current study	Kalamurina	Non-boom	Cons.	Scat	82

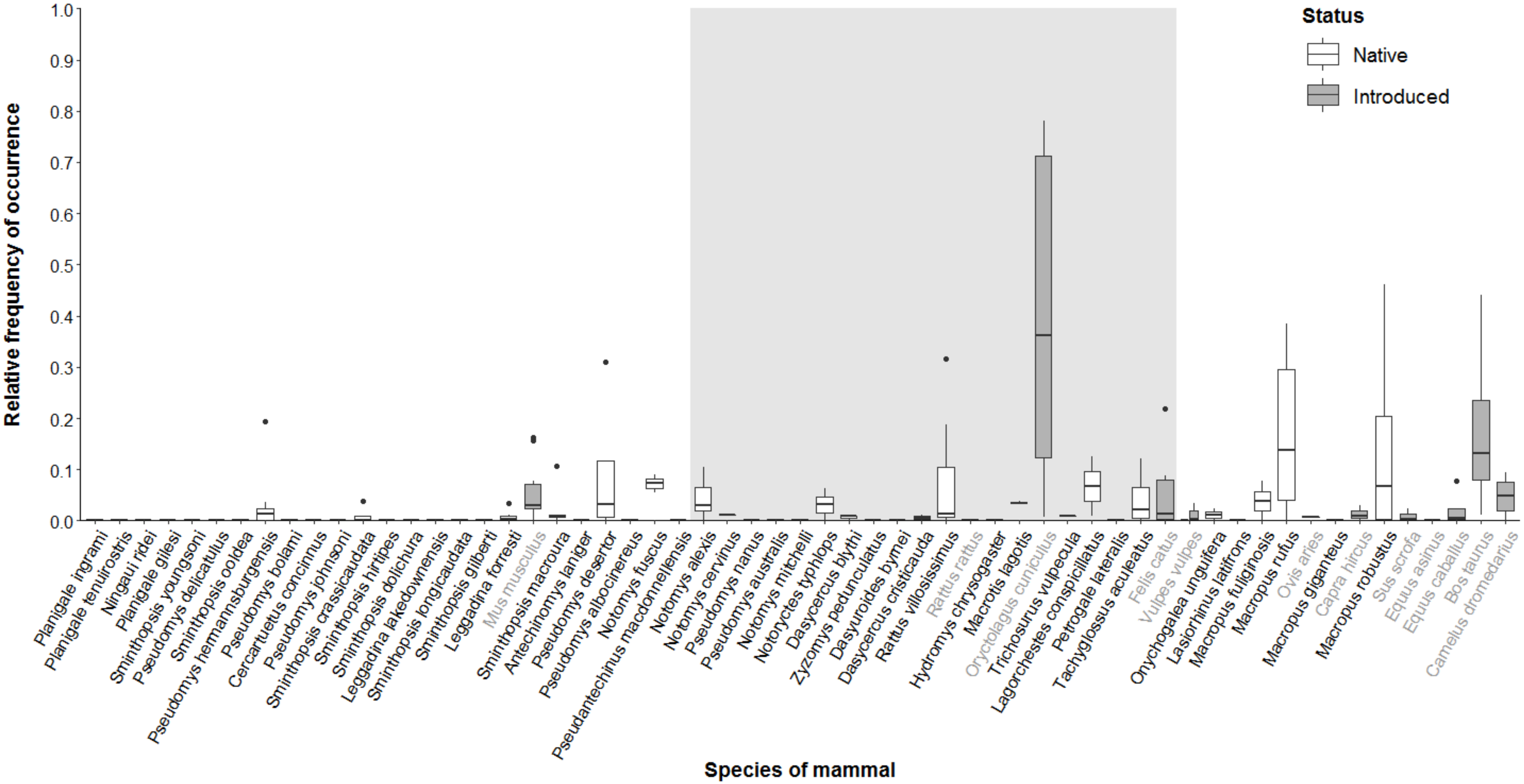

Figure A2.2. Relative frequency of occurrence of terrestrial mammals in the diet of dingoes in the arid zone. All terrestrial mammals that were sympatric with dingoes at a study site are represented, regardless of their presence in the diet. Grey boxplots and species names indicate introduced species and the light grey background represents the CWR (medium size class).

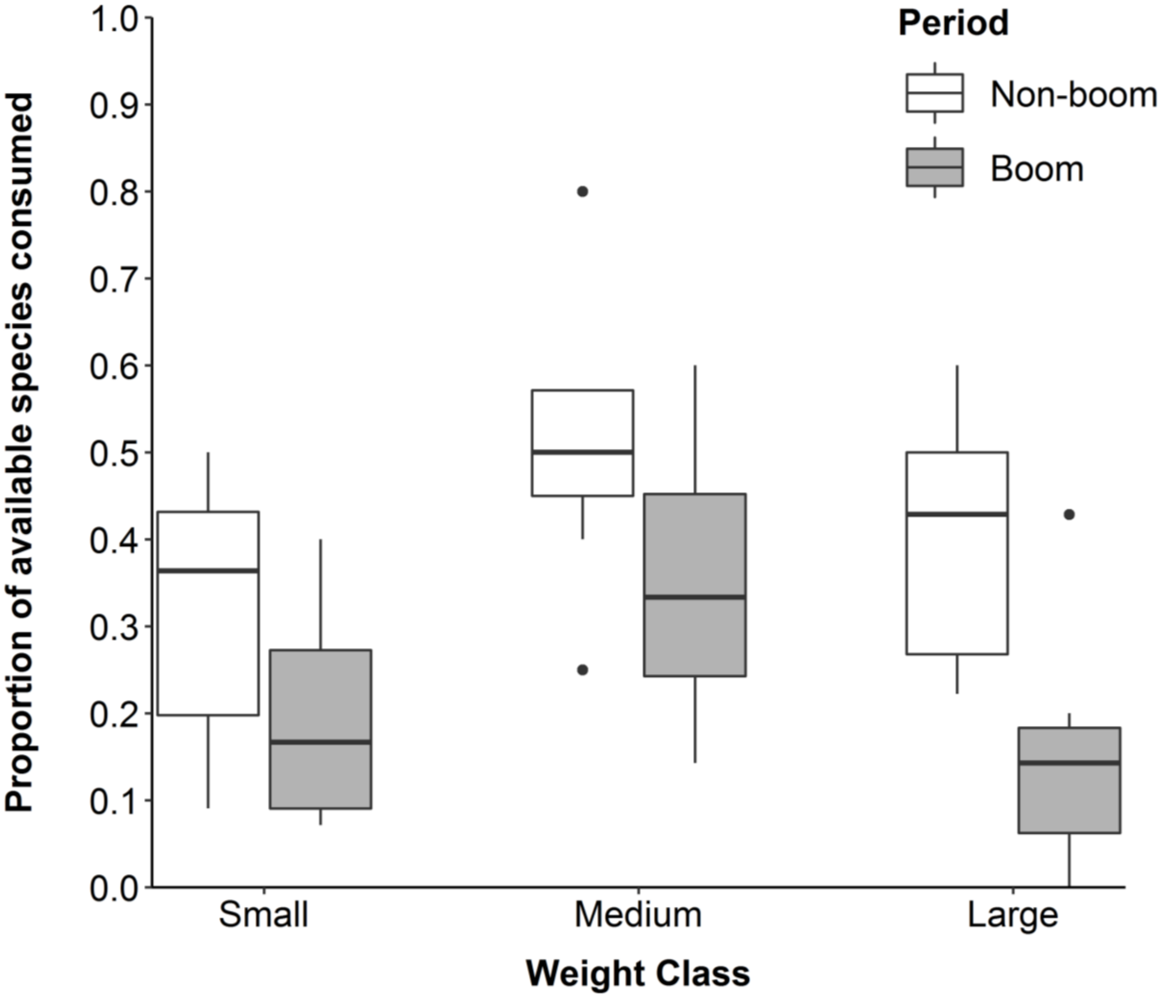

Figure A2.3. Proportion of species recorded in the diet of dingoes relative to those extant and presumably available as potential prey. All terrestrial mammals were considered to be potential prey and their presence at a site was determined by their distribution in Aitken et al. (2013), unless otherwise indicated by the individual study. Only data from sites with dietary samples from both periods were analysed (n = 14).

Table A2.4. Results of the generalized linear model for the effect of major land use (conservation and pastoralism) on the frequency of occurrence of the most commonly recorded species in dingo diet. Negative estimates indicate the species was recorded more frequently in the diet of dingoes from conservation areas, and positive estimates indicate a higher FO at pastoral sites. Significant p values are highlighted in bold.

Species	Estimate	SE	*p*-value
Pseudomys hermannsburgensis	**-2.681**	**0.285**	**< 0.001**
Mus musculus	0.391	0.269	0.147
Sminthopsis macroura	**1.610**	**0.714**	**0.024**
Leggadina forresti	**-3.140**	**0.674**	**< 0.001**
Notomys alexis	0.152	0.306	0.619
Rattus villosissimus	**-0.824**	**0.182**	**< 0.001**
Oryctolagus cuniculus	0.113	0.124	0.364
Tachyglossus aculeatus	**-1.983**	**0.344**	**< 0.001**
Felis catus	**-1.279**	**0.234**	**< 0.001**
Macropus rufus	**-0.400**	**0.170**	**0.019**
Macropus robustus	**-2.677**	**0.177**	**< 0.001**
Bos taurus	**1.073**	**0.312**	**0.001**

Table A2.5. Model summary for the per-species probability of occurring in a dietary sample using only species that were present in the diet of dingoes. Shown are coefficient estimates, standard errors (SE) and p-values from our generalised linear mixed-effects model, which assumed correlated intercepts and period effects by species. Significance is indicated in bold.

Model	Variables	Estimate	SE	*p*-value
P(occurrence) ~ (1 + Period | Species) + Class + Class:Period	(Intercept)	-4.114	0.683	< 0.001
	Medium	-0.126	0.929	0.892
	Large	0.309	1.012	0.760
	Small:Boom	-0.338	0.556	0.544
	Medium:Boom	-0.712	0.629	0.258
	Large:Boom	**-1.951**	**0.765**	**0.011 ***

Table A2.6. Species level probability of presence ±95% CI for each species derived from the fitted mixed-effects model. Key species are highlighted in grey and are also indicated in Fig.4 5.

Species	Boom [LCL,UCL]	Non-boom [LCL,UCL]
Pseudomys hermannsburgensis	0.006 [0.002, 0.018]	0.008 [0.006, 0.011]
Sminthopsis crassicaudata	0.001 [0, 0.008]	0.001 [0, 0.002]
Leggadina forresti	0.001 [0, 0.008]	0.002 [0.001, 0.003]
Sminthopsis macroura	0.005 [0.002, 0.013]	0.036 [0.031, 0.041]
Mus musculus	0.156 [0.12, 0.2]	0.062 [0.056, 0.07]
Pseudomys desertor	0.002 [0, 0.016]	0.003 [0.001, 0.006]
Notomys fuscus	0.119 [0.084, 0.164]	0.073 [0.065, 0.081]
Notomys alexis	0.015 [0.006, 0.04]	0.066 [0.051, 0.084]
Notomys cervinus	0.004 [0, 0.187]	0.012 [0.002, 0.069]
Pseudomys australis	0 [0, 0.007]	0.001 [0, 0.003]
Dasycercus blythi	0.001 [0, 0.05]	0.003 [0.001, 0.016]
Dasycercus cristicauda	0.002 [0, 0.089]	0.006 [0.001, 0.037]
Rattus villosissimus	0.329 [0.27, 0.394]	0.074 [0.066, 0.082]
Oryctolagus cuniculus	0.203 [0.171, 0.24]	0.385 [0.371, 0.399]
Tachyglossus aculeatus	0 [0, 0.004]	0.001 [0, 0.002]
Felis catus	0.006 [0.002, 0.021]	0.006 [0.004, 0.008]
Macropus rufus	0.041 [0.028, 0.061]	0.067 [0.06, 0.074]
Macropus robustus	0.001 [0, 0.006]	0.003 [0.002, 0.006]
Sus scrofa	0 [0, 0.003]	0.001 [0.001, 0.003]
Equus caballus	0 [0, 0.01]	0.003 [0.001, 0.009]
Bos taurus	0.029 [0.019, 0.044]	0.142 [0.133, 0.152]
Camelus dromedarius	0 [0, 0.002]	0.001 [0, 0.002]

Table A2.7. Shannon's diversity (H) index for the mammalian portion of dingo diet at each study site, divided into boom and non-boom periods. Higher H values indicate a higher number of mammal species were recorded in dingo diet more evenly.

Study site	Period	Major land use	*H*
Kalamurina	Nonboom	Conservation	1.01
Kalamurina	Boom	Conservation	0.79
Ethabuka	Nonboom	Conservation	1.93
Ethabuka	Boom	Conservation	1.06
Wahgunyah NP	Nonboom	Conservation	0.85
Rangelands	Nonboom	Conservation	1.43
Tennant	Nonboom	Conservation	1.75
MacDonnell Ranges	Nonboom	Conservation	1.90
Erldunda	Nonboom	Pastoralism	1.60
Erldunda	Boom	Pastoralism	0.72
Lambina	Nonboom	Pastoralism	1.37
Lambina	Boom	Pastoralism	0.86
Quinyambie	Nonboom	Pastoralism	0.84
Quinyambie	Boom	Pastoralism	1.18
Todmorden	Nonboom	Pastoralism	1.29
Todmorden	Boom	Pastoralism	1.57
Bunda Plateau	Nonboom	Pastoralism	1.04
Tanami	Nonboom	Pastoralism	2.18
Strzelecki	Nonboom	Pastoralism	1.00
Cordillo Downs	Nonboom	Pastoralism	1.85
Cordillo Downs	Boom	Pastoralism	0.54

Table A2.8. Model summary for the effect of land use and inter-site distance on dietary overlap (Pianka's index). Model estimates, standard errors (SE), and p values for our generalised linear model. Significant effects are indicated in bold.

Model	Variables	Estimate	SE	*p* value
Overlap(Pianka) ~ Distance:Land use + Distance	(Intercept)	0.574	0.004	< 0.001
	Distance	< -0.001	< 0.001	0.96
	Pastoralism	**0.1**	**0.004**	**0.026**
	Conservation/ Pastoralism	0.001	0.004	0.71
	Distance:Conservation/ Pastoralism	< -0.001	< 0.001	0.86
	Distance:Pastoralism	< -0.001	< 0.001	0.72

Table A2.9. Asymptote estimates for the cumulative Shannon diversity of all food items in dingo diet. N is the number of dietary samples, Ĥ is the estimate of the asymptote and n̂ is the estimated number of samples needed to reach the asymptote. A dash indicates a sample size estimate above the total number of dietary samples collected for that site. Information below the solid line represent the sample size estimates not determined by this study.

Site	Period	N	Ĥ95%	*n̂*	Ĥ97.5%	*n̂*	Ĥ99%	*n̂*
Kalamurina	Boom	53	1.497	21	1.460	37	1.482	-
Kalamurina	Nonboom	82	1.758	19	1.804	36	1.832	70
Ethabuka	Boom	89	1.504	37	1.544	63	1.568	-
Ethabuka	Nonboom	133	2.116	27	2.171	51	2.205	109
Cordillo Downs	Nonboom	1311	2.162	34	2.219	64	2.253	132
Cordillo Downs	Boom	377	1.072	46	1.100	79	1.117	200
Lambina	Boom	76	1.411	37	1.448	-	1.471	-
Lambina	Nonboom	71	1.764	22	1.811	36	1.839	64
Todmorden	Boom	279	1.881	37	1.931	68	1.960	136
Todmorden	Nonboom	394	1.737	44	1.783	92	1.810	229
Quinyambie	Boom	259	1.501	33	1.540	66	1.564	161
Quinyambie	Nonboom	2220	1.476	55	1.515	110	1.538	250
Strzelecki	Nonboom	146		40				
Wahgunyah	Nonboom	34		25				
Rangelands	Nonboom	37		15				
MacDonnell Ranges	Nonboom	98		30				

Table A2.10. Pairwise comparisons of dietary overlap (above diagonal) and approximate distance (below diagonal) between sites. Dietary overlap was measured using Pianka's index and distance is given in kilometres. Conservation sites are shown with an asterisk (*).

	Erldunda	Bunda Plateau	Tennant*	Strzelecki	Wahgunyah NP*	Cordillo Downs	Lambina	Todmorden	Tanami	Quinyambie	Rangelands*	Ethabuka*	MacDonnell Ranges*	Kalamurina*
Erldunda		0.71	0.52	0.69	0.62	0.65	0.76	0.66	0.68	0.62	0.57	0.59	0.61	0.60
Bunda Plateau	1000		0.57	0.70	0.54	0.63	0.55	0.61	0.75	0.60	0.49	0.54	0.72	0.62
Tennant*	670	1480		0.60	0.55	0.50	0.54	0.54	0.66	0.50	0.59	0.53	0.57	0.52
Strzelecki	1015	1635	1525		0.57	0.61	0.57	0.65	0.75	0.60	0.49	0.55	0.72	0.58
Wahgunyah NP*	740	650	1400	1005		0.59	0.50	0.51	0.70	0.55	0.44	0.54	0.69	0.64
Cordillo Downs	840	1675	1220	395	1130		0.78	0.66	0.61	0.65	0.59	0.54	0.56	0.54
Lambina	220	1000	875	820	600	715		0.76	0.71	0.60	0.49	0.60	0.65	0.55
Todmorden	275	1045	915	755	610	655	65		0.69	0.57	0.55	0.55	0.70	0.54
Tanami	615	1235	300	1595	1265	1340	835	890		0.63	0.70	0.66	0.63	0.62
Quinyambie	1030	1660	1535	25	1035	390	840	775	1610		0.54	0.52	0.55	0.54
Rangelands*	1855	1005	2085	2635	1655	1635	1925	1980	1785	2655		0.58	0.68	0.56
Ethabuka*	610	1580	820	765	1155	405	590	560	980	770	2465		0.54	0.54
MacDonnell Ranges*	225	1080	465	1205	935	990	445	495	395	1225	1835	680		0.62
Kalamurina*	625	1375	1140	400	825	305	450	385	1195	415	2345	455	810	

Additional detail on study site and morphological analysis of scats

The region’s climate is arid, characterised by very hot summers and mild winters; mean temperatures ranging from 23.1˚ - 37.9˚ in the hottest month (January) and 5.9˚ - 19.7˚ in the coldest month (July; Bureau of Meteorology, 2017). Kalamurina is one of the driest places in Australia with a median annual rainfall of 133.5 mm (Bureau of Meteorology, 2017). It is located in the Simpson-Strzelecki Dunes Bioregion and the dominant landform is sand dunes (< 18 m), with scattered floodplains, claypans and salt lakes. The dune crests and flanks are dominated by sandhill canegrass (*Zygochloa paradoxa*) with an overstorey of scattered shrubs including species of *Acacia* and *Hakea.* The dune swales are characterised by chenopod shrubland where the main vegetation are species of *Acacia*, *Eremophila*, and *Atriplex*. Extensive coolabah (*Eucalyptus coolabah*) woodlands exist along the banks and floodplains of the larger watercourses.

Predator scats were collected year round in 2011 and 2012 (boom), and primarily during autumn and spring of 2016 and 2017 (non-boom). Throughout the study period scats were collected opportunistically along vehicle tracks (c. 150 km), creek lines, sand dunes/ swales, around water sources, and from individuals captured as part of a separate study. Samples of unknown origin were matched to a predator based on size, shape, and scent as described by Triggs (1996), as well as placement in the environment. We estimated the approximate age of each scat by its colour, odour and apparent moisture content; only collecting samples deemed to be younger than three months. A single scat was defined as one or more faecal pellets that appeared to have been deposited in one event. Scats were placed into paper bags and labelled with the location (latitude and longitude), date, predator species and where relevant, individual identification and sex.

We sterilised samples by oven-drying at 60˚ for 24 hours before placing them in individual fabric bags (30 denier) where they were soaked in water and detergent for up to 24 hours prior to being rinsed under running water. After washing and rinsing, only indigestible fragments of prey remained (hair, teeth, bones, scales, claws, feathers, and exoskeletons). Prey remains were initially sorted to the lowest possible taxonomic level with the aid of a dissecting microscope. Small mammals were often identified by jaw bone however, a representative sample of all hair in each scat was examined using cross-sections and whole mounts under a compound microscope (10x and 40x lenses). Identification of hairs was made using a reference collection and the hair analysis software package 'Hair ID- An Interactive Tool for Identifying Australian Mammalian Hair' (Brunner and Triggs, 2002). Reptiles, birds and invertebrates were classified to the class level.

APPENDIX 3. Supplementary material to Chapter 4

Table A3.1. Number of seconds/ acceleration data points that the focal dingo was observed doing each behaviour, summed over eight sampling sessions.

	Individual dingo			
Behaviour	Dingo 1	Dingo 2	Dingo 3	Total
Lat. lying inactive	115	38	14	167
Stern. lying inactive	45	20	0	65
Lat. lying alert	2	0	113	115
Stern. lying alert	194	245	481	920
Sitting	221	41	28	290
Standing	1703	791	1230	3724
Drinking	0	15	23	38
Lat. lying groom	0	0	58	58
Searching	431	253	332	1016
Walking	763	611	569	1943
Collar discomfort	28	16	0	44
Trotting	150	129	139	418
Playing	62	215	16	293
Running	122	82	65	269
Total	3836	2456	3068	9360

Table A3.2. Nine sets of predictor variables were generated to test the effect of variable choice and number on model accuracy.

Predictor set	Number of variables	Predictor variables
1	3	Axes(x,y,z)
2	11	Axes(x,y,z), SMA, WL, DBA(x,y,z), ODBA, VeDBA, Q
3	14	Axes(x,y,z), Absolute(x,y,z), DBA(x,y,z), ODBA, VeDBA, Q, SMA, WL
4	26	Axes(x,y,z), mean(x,y,z), min.(x,y,z), max.(x,y,z), standard deviation(x,y,z), correlation(xy,yz,xz), skewness(x,y,z,Q), kurtosis(x,y,z,Q)
5	32	Axes(x,y,z), mean(x,y,z), min.(x,y,z), max.(x,y,z), standard deviation(x,y,z), correlation(xy,yz,xz), skewness(x,y,z), kurtosis(x,y,z), SMA, WL, DBA(x,y,z), ODBA, VeDBA, Q
6	38	Axes(x,y,z), mean(x,y,z), min.(x,y,z,Q,ODBA,VeDBA,DBA(x,y,z)), max.(x,y,z,Q,ODBA,VeDBA,DBA(x,y,z)), standard deviation(x,y,z,Q), correlation(xy,yz,xz), SMA, DBA(x,y,z), ODBA, VeDBA, Q
7	49	Axes(x,y,z), mean(x,y,z,Q,difference(x,y,z),absolute(x,y,z)), difference(x,y,z), DBA(x,y,z), ODBA, VeDBA, Q, standard deviation(x,y,z,Q), correlation(xy,yz,xz), absolute(correlation(xy,yz,xz)), min.(DBA(x,y,z),ODBA,VeDBA)), max.(DBA(x,y,z),ODBA,VeDBA), SMA, WL, skewness(x,y,z,Q)
8	53	Axes(x,y,z), absolute(x,y,z), mean(x,y,z), standard deviation(x,y,z,Q), correlation(xy,yz,xz,absolute(xy,yz,xz)), min.(x,y,z,Q,DBA(x,y,z),ODBA,VeDBA), max.(x,y,z,Q,DBA(x,y,z),ODBA,VeDBA), absolute(min.(x,y,z),max.(x,y,z)), SMA, WL, skewness(x,y,z,Q), kurtosis(x,y,z,Q)

9	69	Axes(x,y,z), absolute(x,y,z,mean(x,y,z)), mean(x,y,z,Q,difference(x,y,z)), difference(x,y,z), DBA(x,y,z), ODBA, VeDBA, Q, standard deviation(x,y,z,Q), correlation(xy,yz,xz,absolute(xy,yz,xz)), min.(x,y,z,Q,DBA(x,y,z),absolute(x,y,z),ODBA,VeDBA), max.(x,y,z,Q,DBA(x,y,z),absolute(x,y,z),ODBA,VeDBA), SMA, WL, skewness(x,y,z,Q), kurtosis(x,y,z,Q)

Table A3.3. Top 50 best performing Random Forest models, ranked by TSS score. Moving window centred on each data point. Rank 3 (in bold) was selected to be our best model because it possessed high evaluation metrics when using a low number of predictor variables and decision trees (i.e. most parsimonious model with high TSS), and had the lowest range of accuracy measures across the 14 behaviours.

Rank	Predictor variable set (number of predictors)	Moving window size (seconds)	Number of trees	*TSS*	*MCC*	*F*-measure	Precision	Sensitivity	Specificity
1	8 (53)	64	5000	0.87	0.89	0.89	0.91	0.88	0.99
2	8	32	10000	0.87	0.88	0.89	0.91	0.88	0.99
3	4 (26)	64	1000	0.87	0.89	0.89	0.92	0.88	0.99
4	4	64	10000	0.87	0.88	0.89	0.91	0.88	0.99
5	8	64	10000	0.86	0.88	0.89	0.91	0.88	0.99
6	8	64	500	0.86	0.88	0.89	0.91	0.88	0.99
7	4	32	2500	0.86	0.88	0.89	0.91	0.87	0.99
8	4	64	500	0.86	0.88	0.89	0.91	0.87	0.99
9	4	32	1000	0.86	0.87	0.88	0.91	0.87	0.99
10	8	32	1000	0.86	0.87	0.88	0.9	0.87	0.99
11	8	64	2500	0.86	0.88	0.88	0.91	0.87	0.99
12	4	128	10000	0.86	0.87	0.88	0.9	0.87	0.99
13	8	16	10000	0.86	0.88	0.89	0.92	0.87	0.99
14	8	16	5000	0.86	0.88	0.89	0.92	0.87	0.99

15	8	32	2500	0.86	0.87	0.88	0.9	0.87	0.99
16	8	32	5000	0.86	0.87	0.88	0.91	0.87	0.99
17	4	64	2500	0.85	0.87	0.88	0.91	0.87	0.99
18	4	64	5000	0.85	0.87	0.88	0.91	0.86	0.99
19	8	64	1000	0.85	0.87	0.88	0.9	0.86	0.99
20	4	128	5000	0.85	0.87	0.87	0.9	0.86	0.99
21	4	32	500	0.85	0.86	0.87	0.89	0.86	0.99
22	8	128	1000	0.85	0.86	0.87	0.9	0.86	0.99
23	4	32	10000	0.85	0.87	0.88	0.9	0.86	0.99
24	4	128	1000	0.85	0.86	0.87	0.89	0.86	0.99
25	4	16	5000	0.85	0.87	0.88	0.92	0.86	0.99
26	4	128	500	0.85	0.87	0.88	0.9	0.86	0.99
27	4	16	500	0.85	0.87	0.88	0.91	0.86	0.99
28	8	32	500	0.85	0.86	0.87	0.9	0.86	0.99
29	8	16	2500	0.85	0.87	0.88	0.92	0.86	0.99
30	8	16	500	0.85	0.87	0.88	0.91	0.86	0.99
31	4	32	5000	0.84	0.86	0.87	0.9	0.86	0.99
32	8	128	10000	0.84	0.86	0.87	0.9	0.86	0.99
33	4	128	2500	0.84	0.86	0.87	0.9	0.85	0.99
34	6 (38)	32	2500	0.84	0.86	0.87	0.89	0.85	0.99
35	4	16	10000	0.84	0.86	0.87	0.91	0.85	0.99
36	4	16	1000	0.84	0.87	0.88	0.92	0.85	0.99

37	6	32	500	0.84	0.86	0.87	0.9	0.85	0.99
38	6	16	5000	0.84	0.86	0.87	0.91	0.85	0.99
39	6	64	1000	0.84	0.86	0.87	0.89	0.85	0.99
40	8	128	5000	0.84	0.86	0.87	0.9	0.85	0.99
41	6	32	5000	0.84	0.86	0.87	0.89	0.85	0.99
42	8	16	1000	0.84	0.87	0.87	0.91	0.85	0.99
43	9 (69)	32	2500	0.84	0.86	0.87	0.91	0.85	0.99
44	9	32	500	0.84	0.86	0.87	0.89	0.85	0.99
45	6	32	7500	0.84	0.85	0.86	0.89	0.85	0.99
46	4	16	2500	0.83	0.87	0.87	0.92	0.85	0.99
47	6	16	500	0.83	0.86	0.87	0.91	0.85	0.99
48	8	128	500	0.83	0.85	0.86	0.89	0.85	0.99
49	9	32	1000	0.83	0.85	0.86	0.9	0.85	0.99
50	6	16	10000	0.83	0.86	0.87	0.9	0.85	0.99

Table A3.4. Confusion matrix comparing the predicted behaviours (rows) from our best random forest model to true behaviours (columns), confirmed by video recordings. True positive (TP) classifications are denoted in bold and threshold was set at 0.3.

	Lat. lying inactive	Stern. lying inactive	Lat. lying alert	Stern. lying alert	Sitting	Standing	Drinking	Lat. lying groom	Searching	Walking	Collar discomfort	Trotting	Playing	Running
Lat. lying inactive	**17**	0	0	0	0	0	0	0	0	0	0	0	0	0
Stern. lying inactive	0	**6**	0	0	0	0	0	0	0	0	0	0	0	0
Lat. lying alert	0	0	**10**	0	0	0	0	0	0	0	0	0	0	0
Stern. lying alert	0	1	0	**85**	0	3	0	0	0	0	0	0	0	0
Sitting	0	0	0	0	**25**	0	0	0	0	0	0	1	0	0
Standing	0	0	1	0	0	**344**	0	0	2	26	0	6	0	4
Drinking	0	0	0	0	0	0	**3**	0	0	0	0	0	0	0
Lat. lying groom	0	0	0	0	0	0	0	**6**	0	0	0	0	0	0
Searching	0	0	0	2	0	2	0	0	**93**	8	0	0	0	3
Walking	0	0	0	0	3	14	1	0	4	**154**	0	14	1	3
Collar discomfort	0	0	0	0	0	0	0	0	0	0	**4**	0	0	0
Trotting	0	0	0	0	0	0	0	0	0	2	0	**17**	1	1
Playing	0	0	0	0	0	0	0	0	1	0	0	0	**26**	0
Running	0	0	0	0	0	1	0	0	0	1	0	2	0	**14**
Not classified*	0	0	0	0	0	2	0	0	0	0	0	1	0	1

** Denotes omission, where the model did not assign any behaviour to the input data at our chosen threshold of 0.3.*

Table A3.5. Confusion matrix displaying the paired comparisons of the Tukey's HSD test. P-values are presented above the diagonal and difference between the means is presented below the diagonal. Row and column numbers correspond to: Lat. lying inactive (1), Stern. lying inactive (2), Lat. lying alert (3), Stern. lying alert (4), Sitting (5), Standing (6), Drinking (7), Lat. lying groom (8), Searching (9), Walking (10), Collar discomfort (11), Trotting (12), Playing (13), Running (14).

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1		1.00	0.997	0.255	0.174	<0.001	0.078	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
2	4.39		1.00	0.987	0.933	0.095	0.376	0.027	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
3	11.00	6.60		1.00	0.922	0.07	0.538	0.038	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
4	17.85	13.46	6.85		1.00	<0.001	0.709	0.038	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
5	21.91	17.52	10.92	4.06		0.276	0.917	0.192	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
6	34.76	30.36	23.76	16.91	12.84			0.845	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
7	44.61	40.22	33.61	26.76	22.70	9.86		1.00	0.505	0.104	<0.001	<0.001	<0.001	<0.001
8	53.86	49.47	42.86	36.01	31.95	19.10	9.25		0.761	0.168	<0.001	<0.001	<0.001	<0.001
9	74.87	70.47	63.87	57.02	52.95	40.11	30.26	21.01		0.123	<0.001	<0.001	<0.001	<0.001
10	83.98	79.59	72.99	66.14	62.07	49.23	39.38	30.13	9.12		<0.001	<0.001	<0.001	<0.001
11	165.03	160.63	154.03	147.18	143.11	130.27	120.42	111.17	90.16	81.04		1.00	<0.001	<0.001
12	175.82	171.43	164.82	157.97	153.91	141.06	131.21	121.96	100.95	91.83	10.79		<0.001	<0.001
13	237.80	233.41	226.81	219.95	215.89	203.05	193.19	183.94	162.94	153.82	72.78	61.98		<0.001
14	374.32	369.93	363.32	356.47	352.41	339.57	329.71	320.46	299.45	290.34	209.29	198.50	136.52	

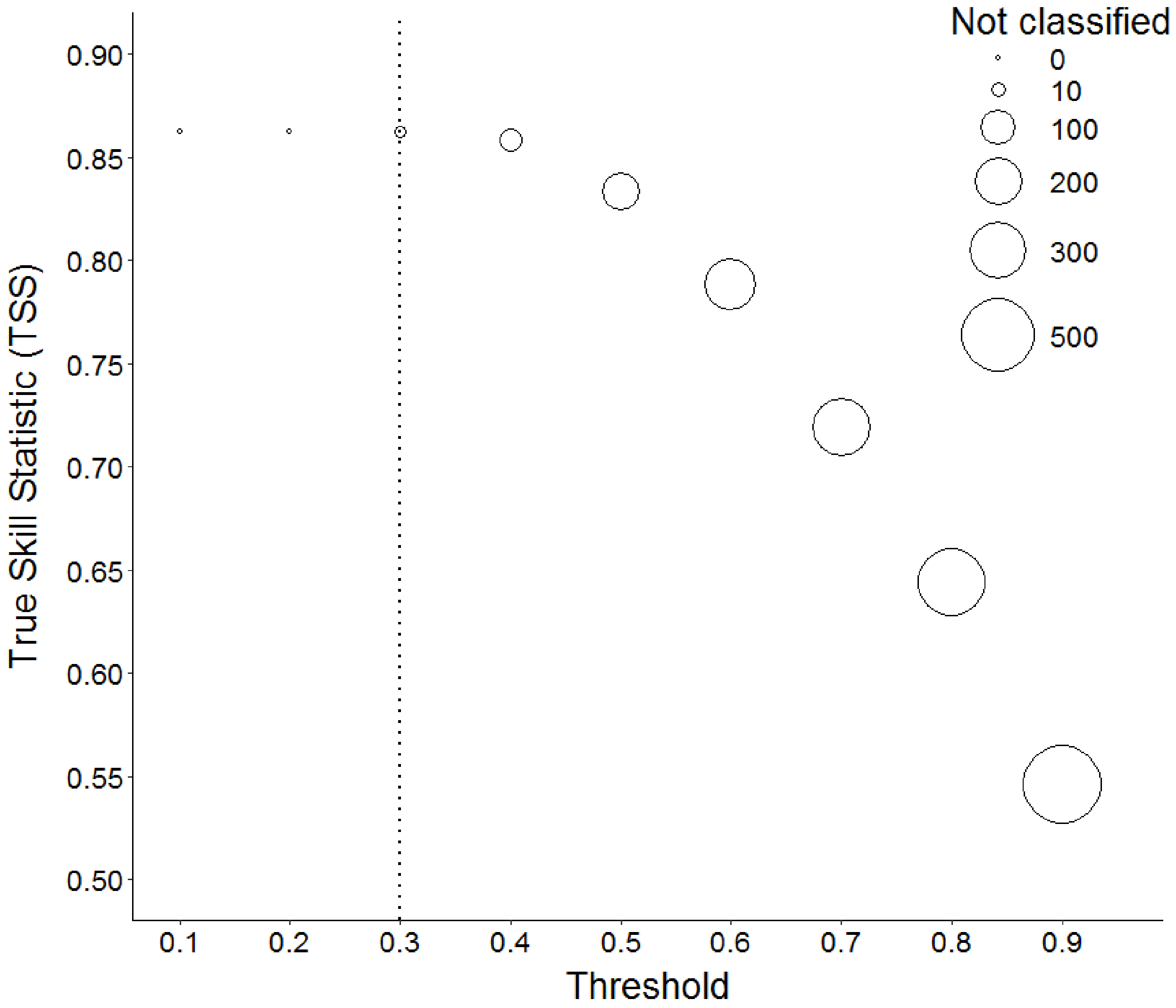

Figure A3.1. The mean predictive ability (TSS) of our best model weighted by the number of samples that could not be classified at each threshold. The dotted line indicates the threshold we assigned to our model. Mean TSS scores were calculated from our ten-fold out-of-sample validation.

APPENDIX 4. Supplementary material to Chapter 5

Table A4.1. Candidate models for estimates of resource selection in dingoes at Kalamurina. Our selected individual model (Model 22) is in bold. Individuals JT06 and JT07 were fit with the same candidate set of models minus any interaction with season (they recorded data from only one season).

Name	Model
Null	1
Model 1	Landscape feature
Model 2	Landscape feature + Landscape feature:Time-of-day
Model 3	Landscape feature + Landscape feature:season
Model 4	Landscape feature + Landscape feature:Temperature
Model 5	Landscape feature + Landscape feature:month
Model 6	Landscape feature + Landscape feature:NDVI
Model 7	Landscape feature + Landscape feature:season + Landscape feature:Temperature + Wind
Model 8	Landscape feature + Landscape feature:rain + Landscape feature:Temperature
Model 9	Landscape feature + Shelters
Model 10	Landscape feature + Shelters + Time-of-day
Model 11	Landscape feature + Landscape feature:season + Shelters
Model 12	Landscape feature + Shelters + season
Model 13	Landscape feature + Shelters:season + Shelters:Time-of-day
Model 14	Landscape feature + Landscape feature:season + Shelters + Dist.watercourses

Model 15	Landscape feature + Landscape feature:season + Shelters + Dist.watercourses:Temperature
Model 16	Landscape feature + Landscape feature:season + Shelters + Dist.watercourses:Time-of-day
Model 17	Landscape feature + Landscape feature:season + Shelters + Dist.watercourses:season
Model 18	Landscape feature + Landscape feature:season + Shelters + Dist.watercourses + Dist.flats
Model 19	Landscape feature + Landscape feature:season + Shelters + Dist.watercourses + Dist.flats + Dist.woodlands
Model 20	Landscape feature + Landscape feature:season + Shelters + Dist.watercourses + Dist.flats + Dist.woodlands + Dist.tracks
Model 21	Landscape feature + Landscape feature:season + Shelters + Dist.watercourses + Dist.flats + Dist.woodlands + Dist.tracks + Dist.salt
Model 22	**Landscape feature + Landscape feature:season + Shelters + Dist.watercourses + Dist.flats + Dist.woodlands + Dist.tracks + Dist.salt + Dist.shrubland**

Table A4.2. Model summary for the effect of landscape features and sex on the distances moved by dingoes, with female and desert woodland as reference categories. Model estimates, standard errors (SE), and p values for our generalised linear model are presented.

Model formula = Distance ~ sex + landscape feature + sex : landscape feature.

Model	Variables	Estimate	SE	*p*-value
	(Intercept)	-0.1491	0.0107	< 0.001
sex	Male	0.1204	0.0393	0.0022
landscape features	Shelter	-0.3308	0.0140	< 0.001
	Sand dunes	0.0688	0.0123	< 0.001
	Flats	0.2445	0.0117	< 0.001
	Salt lakes	1.7566	0.0475	< 0.001
	Low shrubland	0.2475	0.0165	< 0.001
	Tracks	0.9002	0.0248	< 0.001
	Watercourses	0.0579	0.0148	0.0001
sex : landscape features	Male: Shelter	-0.0599	0.0444	0.1776
	Male: Sand dunes	0.0147	0.0409	0.7187
	Male: Flats	-0.0906	0.0404	0.0249
	Male: Salt lakes	0.6932	0.0834	< 0.001
	Male: Low shrubland	-0.0273	0.0512	0.5937
	Male: Tracks	1.0646	0.0706	< 0.001
	Male: Watercourses	-0.0303	0.0502	0.5464

APPENDIX 5. Supplementary material to Chapter 6

Table A5.1. List of candidate models fit with our environmental variables. We ranked our generalised linear mixed-effect models by AICc and R^2.

Rank	Models	AICc	R^2
1	log(ODBA) ~ (1 + Behaviour|ID) + (1|J.day) + Landscape feature + Time of day + Period:Time of day	44486	0.57
2	log(ODBA) ~ (1 + Behaviour|ID) + (1|J.day) + Landscape feature + Time of day + Landscape feature:Time of day	44491	0.57
3	log(ODBA) ~ (1 + Behaviour|ID) + (1|J.day) + Landscape feature + Time of day + Landscape feature:Time of day + Rain	44496	0.57
4	log(ODBA) ~ (1 + Behaviour|ID) + (1|J.day) + Landscape feature + Time of day	44510	0.55
5	log(ODBA) ~ (1 + Behaviour|ID) + (1|J.day) + Landscape feature + Period + Time of day	44516	0.57
6	log(ODBA) ~ (1 + Behaviour|ID) + (1|J.day) + Landscape feature	44574	0.56
7	log(ODBA) ~ (1 + Landscape feature|ID) + Landscape feature + Rain + Behaviour	44649	0.35
8	log(ODBA) ~ (1 + Behaviour|ID) + Landscape feature + Rain	44796	0.54
9	log(ODBA) ~ (1 + Behaviour|ID) + Landscape feature + Rain + Period + Temperature	44812	0.56
10	log(ODBA) ~ (1|ID) + Landscape feature + wind + Behaviour + Landscape feature:Temperature	44853	0.32
11	log(ODBA) ~ (1|ID) + (1|J.day) + Landscape feature + Time of day + Period	47747	0.14
12	log(ODBA) ~ (1|ID) + (1|J.day) + Landscape feature + Time of day	47752	0.14
13	log(ODBA) ~ (1|ID) + (1|J.day) + Landscape feature + Period	47893	0.13
14	log(ODBA) ~ (1|ID) + (1|J.day) + Landscape feature	47898	0.13
15	log(ODBA) ~ (1|ID) + (1|J.day) + Landscape feature + Rain	47903	0.13
16	log(ODBA) ~ (1 + Landscape feature|ID) + Landscape feature + Time of day + Period	47974	0.13
17	log(ODBA) ~ (1|ID) + Landscaped feature + Time of day + Temperature + Period	48090	0.08

18	log(ODBA) ~ (1|ID) + Landscape feature + Time of day + Period	48106	0.08
19	log(ODBA) ~ (1|ID) + Landscape feature + Time of day	48108	0.09
20	log(ODBA) ~ (1|ID) + Landscape feature + Temperature	48236	0.07
21	log(ODBA) ~ (1|ID) + Landscape feature + Wind	48237	0.07
22	log(ODBA) ~ (1|ID) + Landscape feature	48240	0.08
23	log(ODBA) ~ (1|ID) + Landscape feature + Energy + Period	48241	0.10
24	log(ODBA) ~ (1|ID) + Landscape feature:Energy	48632	0.08
25	log(ODBA) ~ 1 + (1|ID)	48825	0.03

Table A5.2. Proportion of each day spent stationary, walking, and running.

Dingo ID	Sex	Stationary	Walking	Running	Season
jt04	F	0.47	0.35	0.18	autumn-winter
jt05	F	0.38	0.23	0.40	autumn-winter
jt07	M	0.54	0.46	< 0.01	autumn-winter
jt32	F	0.97	0.02	0.01	spring-summer
jt34	F	0.93	0.01	0.07	spring-summer
jt36	F	0.87	0.01	0.12	spring-summer
jt37	M	0.88	0.02	0.10	spring-summer

Table A5.3. Model summary showing the effect of landscape features, time of day, and period on dingo activity (ODBA). Model estimates, standard errors (SE) and p-values for our correlated intercepts and slopes linear mixed model are presented. Significance is indicated in bold.

Model	Variables	Estimate	SE	*p* value
log(ODBA) ~ (1 + Behaviour|ID) + (1|J.day) +	**(Intercept)**	**4.818**	**0.055**	**< 0.001**
Landscape feature +	**Flats**	**0.175**	**0.029**	**< 0.001**
Time of day +	**Salt lakes**	**0.593**	**0.120**	**< 0.001**
Period:Time of day	**Shelter**	**-0.495**	**0.040**	**< 0.001**
	Low shrubland	0.055	0.071	0.439
	Tracks	**0.486**	**0.083**	**< 0.001**
	Watercourses	-0.075	0.054	0.166
	Desert woodland	0.026	0.065	0.688
	Night	**-0.174**	**0.035**	**< 0.001**
	Twilight	**0.235**	**0.036**	**< 0.001**
	Day:Winter	0.000	0.071	0.998
	Night:Winter	0.217	0.072	0.005
	Twilight:Winter	-0.174	0.074	0.022