

Resource use and coexistence of sympatric Tasmanian devils and spotted-tailed quolls



Georgina Elizabeth Andersen (MSc, BSc)



Submitted in fulfilment of the requirements for the
Degree of Doctor of Philosophy
School of Biological Sciences
University of Tasmania
May 2016

Statements by the author

Declaration of originality

This thesis contains no material which has been accepted for a degree or diploma by the University or any other institution, except by way of background information and duly acknowledged in the thesis, and to the best of my knowledge and belief no material previously published or written by another person except where due acknowledgement is made in the text of the thesis, nor does the thesis contain any material that infringes copyright.

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The research associated with this thesis was conducted in compliance with the Australian Code of Practice for the Care and Use of Animals for Scientific Purposes. The research presented in this thesis was carried out in accordance with the University of Tasmania Animal Ethics Committee Permit # A12361 and with permission from the Tasmanian Department of Primary Industries, Parks, Water and Environment (DPIPWE) under the scientific permits TFA12166 and TFA13969.

Signed:

Georgina E. Andersen

03/05/2016

Statement of co-authorship

The following people contributed to the work undertaken as part of this thesis:

Georgina Andersen (Candidate), School of Biological Sciences, University of Tasmania, Hobart, Australia

Menna Jones (Primary supervisor), School of Biological Sciences, University of Tasmania, Hobart, Australia

Christopher Johnson (Secondary supervisor), School of Biological Sciences, University of Tasmania, Hobart, Australia

Leon Barmuta (Co-author on chapter 2 and 4), School of Biological Sciences, University of Tasmania, Hobart, Australia

Chapter details and relative author contributions are listed below:

Chapter 2 is in preparation for publication:

Andersen, G.E., Johnson, C.N., Barmuta, L.A., and Jones, M.E. Diet composition and overlap of two sympatric carnivores, the Tasmanian devil and spotted-tailed quoll

Georgina Andersen was the primary investigator and lead author. Chris Johnson and Menna Jones contributed to the idea, the study design and edited chapters. Leon Barmuta assisted with statistical advice.

Chapter 3 is in preparation for *Wildlife Research*:

Andersen, G.E., Johnson, C.N., and Jones, M.E. Spatial ecology of sympatric Tasmanian devils and spotted-tailed quolls.

Georgina Andersen was the primary investigator and lead author. Chris Johnson and Menna Jones contributed to the idea, the study design and edited chapters.

Chapter 4 is in review in *Journal of Applied Ecology*:

Andersen, G.E., Johnson, C.N., Barmuta, L.A., and Jones, M.E. Anthropogenic habitat modification enhances traveling and hunting opportunities for two medium-sized carnivores.

Georgina Andersen was the primary investigator and lead author. Chris Johnson and Menna Jones contributed to the idea, the study design and edited chapters. Leon Barmuta assisted with statistical advice.

Chapter 5 is published in *Behavioural Ecology and Sociobiology*:

Andersen, G.E., Johnson, C.N., and Jones, M.E. Sympatric predator odour reveals a competitive relationship in size-structured mammalian carnivores.

Georgina Andersen was the primary investigator and lead author. Chris Johnson and Menna Jones contributed to the idea, the study design and edited chapters.

We the undersigned agree with the above stated “proportion of work undertaken” for each of the above submitted peer-reviewed manuscripts contributing to this thesis:

Signed:

Menna Jones
Primary Supervisor
School of Biological Sciences
University of Tasmania
4th November 2016

Signed:

Anthony Koutoulis
Head of School
School of Biological Sciences
University of Tasmania
4th November 2016

Acknowledgements

I would first like to thank my supervisors **Menna Jones** and **Chris Johnson** for letting me embark on this great project, which has taught me so much and challenged me in many ways. Thank you Menna for your enthusiasm, support and many discussions on devils and quolls. Thank you Chris for responding to my email enquiring about a PhD and for offering me such an amazing project. You always helped me see the bigger picture and provided sound advice when I needed it.

Much of my PhD was spent in the beautiful Arthur-Pieman Conservation Area (APCA), which quickly became my second Tassie home. A huge thank you to the rangers of the APCA, for all your help over the past 4 years and for always welcoming me back! A special thanks to **Mel Pfeiffer**, who became a good friend and constant support during field work. Thanks for putting up with some major bush bashing expeditions after dropped GPS collars and for chats over morning tea. Thank you **Greg Cash** for providing me with the nicest field accommodation, despite the kookaburra attacks!

I could not have successfully completed field work without the help of all my volunteers. So a massive thank you to all those that helped me check traps at the crack of dawn and radio-track/bush bash come rain or shine. My field work acknowledgements would not be complete without thanking all the devils and quolls that took part in this study. I have had some truly memorable experiences during field work that I will always cherish.

I also would like to thank several funding bodies who made this project possible: The Holsworth Wildlife Research Endowment, the Dr Eric Guiler Tasmanian Devil Research Fund and the Australian Research Council. I was the recipient of the Australian Postgraduate Award and the Tasmanian Devil Elite Scholarship.

To the people at UTAS, a huge thanks goes out to the various office mates that have helped keep me sane, whilst I was in the office: **Halley Durrant**, **Shannon Troy**, **Lisa Cawthen** and **Paul Botwe**. A special thanks to **Halley Durrant**, for all the laughs, the morning coffee chats and just for making being in the office a little more bearable! A

big thanks to **Shannon Troy** for helping me find such an amazing study site, for statistical help and for proof reading my general introduction and discussion. Thanks to the past and present postgrads for your support and friendship especially **Anna Bruniche Olsen, Nick Fountain-Jones, Hugh McGregor, Bronwyn Fancourt, Amy Edwards, Jo McEvoy, Vince Scoleri, Sebastian Comte, David Hamilton and Rowena Hamer.**

I would also like to thank the various staff members in the School of Biological Sciences for help with everything administrative: **Felicity Wilkinson, Adam Stephens, Jenny Sprent, Richard Holmes, Wayne Kelly, Barry Rumbold, Jodi Noble, Clancy Carver and Erik Wapstra.** Thank you to **Barry Wells** for animal welfare advice and teaching me how to sedate feral cats. I'd also like to thank **Katrine Sorensen and Amy Dunlop** for helping to identify prey species from scats. I am also very grateful to **Leon Barmuta and Joanna Potts** for statistical advice and R code help. I would have been seriously stuck without your help!

Thanks to the soccer team at uni for providing some much needed distraction during the write up and for giving me a good excuse to kick something and occasionally someone, oops 😊

To my friends back in Denmark, **Mette Richner, Inge Findorf, Louise Toft Iversen and Maria Jellesmark,** I cannot thank you enough for your love and support throughout the years. Thanks for always remaining my friends no matter where in the world my travels take me!

I am eternally grateful to my parents and sister for your unconditional love and support. You have always encouraged me to follow my dreams and helped me along the way whenever I needed it.

Finally, I would like to dedicate this thesis to the late **Geoff King,** the king of conservation in the North West. My first field season would have been a lot harder without your knowledge of the devils and quolls in the APCA and your help whenever I needed it. As we used to say “long live the devils of Arthur River”

Abstract

Interactions between sympatric carnivores are among the key factors influencing community structure and function, and strongly affecting the population dynamics, distribution and behaviour of the interacting species. Interspecific competition occurs in two ways: exploitation competition occurs when a resource unit is consumed by one species so it cannot be consumed by another; interference competition involves direct aggressive encounters (e.g. fighting) or the threat of aggression, thereby excluding a competitor from a resource. The strength of competition between carnivores varies with factors such as body size, diet and population density. Interspecific competition is often asymmetrical such that the smaller carnivore is most affected. Due to the competitive effects that apex predators can have on sympatric carnivores, their removal from a system can result in a ‘mesopredator release’, which in turn can lead to increased predation on smaller prey species.

To minimise competition and facilitate coexistence, the subordinate species can either avoid spatial overlap with the dominant species or modify temporal or behavioural patterns to reduce the chance of encounters and interactions, but still allow for spatial overlap. The intensity of competition can be reduced in species that have co-existed for a long time through coevolution of divergent ecomorphological and behavioural traits that influence the size and type of prey that are eaten. Current competition can be difficult to measure, as competition may only occur when resources are severely limited such as during drought, and can be subtle where there is a long coevolutionary history among the species. As interspecific competition between carnivores can strongly influence abundance and distribution, understanding how carnivores interact and the extent that competition might influence their ecology and demography is crucial in managing and conserving them.

The Tasmanian devil (*Sarcophilus harrisii*) is Tasmania’s largest marsupial carnivore (5 - 14kg) and coexists with the smaller spotted-tailed quoll (*Dasyurus maculatus*) (0.9 - 5kg). The devil population is currently declining due to a fatal transmissible cancer (devil facial tumour disease, or DFTD) and it has been hypothesized that this could result in a mesopredator release of quolls. There is a

paucity of evidence on the mechanisms by which these species coexist and how interactions may influence distribution, habitat use and temporal activity of the smaller carnivore. I investigated the feeding ecology, movement behaviour, habitat utilisation and interactions between devils and quolls to aid the management and conservation of both species in the wild.

First, I investigated diet composition and overlap of devils and quolls by analysing scats from several sites across Tasmania. Devils and quolls prey predominately on Tasmanian pademelon (*Thylogale billardierii*), Bennett's wallaby (*Macropus rufogriseus*) and birds but also consume a wide range of prey species at lower frequencies. This suggests that they are flexible and opportunistic foragers. Diet overlap was very high (Pianka index: 0.92).

Second, I investigated whether there was temporal separation or spatial separation at the home-range level between devils and quolls. I did this at a site that is still free of DFTD and where devil and quoll densities are high. Using GPS collars, I found little spatial segregation at the home-range and core-area level between devils and quolls. Devils and quolls exhibited different activity patterns during the night. Devils were active from dusk until 4am, while quolls were most active in the early and latter parts of the night. This pattern of activity could allow quolls to avoid agonistic encounters with devils, but could also reflect the different hunting modes of the two species.

Third, I investigated the selection of habitat types and linear features by both devils and quolls in the same landscape. I found that both species respond to moderate anthropogenic modification of intact habitats to enhance movement and facilitate prey acquisition. They used the pasture/cover interface for foraging and roads for movement and foraging. Devils utilised fence lines, while quolls showed little preference for them. Devils and quolls used all vegetation types and did not avoid the agricultural matrix. However, living in these landscapes makes them susceptible to human persecution and collision with vehicles. Human tolerance and mitigation measures to reduce the effect of road kill combined with maintaining connectivity in the agricultural matrix should be the focus of management strategies in these habitats. While moderate landscape alteration can enhance the natural features that devils and quolls use to forage, there is

likely to be a threshold of fragmentation beyond which devils and quolls may not be able to exist.

Fourth, I assessed the behavioural responses of free-living devils and quolls to one other's odour to help understand their behavioural interactions and test mechanisms of competitive interaction. Behavioural responses exhibited by devils and quolls are indicative of a dominant predator-mesopredator relationship and suggest the potential for interspecific competition.

This study found an extensive overlap of resource use, which suggests that current competition is not occurring at my study site. Bennett's wallaby and Tasmanian pademelons, which are the preferred prey species of devils and quolls, both reach high population densities in fragmented areas, such as my study site, and could facilitate coexistence. When resources are abundant, losing devils from an ecosystem is unlikely to result in a mesopredator release of quolls. This study also enhances our understanding of devil and quoll spatial ecology and reveals several conservation and management implications in fragmented areas.

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Chapter 1 General introduction

1.1 The role of large carnivores in structuring communities

Multi-predator systems generally consist of an apex predator (a species with no predators of its own, residing at the top of the food chain) and several mesopredators (smaller predators, occurring in trophic links below the apex predator) that may interact with one other in complex ways. Large mammalian predators have experienced population and range decline during the previous two centuries, due to human persecution together with habitat loss and fragmentation (Morrison *et al.* 2007; Ripple *et al.* 2014). As apex predators interact strongly with many other species in food webs, they play an important ecological role and their removal can have cascading effects that potentially result in loss of biodiversity (Ritchie and Johnson 2009).

Apex predators are often considered to be keystone species because they can have positive effects on biodiversity due to their top-down control on ecosystems through competitive interactions and direct predation (Ritchie and Johnson 2009). Apex predators may regulate ecosystems both by limiting herbivore populations and by suppressing mesopredators (Prugh *et al.* 2009; Estes *et al.* 2011; Ritchie *et al.* 2012). Apex predators have been shown to limit herbivore populations through predation, which reduces browse pressure on vegetation, which in turn increases plant biomass providing food and shelter for other species (Hebblewhite *et al.* 2005; Letnic *et al.* 2009). Furthermore, loss of apex predators can lead to ‘mesopredator release’ (Soule *et al.* 1988) of native or invasive mesopredators, which in turn can result in increased predation pressure on smaller prey species (Prugh *et al.* 2009; Ritchie and Johnson 2009). Mesopredator release has been documented in a wide range of systems and species (Ritchie and Johnson 2009). The majority of studies indicate that this outcome is a common result of loss of apex predators throughout the world. Due to the important effects of apex predators on ecosystems, there is a growing interest worldwide in restoring them where they have disappeared, to manipulate ecological processes and species abundances and thereby achieve biodiversity conservation goals (Estes *et al.* 2011).

While apex predators can exert top-down forces to regulate ecosystems, bottom-up effects and anthropogenic habitat alteration are also important drivers of mesopredator and prey populations, and should also be considered when evaluating the roles of apex predators in ecosystems. Bottom-up effects, including habitat loss and fragmentation, can affect the magnitude and direction of predatory and competitive interactions through changes in resource availability and habitat complexity. For example, resource abundance can temporarily free prey populations from predator regulation and also alter interactions between predators (Letnic and Dickman 2010). Elmhagen and Rushton (2007) found a mesopredator release of the red fox (*Vulpus vulpus*) following the decline of its top predators (the gray wolf (*Canis lupus*) and Eurasian lynx (*Lynx lynx*)) but demonstrated that ecosystem productivity determined the strength of the mesopredator response.

Anthropogenic disturbances through changes to primary productivity and persecution of carnivores may reduce or remove the cascading effects of apex predators. For example, high human activity partially excluded gray wolves from a section of Banff National Park, which resulted in an increase of the elk (*Cervus elaphus*) population and decrease of aspen (*Populus tremuloides*) recruitment and willow (*Salix* spp.) production through increased browsing intensity (Hebblewhite *et al.* 2005). Similarly, Mexican wolves (*Canis lupus baileyi*) in southwestern North America have not yet attained an ecologically effective density allowing them to control elk populations due to ongoing conflicts with livestock grazing (Beschta and Ripple 2010). In addition, the presence of anthropogenic food resources can result in behavioural or population induced changes to predators and trophic cascades (Newsome *et al.* 2015).

1.2 Interspecific competition among mammalian carnivores

Interspecific competition occurs when sympatric species compete for the same limited resource. Interspecific competition has the potential to alter population dynamics through effects on fecundity and survivorship, which in turn influences abundance (Holt and Polis 1997; Donadio and Buskirk 2006). The strength of competition between carnivores may vary with factors such as body size, diet and population density (Donadio and Buskirk 2006). Interspecific competition is often asymmetrical such that the smaller/subordinate carnivore is affected the most (Donadio and Buskirk 2006).

Competition can take two main forms: (1) exploitation competition, in which one species is more efficient at depleting a shared resource, thereby depriving another species of that resource and affecting its fitness (Case and Gilpin 1974) and (2) interference competition, in which one species physically excludes another from using a particular resource (Case and Gilpin 1974). Extreme aggressive interference competition can lead to intraguild killing. If the predator killed is eaten, such competition also constitutes predation.

Exploitative competition in carnivores is difficult to quantify. Manipulative experiments are generally required to demonstrate the presence of exploitation competition, and it may occur only intermittently at times of extreme resource limitation, such as during drought. Manipulative experiments in invertebrates (Johansson 1993; Fincke 1994) and some small vertebrates (Hughes *et al.* 1994; Stapp 1997) have been performed to reveal competition. Such experiments are harder to perform in large mammalian carnivores due to their high mobility, low population density and the logistics and cost involved with such experiments. Exploitative competition, however, can be inferred in cases such as where lions (*Panthera leo*) and hyenas (*Crocuta crocuta*) steal food from African wild dogs (*Lycaon pictus*) and cheetahs (*Acinonyx jubatus*). This results in substantial hunting costs to the wild dog and cheetah, which can affect their fitness (Creel *et al.* 2001). In contrast, interference competition and intraguild predation among carnivores are well documented. They are easier to detect and measure and likely to occur across a wider range of resource availability. Palomares and Caro (1999) reviewed instances of interspecific killing among mammalian carnivores and identified 97 pairwise interactions, involving 54 different victim and 27 killer species. In some carnivores, intraguild predation has a considerable impact on mortality rates. For example, predation by coyotes (*Canis latrans*) was the major cause of death for kit foxes (*Vulpes macrotis*) and swift foxes (*Vulpes velox*) (Ralls and White 1995; Sovada *et al.* 1998).

Interference competition can cause the subordinate species to adopt one of two strategies to reduce negative encounters with the dominant competitor and facilitate coexistence: (1) avoid spatial overlap or; (2) modify temporal or behavioural patterns to reduce the chance of encounters and interactions within the same landscape. Avoidance behaviour has been found in coyotes, which avoid gray wolves; red foxes which avoid coyotes (Fedriani *et al.* 2000; Gosselink *et al.* 2003); and cheetahs which avoid lions and hyenas (Durant 1998; Durant 2000). Intraguild predation on the subordinate species

occurs in all of these cases (Palomares and Caro 1999). However, killing events appeared to be rare and the energy costs of avoidance by the subordinate species may be more important in creating the overall effect of the apex predator on distribution and population size of the mesopredator. Coyote densities were higher in areas where gray wolf densities were low and coyote home ranges were found outside or on the margins of gray wolf pack territories (Fuller and Keith 1981; Thurber *et al.* 1992). These behavioural changes by the subordinate carnivore can result in energetic and/or nutritional costs, as it is obliged to forage in suboptimal conditions. On a population level this can lead to reduced abundance (Ritchie and Johnson 2009). For example, African wild dogs and cheetahs can be found at lower densities in areas where prey are very abundant due to the presence of their competitors, such as lions and spotted hyenas (Laurenson *et al.* 1995; Mills and Gorman 1997).

Coexisting species that overlap geographically often diverge in one or more morphological, ecological or behavioural traits that results in partitioning of resources and reduces interspecific competition (Brown and Wilson 1956). Character displacement can result in a divergence of dental morphology and/or body size (Davies *et al.* 2007). Examples of divergence in behavioural characters include activity time or habitat preference (Durant 1998; Harrington *et al.* 2009). Ecomorphological adaptations to exploit foraging niches can result in parallel evolution on different continents that are isolated from each other, of carnivore assemblages comprising different guilds that exploit particular niches. The classic placental guilds and their marsupial equivalents being cursorial/terrestrial, pursuit and pounce/pursuit predators (Family Canidae; F. Thylacinidae), arboreal ambush predators (F. Felidae, F. Thylacoleonidae), small (F. Viverridae, Mustelidae and Procyonidae; Genus *Dasyurus* in the F. Dasyuridae) and scavenger (F. Hyaenidae; G. *Sarcophilus* in the F. Dasyuridae) (Jones 2003). Exploitation of specialist niches leads to reduced competition between species, for example between arboreal and terrestrial predators. This is associated with greater differentiation in the sizes or types of food resources captured and consumed by coexisting predator species.

As interspecific competition between mammalian carnivores can strongly influence abundance and distribution, understanding how carnivore species interact is crucial in managing and conserving carnivores. In addition to competitive interactions that limit carnivore populations, anthropogenic habitat alteration can further affect carnivore populations and their interactions.

1.3 Anthropogenic impacts on carnivores

Exponential expansion of human populations resulting in escalating use of land and resources have resulted in destruction and fragmentation of habitats in many parts of the world, as a result of effects such as creation of road networks, clearing of native vegetation for agriculture, and development of cities. These changes have endangered many native species and driven some to extinction. Apex predator populations are declining globally due to anthropogenic impacts (Ripple *et al.* 2014). This is significant for ecosystems because of the strongly interactive roles of predator species. Mammalian predators are especially susceptible to human disturbance and habitat destruction because they typically live at low population densities, have large home ranges and large body sizes, as well as external anthropogenic threats i.e. hunting and persecution (Purvis *et al.* 2000; Woodroffe 2001; Crooks 2002; Cardillo *et al.* 2004). Trophic cascades have been linked to change in abundance for 7 of the 31 large mammalian carnivores and human actions have contributed to their decline (Ripple *et al.* 2014).

Despite their demanding ecological requirements, some larger carnivores and mesopredators are able to survive and even thrive in modified habitats. Species such as pumas (*Puma concolor*), gray wolves, brown bears (*Ursus arctos*), leopards (*Panthera pardus*) and striped hyenas (*Hyaena hyaena*) have all exhibited population increase and range expansion in human-modified landscapes (Boitani *et al.* 2010; Latham *et al.* 2011; Mace *et al.* 2012; Athreya *et al.* 2013; Knopff *et al.* 2014b). For these species, linear structures created by human modification of landscapes may facilitate movement and concentrate food resources (James and Stuart-Smith 2000; McKenzie *et al.* 2012). The availability of human-provided foods can benefit carnivores, and 36 terrestrial carnivore species in 34 different countries have been found to utilize these food resources (Newsome *et al.* 2015). In addition, to native mesopredators, invasive mesopredators, such as feral cats and red foxes can also benefit from modified landscapes and anthropogenic resources (Denny *et al.* 2002; Shapira *et al.* 2008; Towerton *et al.* 2011; Graham *et al.* 2012; Newsome *et al.* 2015). As carnivores respond differently to anthropogenic disturbances, an understanding of how they select habitats in human-modified landscapes is critical to the appropriate conservation and management of carnivores.

1.4 Carnivores in Tasmania, Australia

Unlike on the Australian mainland, Tasmania's native fauna has remained relatively unchanged since European settlement. The only known mammalian extinction in the last century is the largest carnivorous marsupial, the thylacine/Tasmanian wolf (*Thylacinus cynocephalus*), for which the last confirmed record in the wild was 1933 (Guiler 1985). Tasmania's current marsupial carnivore guild consists of the Tasmanian devil (*Sarcophilus harrisii*), the spotted-tailed quoll (*Dasyurus maculatus*) and the eastern quoll (*Dasyurus viverrinus*). However, two of these species are currently experiencing population declines. The devil is listed as endangered on the IUCN red list of threatened species (Hawkins *et al.* 2008), due to a transmissible cancer (devil facial tumour disease; DFTD) and has experienced large population declines since 1996 (Hawkins *et al.* 2006). The Tasmanian spotted-tailed quoll is listed as rare under the *Threatened Species Protection Act 1995* (TSPA 1995) and the eastern quoll population has also declined recently (Fancourt *et al.* 2013).

There are currently no published studies on whether the extinction of the thylacine from Tasmania caused a mesopredator release of devils and/or quolls. The extinction of the thylacine and devil from mainland Australia presumably led to character release in spotted-tailed quolls (Jones 1997), which suggests that it might have had a similar effect on devils and quolls in Tasmania.

1.1.1 Life history of Tasmanian devils

Tasmanian devils are a medium-sized, sexually dimorphic (male 7.5-14.0kg; female 4.6-9.0kg) carnivore (Jones 2008). They are the largest living carnivorous marsupial and apex predator following the extinction of thylacines (*Thylacinus cynocephalus*). Devils breed during February and March, and after a gestation of 21 days a litter of 4 young is born and attaches to the teats. Females become sexually mature at around two years of age, while males may not mate until they are three or four years old. Devils live to around six years in the wild (Jones 2008).

Devils are solitary and nocturnal, and have large home ranges averaging 1300 ha (Pemberton 1990). They are pounce-pursuit predators (Jones 2003) that are capable of short fast pursuits and hunt with a moving search (Pemberton 1990). They have a

diverse diet but predominately consume larger-bodied mammals (Jones and Barmuta 1998; Pemberton *et al.* 2008). They are also highly effective scavengers, with skull, dental and muscular adaptations for consuming the hard parts of carcasses such as bones and thick skin (Jones 1997).

1.1.2 Life history of spotted-tailed quolls

Spotted-tailed quolls are the second largest of the carnivorous marsupials, weighing on average 3.5kg for males and 1.8kg for females (Jones *et al.* 2001). They breed seasonally, between late May and early August. Gestation is approximately 21 days and litter size ranges between 2 and 6 (Jones *et al.* 2001). Young become entirely independent at 18-21 weeks old and are sexually mature at 12 months (Belcher 2008).

Quolls are morphologically adapted to climbing, spend a significant proportion of their movement above ground and regularly consume arboreal prey (Jones and Barmuta 2000; Jones 2003; Glen and Dickman 2006a). They have limb ratios indicative of a slow-running, ambush predator of closed habitats (Jones and Stoddart 1998). They consume small to medium-sized mammals, among other prey (Belcher 1995; Jones and Barmuta 1998; Belcher and Darrant 2006; Glen and Dickman 2006a). Quolls are solitary animals that occupy large home ranges of several hundred to several thousand hectares (Belcher and Darrant 2004; Claridge *et al.* 2005; Glen and Dickman 2006b). Females are territorial and actively defend their home ranges from other females (Belcher and Darrant 2004; Glen and Dickman 2006b). However, female offspring are tolerated, and female young remain within the natal home range after weaning (i.e., female natal philopatry) (Belcher and Darrant 2004). Males are not territorial, and their home ranges, which are larger than those of individual females, overlap those of several females as well as other males (Belcher and Darrant 2004; Claridge *et al.* 2005; Glen and Dickman 2006b).

1.1.3 Ecological interactions between Tasmanian devils and spotted-tailed quolls

Tasmanian devils and spotted-tailed quolls have coevolved as part of a marsupial guild of predators and in isolation from placental, mammalian analogues (Jones 2003). This has resulted in ecomorphological evolution to both exploit similar hunting and activity

niches as placental carnivores do on other continents, and for divergence amongst the Australian marsupial taxa to reduce niche overlap. Devils have evolved to exploit the facultative scavenger niche, with strong jaw musculature and robust teeth, while spotted-tailed quolls are arboreally adapted (Jones 2003). Competitive character displacement in the trophic structures proximal to killing prey in mainland Australia versus Tasmanian guilds of marsupial carnivores suggests that competition has occurred over an evolutionary time scale (Jones 1997). That competition still occurs between Tasmanian devils and spotted-tailed quolls is suggested by:

(1) *Diet overlap.* Jones and Barmuta (1998) found that dietary overlap among Tasmanian devils and spotted-tailed quolls was dependent on sex and age class. Devils consumed larger prey species such as Bennett's wallaby and wombats, while quolls consumed mammals of all sizes. Female and sub-adult devils showed significant overlap with male spotted-tailed quolls but no significant overlap with females. This suggests that competition could occur if resources become limited. The degree of overlap was also affected by seasonal variations in the diet, with the greatest overlap in late winter when there are no juveniles of prey species available (Jones and Barmuta 1998). Where dietary overlap is greatest, habitats are partitioned and different prey species are consumed to reduce competition.

(2) *Habitat partitioning.* A spool and line study by Jones & Barmuta (2000) in Tasmania, showed a higher degree of arboreal use in spotted-tailed quolls. The ability of quolls to climb might provide a means of escape if a devil is encountered and thereby reduce the severity of interference competition. Vertical habitat partitioning on its own does not provide evidence for current competition but arboreality is a niche dimension that quolls could utilise to minimise competition.

(3) *Difference in relative abundance.* Devils are numerically more abundant than spotted-tailed quolls (Jones and Barmuta 1998).

(4) *Hierarchical dominance behaviours at carcasses.* Carcasses are potential foci for contest competition between devils and quolls with devils being more dominant and displace quolls (Jones and Barmuta 1998).

1.1.4 The potential for mesopredator release following the decline of the Tasmanian devil

It is important now to understand the relationships between the carnivores in Tasmania. The Tasmanian devil has experienced large population declines, due to a consistently fatal transmissible cancer (Hawkins *et al.* 2006). It has been hypothesised that the decline of the devil will result in a mesopredator release of not only spotted-tailed quolls but feral cats as well (Jones *et al.* 2007; Hollings *et al.* 2014). An increase in an invasive mesopredator such as the feral cat can have detrimental effects on small mammal populations. As a mesopredator, feral cats have been part of the Tasmanian carnivore guild since 1980 (Abbott 2002), yet the role and significance of cats in Tasmania is unknown. Further, while Tasmania presents as a favourable environment for the proliferation of feral cats, current information on the extent to which feral cats have become established as a mesopredator, or indeed actual cat numbers in Tasmania, is poor. The similar body size and prey composition of feral cats and spotted-tailed quolls suggest that exploitation and interference competition is likely to occur (Dickman 1996; Jones and Barmuta 1998; Jones and Barmuta 2000), and there are reports of both species killing one another (Peacock and Abbott 2014).

In addition, devils could possibly play a role in preventing the European red fox (*Vulpes vulpes*) from becoming established and thereby protecting species abundance and diversity (Jones *et al.* 2007). There have been several introductions of the fox to Tasmania over the previous 100 years, but there has yet to be any conclusive evidence of an extant population (Saunders *et al.* 2006).

In order to predict the cascading effects of apex predator removal, the interactions amongst apex predators, mesopredators and prey species must be identified. This has not been fully investigated for the Tasmanian carnivore guild and confounds insight into and managerial options for devils in the current circumstances; in particular, restoration of devils into the wild. Given the detrimental impacts feral cats have on wildlife, I intended to study them as well as devils and quolls but because they occurred at a relatively low abundance at my study site and because they were difficult to catch insufficient data was collected to include them in formal analyses. The interaction between devils and quolls, considering both the potential for competition and the nature of coexistence as shown by similarities and differences in resource use- diet, and movement in relation to habitat and landscape features in sites where the two species

overlap, therefore provide the ecological background and theoretical framework for my study.

1.5 Thesis aims

The overall aim of this thesis was to enhance understanding of the ecological interactions between the Tasmanian devil and the spotted-tailed quoll in Tasmania, Australia. This thesis builds upon Jones and Barmuta's work by including a state-wide diet analysis, fine scale analyses of movement in intact and fragmented habitats, home range size and activity time analyses of devils and quolls. I had four specific aims:

1. To determine trophic dietary breadth and overlap between Tasmanian devils and spotted-tailed quolls by analysing scats, from several sites across Tasmania. This will help us understand if resource partitioning occurs to facilitate coexistence and reveal the potential for competition (Chapter 2).
2. To examine the degree of home range and core area overlap between devils and quolls and to investigate nightly activity patterns (Chapter 3). This will be investigated through simultaneously GPS collaring devil and quolls, when both species are invested in maternal care as energetic demands are at their highest. It will help us understand whether quolls avoid establishing their home range or core area within devils and whether temporal partitioning occurs. It will also provide us with basic knowledge on Tasmanian devil and Tasmanian spotted-tailed quoll spatial ecology, which is currently sparse.
3. To examine the response and movement patterns of two medium-sized carnivores, with different ecomorphological niches: a specialist scavenger, the Tasmanian devil and an arboreal specialist, the spotted-tailed quoll, to anthropogenic landscape modification (Chapter 4). Using GPS tracking, in a conservation area and agricultural landscape, I will investigate how animals use linear features such as the interface between pasture and vegetation, fences and roads and different vegetation types. As habitat loss and fragmentation affects many carnivore species, this study will help us understand how it might affect devils and quolls and provide management recommendations.

4. To investigate the behavioural responses of two native species, the larger Tasmanian devil and the smaller spotted-tailed quoll to each other's odour and to the introduced predator, the feral cat to establish whether a size-based dominance hierarchy exists (Chapter 5). I will use an experimental array of camera traps, in which carnivore scats are added as treatments. This experiment will help us understand predator interactions and potential for interspecific competition.

1.6 Thesis structure

The thesis contains six chapters and chapters 2-5 are written as separate articles for publication. Therefore, there is some repetition across the chapters in descriptions of study site and background information on the study species. Chapter 4 is currently in review and Chapter 5 is published.

Chapter 2 Diet composition and overlap of two sympatric carnivores, the Tasmanian devil and spotted-tailed quoll



This chapter is currently in preparation for publication:

Andersen, G.E., Johnson, C.N., Barmuta, L.A., and Jones, M.E. Diet composition and overlap of two sympatric carnivores, the Tasmanian devil and the spotted-tailed quoll.

2.1 Abstract

Australia's native mammalian fauna includes only two 'hypercarnivores' (species which feed predominantly on vertebrate flesh): the Tasmanian devil (*Sarcophilus harrasii*) and spotted-tailed quoll (*Dasyurus maculatus*). These species co-exist in Tasmania, Australia, and could compete with one another for food. The Tasmanian devil is currently declining due to a fatal transmissible cancer. The goal of this study was to analyse the diet of both species across their range in Tasmania, as a basis for understanding how devil decline might affect abundance and distribution of quolls through release from competition. We used faecal analysis to describe diets of one or both species at 13 sites across Tasmania. We compared diet type and breadth between species, and tested geographic trends by searching for relationships between diet and rainfall. Dietary items were classified into 6 broad categories: large mammals ($\geq 7.0\text{kg}$), medium-sized mammals (0.5 - 6.9kg), small mammals ($< 0.5\text{kg}$), birds, reptiles and invertebrates. Diet overlap based on prey size category was high. Quoll diets were broader than devils at all but one site. Devils consumed more large and medium-sized mammals and quolls more small mammals, reptiles and invertebrates. Medium-sized mammals (mainly Tasmanian pademelon *Thylogale billardierii*), followed by large mammals (mainly Bennett's wallaby *Macropus rufogriseus*) and birds, were the most important prey groups for both species. Diet composition varied across sites, suggesting that both species are flexible and opportunistic foragers, but was not related to rainfall for devils. Quolls included more large mammals but fewer small mammals and invertebrates in their diet in the eastern drier parts of Tasmania where devils have declined. This suggests that a competitive release of quolls may have occurred and the substantial decline of devils has provided more food in the large mammal category for quolls. Conversely, it suggests that if resources become limited in areas of high devil density, interspecific competition could occur.

2.2 Introduction

Knowledge of diet is fundamental in understanding the ecological impacts and interactions of carnivore species (Klare *et al.* 2011). Carnivore diets are influenced by the diversity, abundance and availability of prey resources, which may vary in space or time. Carnivore density is positively correlated with prey biomass (Carbone and

Gittleman 2002) but is also influenced by competitive interactions with other carnivores (Palomares and Caro 1999).

Ecologically and morphologically similar species are most likely to compete but can coexist in a stable environment through partitioning diet, habitat or time to reduce competition (Gause 1934; Pianka 1973; Janssen *et al.* 2007; Vanak *et al.* 2013). Without such partitioning, one species could exclude another (Hardin 1960). Within the same habitat, carnivores can partition resources by consuming prey of different sizes (Andheria *et al.* 2007; Davis *et al.* 2015), through vertical partitioning of habitat due to differential use of trees (Emmons 1980; Estrada and Coates-Estrada 1985), or by being active at different times of the diel cycle; the latter will only result in food resource partitioning if different prey are active at different times of day.

High dietary overlap between sympatric carnivores indicates the potential for both exploitation and interference competition. It can also result in aggressive interactions, because carnivores searching for the same prey item are more likely to encounter one another and may be under higher selective pressure to eliminate competitors (Polis *et al.* 1989; Donadio and Buskirk 2006). Body size influences the outcome of these interactions; typically the larger carnivore dominates and excludes the smaller carnivore (Donadio and Buskirk 2006). If the competing species are of different body sizes, population decline of the larger dominant carnivore can result in a ‘mesopredator release’ of the smaller carnivore (Soule *et al.* 1988; Ritchie and Johnson 2009). Extensive dietary overlap does not necessarily result in interspecific competition, however, which is more likely to occur when a shared resource is in limited supply (Schoener 1986), such as during drought or when prey abundance is low (Holt and Polis 1997).

On the Australian island of Tasmania, the Tasmanian devil (*Sarcophilus harrisii*) (5 - 14kg; Jones 2008) occurs sympatrically with the smaller spotted-tailed quoll (*Dasyurus maculatus*) (0.9 - 5kg; Belcher 2008). The spotted-tailed quoll has a more extreme sexual size dimorphism (male:female = 2.0) than devils (male:female = 1.3) (Jones 1995). The devil is of particular interest, as it has undergone a severe and rapid population decline since the emergence of a novel transmissible cancer (devil facial tumour disease; DFTD), first detected in 1996 (Hawkins *et al.* 2006). The decline of Tasmania’s largest mammalian predator could lead to ecosystem-wide changes

(Hollings *et al.* 2014; Hollings *et al.* 2015; Hollings *et al.* 2016), possibly including mesopredator release of spotted-tailed quolls (Jones *et al.* 2007).

There has been no comprehensive study of diet composition and overlap of Tasmanian devils and Tasmanian spotted-tailed quolls across their ranges, which could reveal the extent of the potential for competition and how this might translate to a change in quoll abundance following devil decline. Jones and Barmuta (1998) analysed diet overlap among the three extant Tasmanian marsupial carnivores (the devil, and the spotted-tailed and eastern quoll (*D. viverrinus*)) at a single site in an alpine environment (750 – 950 m altitude). They found high overlap between devils and male spotted-tailed quolls, both species predominantly eating medium and large-sized mammals (e.g. Tasmanian pademelons *Thylogale billardierii*, brushtail possums *Trichosurus vulpecula*, Bennett's wallabies *Macropus rufogriseus* and common wombats *Vombatus ursinus*). Female spotted-tailed quolls did not overlap with devils but had high diet overlap with eastern quolls at this alpine site where there are few medium-sized terrestrial mammalian prey and no invertebrates in the diet of any carnivore species in the winter (Jones and Barmuta 1998). Another study by Pemberton *et al.* (2008) examined the diet of Tasmanian devils at six sites in coastal and inland locations in western Tasmania and found that the most common prey items were birds, brushtail possums and ringtail possums (*Pseudocheirus peregrinus*), Tasmanian pademelons and Bennett's wallabies.

The aim of this study was to assess partitioning of food resource between Tasmanian devils and spotted-tailed quolls through analyses of diet and prey selectivity across their shared distributional range. More specifically we aim to: (1) determine which prey species are consumed and the relative importance of these for devils and quolls, (2) examine diet breadth and diet overlap to understand resource partitioning patterns across the sympatric range of these two predators, and (3) examine if the species' diets vary geographically. Most of Tasmania's native mammals which are potential prey species are widely distributed across the state, although a few species (e.g. bettongs *Bettongia gaimardi*) are restricted in distribution to the drier eastern half (Rounsevell *et al.* 1991). Rainfall is a strong bottom-up factor influencing the abundance of most prey species (Hollings *et al.* 2014) so we expect that the east to west positive gradient in rainfall could influence the diets of, and dietary overlap between devils and quolls. The progressive spread and severe population decline of Tasmanian

devils from DFTD could affect diets of both species, if diet is density-dependent in the Tasmanian devil and if the availability of prey for spotted-tailed quolls is affected by density of devils. However, effects of DFTD on diet will be difficult to distinguish from effects of rainfall, because disease-caused population decline has proceeded from east to west in Tasmania, matching the rainfall gradient. As rainfall varied more continuously across Tasmania, and our sites were either not affected by disease or diseased for more than seven years, we chose to include rainfall as the descriptor variable in analyses.

2.3 Materials and Methods

2.3.1 Study sites

Scats were collected from 13 sites across Tasmania (Fig. 2.1) between 1990 and 2015, sampling the full range of environments in which these species occur. Tasmania has a cool temperate climate with a rainfall gradient increasing from east to the west and south, and rainfall and temperature gradients increasing from coast to alpine. Sites covered the full extent of the rainfall gradient, ranging from 423mm at Ross and 534mm at Freycinet in the east, 1318mm at Oldina and 1071mm at Arthur River in the northwest, to 1142mm at Snug in the south, 2143mm at Melaleuca in the southwest and 1822mm at Cradle Mountain, the alpine region (Table 2.1). We sampled four sites on the coast (Woolnorth, wukalina/Mount William, Freycinet and Arthur River) and two in alpine to subalpine environments (Cradle Mountain and kunanyi/Wellington Park). We also sampled both intact natural environments and agricultural areas adjacent to forest. Six sites were largely natural: wukalina/Mt William National Park, Freycinet National Park, kunanyi/Wellington Park, Snug Tiers, Cradle Mountain National Park, Melaleuca in the Franklin-Gordon Wild Rivers National Park, while a seventh site, Arthur River in the Arthur-Pieman Conservation Area was adjacent to agricultural land. The other six sites were in agricultural landscapes: Ross and Epping Forest in the Tasmanian Midlands, Elderslie in the Derwent valley, Meander, Oldina and Woolnorth. Dominant vegetation types at each site were obtained from Reid et al. (1999) and varied across sites (Table 2.1).

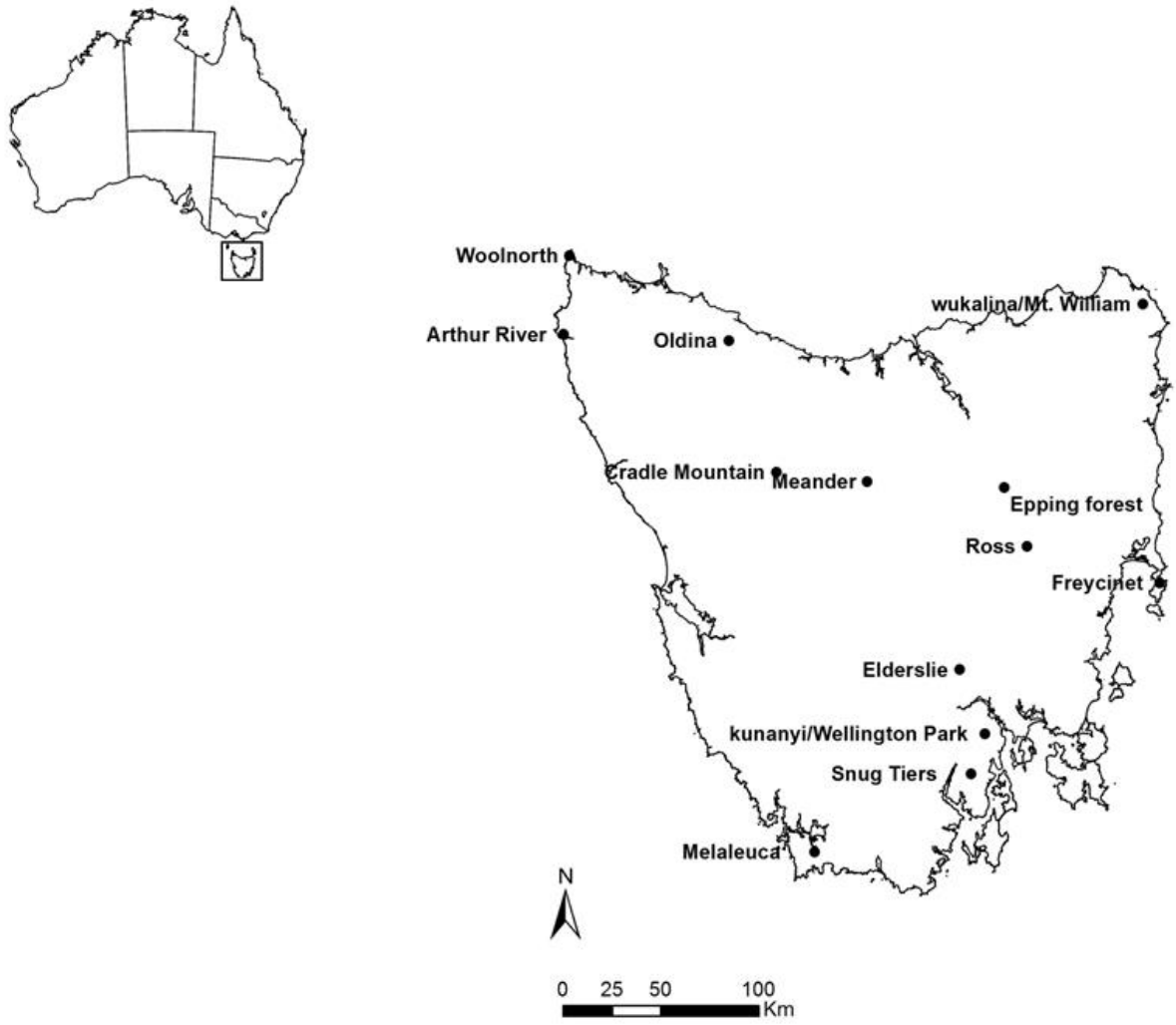


Fig 2.1. Map of study sites in Tasmania, Australia, where scats were collected.

Table 2.1. Details of the site, year(s) of scat collection, location, dominant vegetation types, mean rainfall (mm) over the five years preceding the period of scat collection and year of devil facial tumour disease outbreak (DFTD) for each of the thirteen sites, where scats were collected. n = number of devil (TD) and quoll (STQ) scats collected.

Site	Year(s) of collection	n	Coordinates	Dominant vegetation	Mean rainfall (mm)	DFTD arrival
Arthur River	2012; 2013	125 (TD) 36 (STQ)	41°05'S, 144°66'E	Dry coastal vegetation; moorland and scrubland wet eucalypt forest	1071	DFTD free
Woolnorth	2012	36 (TD)	40°69'S, 144°72'E	Wet eucalypt forest; cleared land; moorland and scrubland; farmland	771	DFTD free
Oldina	2012	28 (TD)	41°08'S, 145°67'E	Wet eucalypt forest; farmland	1318	2014
wukalina/Mount William	2012	7 (TD)	40°94'S, 148°25'E	Dry coastal vegetation; dry sclerophyll forest; woodland and native grassland	925	1995
Freycinet	2012; 2014	30 (TD) 11 (STQ)	42°20'S, 148°31'E	Dry coastal vegetation dry sclerophyll forest; woodland and native grassland	534	2000
Elderslie	2012	16 (TD)	42°60'S, 147°07'E	Dry sclerophyll forest; woodland and native grassland; cleared land	961	2005
Snug Tiers	2012	27 (TD)	43°07'S, 147°26'E	Wet eucalypt forest; cleared land; dry sclerophyll forest; woodland and native grassland; farmland	1142	2014
Meander	2001	29 (TD) 19 (STQ)	41°72'S, 146°61'E	Wet eucalypt forest; cleared land; dry sclerophyll forest; woodland and native grassland; farmland	961	2003-2004
kunanyi/Wellington Park	2013; 2015	13 (TD)	42°88'S, 147°12'E	Wet eucalypt forest; dry sclerophyll forest	933	2003
Epping forest	2011	17 (STQ)	41°76'S, 147°35'E	Native grassland; dry sclerophyll forest	499	2001-2002

Ross	2011	8 (STQ)	42°03'S, 147°49'E	Native grassland; dry sclerophyll forest; farmland	423	2001-2002
Melaleuca	2014	10 (STQ)	43°42'S, 146°16'E	Wet eucalypt forest; moorland and scrubland	2143	DFTD free
Cradle Mountain	1990-1993	349 (TD) 76 (STQ)	41°68'S, 145°95'E	Wet eucalypt forest; moorlands; native grassland	1822	2004

2.3.2 Scat collection and prey identification

The majority of devil and quoll scats were obtained from animals that were trapped overnight in PVC pipe traps (diameter 315mm x length 875mm) and released the next morning. This sampling strategy provided confidence in species identification of the scats. Scats were stored frozen at -20°C and the location, date and sex of the animal were recorded. It is unlikely that bait consumption affected our diet analyses as traps were baited with meat which leaves no residue in the scats. Scats were also opportunistically collected at some sites (kunanyi/Wellington Park, Melaleuca, Epping Forest and Ross), where we wanted representation but there were no trapping programs. Scats were not collected from latrines. These scats were identified based on size, shape, colour, the presence size and digestion state of bone fragments, and odour. Devil scats are quite distinctive from those of quolls as only devil consume and digest large amounts of bone, which gives a grey tinge to scat colour and there are frequently shards of sizeable animal bones in the scat. Both species were present at all sites but we were unable to collect sufficient scats of one species at some sites. We included the diet data recorded from scats collected from trapped animals at Cradle Mountain between 1990-1993 (Jones and Barmuta (1998)).

The prey species present in the scats were identified by microscopic identification of undigested hair in the scat samples. Scats were immersed in hot water, left to soften for 24 hours and then washed through a 1mm sieve. Fur, feathers, bones and invertebrates remained and were dried in an oven at 60°C for 24 hours, a temperature at which the viability of parasite spores and oocytes would be reduced. Mammalian prey species were identified from hair, by a combination of the cross-sectional size, shape and pattern of the medulla and cortex observed at 100 and 400 times magnification under a transmission microscope, the scale patterns on the surface of the hair, and the colour, length and appearance of the hair. Identification was carried out to the lowest possible taxonomic level by comparison with known reference material and identification guides and keys (Brunner 1974; Taylor 1985; Brunner 2002). Diet items were classified into 6 broad categories: large mammals ($\geq 7.0\text{kg}$), medium mammals (0.5 - 6.9kg), small mammals ($< 0.5\text{kg}$), birds, reptiles and invertebrates. The mammal size classes are similar to those used by other Australian dietary studies (Glen and Dickman 2006a; Glen *et al.* 2011; Davis *et al.* 2015). Mammalian prey were placed in size categories based on the maximum body mass

listed by Menkhorst and Knight (2011) (Table 2.2). While the majority of species can be accurately identified from hair samples, this is not always the case (Lobert *et al.* 2001). We were unable to distinguish between hair of antechinus species (swamp antechinus *Antechinus minimus* and dusky antechinus *A. swainsonii*) and instead grouped them as their genus name. Birds, reptiles and invertebrates were not classified to species and were treated as single prey items. We assumed that the presence of devil hair in devil samples, and quoll hair in quoll samples, was due to grooming and these were not included as a prey item in analyses. The presence of quoll hair in devil samples and devil hair in quoll samples were not included in analyses as prey but were noted as evidence of intraguild predation. Remains of vegetation were also not included in analyses, as they were considered to function in digestion rather than being consumed for nutritional value (Vieira and Port 2007).

2.3.4 Diet composition

To ensure we obtained sufficient number of scats to describe the diets of each species, we calculated dietary diversity (H) using the Brillouin index (Brillouin 1956) based on the 6 broad dietary categories described above using the formula:

$$H = (\ln(N!) - \sum \ln(n_i!)) / N,$$

where H is the diversity, N is the total number of scats analysed at the site and n_i is the number of individual scat items in the i th category. We randomized the order of samples and plotted cumulative dietary diversity against sample size. Sample size was deemed to be sufficient if the curve reached an asymptote.

For individual prey items and prey categories we calculated frequency of occurrence (the percentage of scats in which a certain food item was found, including trace items) and percentage volume (the volume of a certain type of food in the scats expressed as a percentage of the total volume of all prey items in the scats). Percent volume of each prey item in scats was estimated visually (McDonald and Fuller 2005). Frequency of occurrence may overestimate the dietary contribution of small mammalian prey, whereas the percentage volume may underestimate consumption of items that are easily digested. It is therefore recommended to use both metrics (Glen and Dickman 2006a; Klare *et al.* 2011).

We examined differences in the frequency of occurrence of the six prey categories between predators by pairwise comparison using chi-square contingency tests. We also pooled the frequency of occurrence of arboreal mammalian prey (e.g. brushtail, ringtail and pygmy possums and sugar gliders) *versus* ground-dwelling prey and compared the difference using a chi-square test.

2.3.5 Trophic niche breadth and diet overlap

We estimated dietary niche breadth for each species across Tasmania and at each site, and diet overlap between devils and quolls, based on the use of the six dietary categories (large mammals, medium mammals, small mammals, birds, invertebrates and reptiles). At sites where information on the sex of animals was known, we estimated dietary niche breadth and overlap for each sex and species combination. Dietary niche breadth (B_A) was calculated using Levins (1968) index:

$$B_A = (1/\sum p_i^2) - 1/(n-1),$$

where p_i = proportion of occurrence of each prey category in the diet and n = number of possible prey categories. This measure of niche breadth ranges from 0 (narrow niche) to 1 (broad niche). Dietary overlap was calculated using Pianka's index (Pianka 1973):

$$O_{jk} = \sum p_{ij}p_{ik} / (\sum p_{ij}^2 \sum p_{ik}^2)^{0.5},$$

where O is the index of overlap, j and k are the species being compared and p_i is the frequency of occurrence of each dietary item. This index ranges from 0 (no overlap) to 1 (complete overlap).

2.3.6 Effect of rainfall on diet composition

As abundance of the different mammalian prey species in Tasmania is influenced by rainfall (Hollings *et al.* 2014), we examined the effect of rainfall on the presence or absence of the six diet categories. We were also interested in determining whether devil density affects diet but preliminary analysis revealed that rainfall and DFTD (0 = if absent at a site and 1 = if present at a site) were correlated (Pearson's r -value = -0.75, $p > 0.05$, $n = 12$). Therefore, we included only rainfall in our models as it has a more continuous variation across sites. For both devils and quolls, we performed a

generalised linear mixed model (GLMM) for each prey category (using the ‘lme4’ library in R version 3.1.3). The average rainfall (mm) over the five years preceding collection of scats was included as a fixed factor and site was included as a random factor. Tasmanian pademelons, a key prey item in the diet of devils and quolls (Jones and Barmuta 1998), reproduce annually and are sexually mature at 14-15 months (Rose and McCatney 1982). Therefore, we chose five years to allow for demographic lags in prey population sizes to change in rainfall. Rainfall was centred to avoid large correlation with sites.

2.4 Results

We collected 660 Tasmanian devil scats from 10 sites and 177 spotted-tailed quoll scats from 7 sites (Table 2.1). Both devil and quolls scats were collected at 4 sites (Meander, Freycinet, Arthur River and Cradle Mountain). At the time of scat collection, DFTD was present, for a minimum of seven years, at Elderslie, Freycinet, wukalina/Mount William, kunanyi/Wellington Park, Epping Forest and Ross, and absent at Arthur River, Woolnorth, Oldina, Snug Tiers, Meander, Melaleuca and Cradle Mountain (Table 2.1). Dietary diversity estimates for devils and quolls reached an asymptote with increasing sample size for both species (Fig. 2.2).

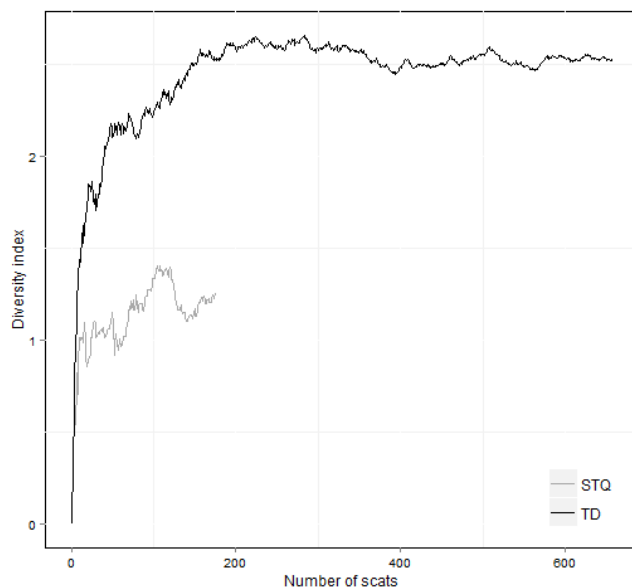


Fig 2.2. Brillouin diversity index of devil (TD) and quoll (STQ) diets with increasing sample size of scats across Tasmania, Australia.

2.4.1 Diet composition

Devils consumed a total of 26 prey taxa and quolls consumed a total of 22 prey taxa. All six major food categories were represented (Table 2.2). Of all devil scats, 69% contained one prey item, 25.8% contained two prey items, 4.4% contained three prey items and 0.8% contained four prey items. Of all quoll scats, 63.3% contained one prey item, 28.8% contained two prey items, 6.8% contained three prey items and 1.1% contained five prey items. Mammals dominated the diet of devils and quolls in terms of both frequency of occurrence and volume (Table 2.2) with 23 and 19 mammal species identified in the diet of devils and quolls, respectively (Table 2.2). Tasmanian pademelon and Bennett's wallaby were the most important mammalian prey species in terms of frequency of occurrence and volume in the diet of devils and quolls (Table 2.2). While the most important prey groups for both devils and quolls were medium mammals, followed by large mammals and birds (Table 2.2), the frequency of occurrence of these differed. Devils consumed more large ($\chi^2 = 2.72, p = 0.091$) and medium mammals ($\chi^2 = 8.17, p = 0.004$) than quolls did (Fig. 2.3). Conversely, quolls consumed significantly more small mammals ($\chi^2 = 10.22, p = 0.001$), reptiles ($\chi^2 = 9.55, p = 0.002$) and invertebrates ($\chi^2 = 68.82, p = 0.041$) than devils (Fig. 2.3). Small mammals and birds occurred at intermediate frequencies in the diet of both devils and quolls, but in terms of volume constituted little in the bulk of scats (Table 2.2). Reptiles occurred at low frequencies in the diet of both devils and quolls (1.2% and 5.1 %, respectively; Table 2.2). Invertebrates were recorded in extremely low frequencies in the diet of devils (2.7%) but at intermediate frequencies in the diet of quolls (22%) (Table 2.2). The frequency occurrence of arboreal mammalian prey species was 15.8% in quolls scats and 20% in devil scats (Fig. 2.3) but this difference was not significant ($\chi^2 = 1.48, p = 0.221$). Four devil scats from Cradle Mountain contained spotted-tailed quoll fur.

Table 2.2. Percent frequency occurrence (%F) and relative volume (%V) of prey items in the diets of Tasmanian devils (n = 902 prey items and 660 scats) and spotted-tailed quolls (n = 258 prey items and 177 scats), across Tasmania, Australia.

Common name	Scientific name	Devils		Quolls	
		%F	%V	%F	%V
Large mammals		39.4	34.4	31.1	27.4
Common wombat	<i>Vombatus ursinus</i>	12.6	10.6	1.1	1.1
Bennett's wallaby	<i>Macropus rufogriseus</i>	24.5	22.4	27.7	24.3
Sheep	<i>Ovis aries</i>	0.6	0.3	1.7	1.5
Goat	<i>Capra hircus</i>	0.2	0.2	-	-
Cow	<i>Bos taurus</i>	0.6	0.4	0.6	0.5
Horse	<i>Equus caballus</i>	0.3	0.2	-	-
Dog	<i>Canis familiaris</i>	0.6	0.2	-	-
Medium mammals		61.0	53.4	41.9	37.5
Tasmanian pademelon	<i>Thylogale billardierii</i>	40.6	39.0	20.9	18.7
Brushtail possum	<i>Trichosurus vulpecula</i>	6.2	5.0	6.2	4.8
Ringtail possum	<i>Pseudocheirus peregrinus</i>	11.5	7.2	6.2	5.4
Bettong	<i>Bettongia gaimardi</i>	0.3	0.3	-	-
Potoroo	<i>Potorous tridactylus</i>	0.9	0.9	-	-
Southern brown bandicoot	<i>Isodon obesulus</i>	0.5	0.3	1.1	1.4
Echidna	<i>Tachyglossus aculeatus</i>	0.8	0.4	1.1	1.1
Platypus	<i>Ornithorhynchus anatinus</i>	-	-	0.7	0.6
Rabbit	<i>Oryctolagus cuniculus</i>	0.2	0.2	5.7	5.5
Small mammals		10.4	5.05	21.1	16.3
Water rat	<i>Hydromys chrysogaster</i>	0.3	0.3	-	-
Black rat	<i>Rattus rattus</i>	0.2	0.1	0.6	0.5
Swamp rat	<i>Rattus lutreolus</i>	0.3	0.1	1.7	1.7
House mouse	<i>Mus musculus</i>	-	-	0.6	0.6
Pygmy possum	<i>Cercartetus concinnus</i>	0.3	0.03	2.8	1.4
Sugar glider	<i>Petaurus breviceps</i>	2.0	0.9	0.6	1.1
Antechinus	<i>Antechinus</i> sp.	5.0	2.4	5.7	4.3
Long-tailed mouse	<i>Pseudomys higginsii</i>	2.1	1.2	5.7	5.2
White-footed dunnart	<i>Sminthopsis leucopus</i>	0.2	0.02	3.4	1.5

Birds	22.1	7.0	24.3	11.0
Reptiles	1.2	0.1	5.1	1.0
Invertebrates	2.7	0.1	22.6	5.5

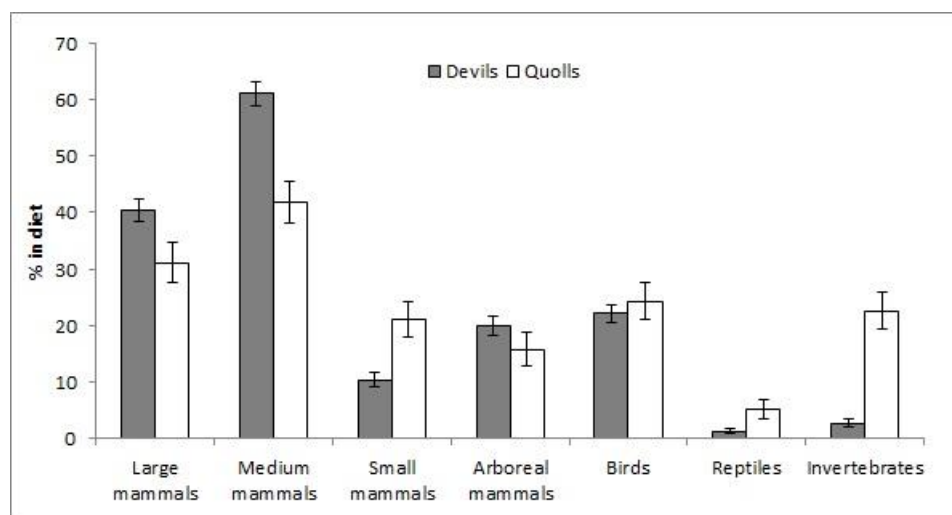


Fig 2.3. Frequency of occurrence (mean \pm s.e.) of large, medium, small and arboreal mammalian prey species and birds, reptiles and invertebrates in devil and quoll scats.

2.4.2 Trophic niche breadth and diet overlap

Niche breadth (B_A) was greater for quolls than devils when data from all sites were pooled and in all sites except for Freycinet (Table 2.3). Devil and quoll niche breadth was greatest at Cradle Mountain (Table 2.3). Niche breadth was lowest for devils at kunanyi/Wellington Park and lowest for quolls at Epping Forest (Table 2.3). The diet of devils and quolls overlapped extensively when data from all sites was pooled and in all sites (Table 2.3).

Female devils had a broader niche breadth than male devils at Freycinet and Cradle Mountain, whereas males had a broader niche breadth at Arthur River, Snug Tiers and Woolnorth (Table 2.4). Female devils also had a broader niche breadth than males at Elderslie but this should be interpreted with caution due to the low sample size (Table 2.4). Niche breadth was the same for both sexes at Oldina (Table 2.4). Male quolls had a broader niche than female quolls at Arthur River and Cradle Mountain, whereas females had a broader niche at Freycinet but this should be interpreted with

caution due to the low sample size (Table 2.4). There was extensive diet overlap among sex and species combinations at all sites except for diet overlap between female quolls and devils of either sex at Cradle Mountain (Table 2.4).

Table 2.3. Trophic niche breadth (Levins' index) and diet overlap (Pianka's index) between Tasmanian devils and spotted-tailed quolls for each site in Tasmania, Australia.

Site	Devil	Quoll	Overlap
All	0.437	0.795	0.917
Arthur River	0.289	0.573	0.850
Freycinet	0.417	0.393	0.954
Cradle Mountain	0.542	0.848	0.779
Meander	0.335	0.483	0.866
wukalina/Mount William	0.195	-	-
Oldina	0.127	-	-
Ross	-	0.581	-
Epping Forest	-	0.326	-
Elderslie	0.271	-	-
Snug Tiers	0.194	-	-
Woolnorth	0.316	-	-
kunanyi/Wellington Park	0.033	-	-
Melaleuca	-	0.349	-

Table 2.4. Trophic niche breadth (Levins' index) for each sex (F=Females and M=Males) of Tasmanian devils and spotted-tailed quolls and diet overlap (Pianka's index) for each combination of sexes and species. Number of scats (n) for each sex at each site is included in parentheses.

		Arthur River	Freycinet	Cradle Mountain	Oldina	Elderslie	Snug Tiers	Woolnorth
Devil	F	0.185 (70)	0.435 (16)	0.563 (163)	0.127 (14)	0.467 (7)	0.186 (19)	0.294 (23)
	M	0.281 (55)	0.340 (14)	0.520 (186)	0.127 (14)	0.103 (9)	0.210 (8)	0.310 (13)
Quoll	F	0.448 (7)	0.400 (5)	0.501 (17)	-	-	-	-
	M	0.580 (30)	0.316 (6)	0.885 (58)	-	-	-	-
Overlap	Devil _{FM}	0.973	0.940	0.990	1.000	0.832	0.995	0.919
	Quoll _{FM}	0.916	0.861	0.842	-	-	-	-
	Devil _M -Quoll _M	0.835	0.998	0.836	-	-	-	-
	Devil _F -Quoll _F	0.928	0.857	0.487	-	-	-	-
	Devil _M -Quoll _F	0.930	0.865	0.488	-	-	-	-
	Devil _F -Quoll _M	0.768	0.917	0.838	-	-	-	-

2.4.3 Geographic variation in diets

Diets of devils and quolls varied across sites but Tasmanian pademelon and Bennett's wallaby were consistently important (Table 2.5 and Table 2.6). The frequency of large mammals in the diet of devils was high (32.8% - 60%) at Arthur River, Woolnorth, Freycinet, Meander and Cradle Mountain, intermediate (7.4% - 18.8%) at Elderslie, kunanyi/Wellington Park, wukalina/Mount William and Snug Tiers and absent from Oldina (Table 2.5). The frequency of medium-sized mammals was high for all sites (51.3% - 100.1%) (Table 2.5). Small mammals occurred in the diet of devils only at Elderslie, Meander and Cradle Mountain, ranging from a low 6.3% at Elderslie to intermediate 18.4% at Cradle Mountain (Table 2.5). The volume of large, medium and small mammals followed a similar pattern to frequency of occurrence (Table 2.5). Birds varied from a low frequency of 6.9% at Meander to a high 46.7% at Freycinet and were absent at kunanyi/Wellington Park. They occurred at low volumes in all sites (Table 2.5). Reptiles occurred only at extremely low frequencies in the diet of devils at Arthur River (0.8%) and Cradle Mountain (2.6%), whereas invertebrates were only found at Freycinet (3.3%) and Cradle Mountain (4.6%) (Table 2.5). Both reptiles and invertebrates occurred in extremely low volumes (Table 2.5).

For quolls, the frequency of large mammals was high at Arthur River (38.9%), Epping Forest (35.3%), Freycinet (54.6%) and Meander (63.2%) but intermediate at Cradle Mountain (21.3%) and Ross (12.5%) and absent at Melaleuca (Table 2.6). The frequency of medium mammals was high at all sites ranging from 31.6 % at Meander to 80% at Melaleuca (Table 2.6). The frequency of small mammals in the diet of quolls varied across sites from a high frequency at Cradle Mountain (39.9%) to a low frequency at Meander (5.3%), and small mammals were not consumed at Epping Forest or Freycinet (Table 2.6). As with devils, the volume of large, medium and small mammals followed a similar pattern to the frequency of occurrence (Table 2.6). Birds occurred in the diet of quolls at all sites and their frequency ranged from 17.3% at Cradle Mountain to 41.2% at Arthur River (Table 2.6). Reptiles occurred only at Cradle Mountain at an intermediate frequency (12%) (Table 2.6). Invertebrates occurred in the diet of quolls at all sites except for Epping Forest. They ranged from high frequency at Melaleuca (70%) to a low frequency at Freycinet (9.1%) (Table 2.6). The volume of birds and invertebrates ranged from low to intermediate values (Table 2.6).

Table 2.5. Percent frequency occurrence (%F) and relative volume (%V) of prey items, in Tasmanian devil scats for each site.

Common name	Scientific name	Arthur River		Woolnorth		Freycinet		Elderslie		Wellington park		Mount William		Meander		Oldina		Snug Tiers		Cradle Mountain	
		%F	%V	%F	%V	%F	%V	%F	%V	%F	%V	%F	%V	%F	%V	%F	%V	%F	%V	%F	%V
Large Mammals		32.8	32.5	33.3	32.5	60.0	45.1	18.8	18.1	7.7	7.7	14.3	12.8	38.1	38.8	0	0	7.4	6.7	49.1	40.6
Common wombat	<i>Vombatus ursinus</i>	2.4	2.4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	22.9	19.1
Bennett's wallaby	<i>Macropus rufogriseus</i>	30.4	30.1	33.3	32.5	50.0	42.7	18.8	18.1	7.7	7.7	14.3	12.8	27.6	27.3	0	0	7.4	6.7	23.5	20.4
Sheep	<i>Ovis aries</i>	0	0	0	0	10.0	2.4	0	0	0	0	0	0	3.5	3.5	0	0	0	0	0	0
Goat	<i>Capra hircus</i>	0	0	0	0	0	0	0	0	0	0	0	0	3.5	3.5	0	0	0	0	0	0
Cow	<i>Bos taurus</i>	0	0	0	0	0	0	0	0	0	0	0	0	3.5	3.5	0	0	0	0	0.9	0.4
Horse	<i>Equus caballus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.6	0.3
Dog	<i>Canis familiaris</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1.2	0.4
Medium Mammals		67.2	66.2	66.7	64.8	56.7	45.1	75.0	73.8	91.9	91.9	85.7	84.3	51.9	51.8	100.1	96.5	92.6	88.9	51.3	38.9
Tasmanian pademelon	<i>Thylogale billardierii</i>	61.6	60.7	61.1	59.2	36.7	32.9	75.0	73.8	76.9	76.9	85.7	84.3	27.6	27.6	92.9	89.3	92.6	88.9	20.3	18.6
Brushtail possum	<i>Trichosurus vulpecula</i>	0.8	0.7	5.6	5.6	10.0	7.9	0	0	15.4	15.4	0	0	10.4	10.3	3.6	3.6	0	0	8.3	6.3
Ringtail possum	<i>Pseudocheirus peregrinus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3.6	3.6	0	0	21.5	13.3
Bettong	<i>Bettongia gaimardi</i>	0	0	0	0	0	0	0	0	0	0	0	0	6.9	6.9	0	0	0	0	0	0
Potoroo	<i>Potorous tridactylus</i>	3.2	3.2	0	0	3.3	3.4	0	0	0	0	0	0	3.5	3.5	0	0	0	0	0	0
Southern brown	<i>Isodon</i>	0	0	0	0	0	0	0	0	0	0	0	0	3.5	3.5	0	0	0	0	0.6	0.3

bandicoot	<i>obesulus</i>																				
Echidna	<i>Tachyglossus aculeatus</i>	0.8	0.8	0	0	6.7	0.9	0	0	0	0	0	0	0	0	0	0	0	0	0.6	0.4
Rabbit	<i>Oryctolagus cuniculus</i>	0.8	0.8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Small mammals		0	0	0	0	0	0	6.3	5.6	0	0	0	0	10.4	10.1	0	0	0	0	18.4	8.7
Water rat	<i>Hydromys chrysogaster</i>	0	0	0	0	0	0	0	0	0	0	0	0	6.9	6.6	0	0	0	0	0	0
Black rat	<i>Rattus rattus</i>	0	0	0	0	0	0	6.3	5.6	0	0	0	0	0	0	0	0	0	0	0	0
Swamp rat	<i>Rattus lutreolus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.6	0.2
Antechinus	<i>Antechinus</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9.5	4.5
Long-tailed mouse	<i>Pseudomys higginsii</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4.0	2.3
White-footed dunnart	<i>Sminthopsis leucopus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.3	0.1
Pygmy possum	<i>Cercartetus concinnus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.6	0.1
Sugar glider	<i>Petaurus breviceps</i>	0	0	0	0	0	0	0	0	0	0	0	0	3.5	3.5	0	0	0	0	3.4	1.5
Birds		8.8	1.1	27.8	2.8	46.7	9.3	25.0	2.5	0	0	28.6	2.9	6.9	0.7	35.7	3.6	44.4	4.5	23.2	10.9
Reptiles		0.8	0.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2.0	0.2
Invertebrates		0	0	0	0	3.3	0.3	0	0	0	0	0	0	0	0	0	0	0	0	4.6	0.7
No. items		138		46		48		20		13		9		31		38		39		518	
No. scats		125		36		30		16		13		7		29		28		27		349	

Table 2.6. Percent frequency occurrence (%F) and relative volume (%V) of prey items, in spotted-tailed quoll scats for each site.

Common name	Scientific name	Arthur River		Epping forest		Freycinet		Melaleuca		Ross		Meander		Cradle Mountain	
		%F	%V	%F	%V	%F	%V	%F	%V	%F	%V	%F	%V	%F	%V
Large mammals		38.9	33.3	35.3	34.7	54.6	45.5	0	0	12.5	6.3	63.2	55.3	21.3	17.6
Common wombat	<i>Vombatus ursinus</i>	0	0	0	0	9.1	9.1	0	0	0	0	0	0	1.3	1.2
Bennett’s wallaby	<i>Macropus rufogriseus</i>	38.9	33.3	23.5	22.9	36.4	36.4	0	0	12.5	6.3	57.9	51.6	20.0	16.4
Sheep	<i>Ovis aries</i>	0	0	11.8	11.8	0	0	0	0	0	0	5.3	3.7	0	0
Cow	<i>Bos taurus</i>	0	0	0	0	9.1	7.3	0	0	0	0	0	0	0	0
Medium mammals		44.5	59	58.8	57.8	36.4	31.8	80.0	58.9	50.0	50.0	31.6	31.4	34.6	30.2
Tasmanian pademelon	<i>Thylogale billardierii</i>	36.1	30.0	0	0	18.2	18.2	70.0	48.9	37.5	37.5	26.3	26.2	9.3	9.3
Brushtail possum	<i>Trichosurus vulpecula</i>	0	0	5.9	5.8	18.2	13.6	0	0	12.5	12.5	0	0	9.3	6.7
Ringtail possum	<i>Pseudocheirus peregrinus</i>	0	21.2	0	0	0	0	0	0	0	0	0	0	14.7	12.9
Southern brown bandicoot	<i>Isodon obesulus</i>	5.6	5.4	0	0	0	0	0	0	0	0	0	0	0	0
Echidna	<i>Tachyglossus aculeatus</i>	0	0	0	0	0	0	10.0	10.0	0	0	0	0	1.3	1.3
Platypus	<i>Ornithorhynchus anatinus</i>	0	0	0	0	0	0	0	0	0	0	5.3	5.2	0	0
Rabbit	<i>Oryctolagus cuniculus</i>	2.8	2.4	52.9	51.8	0	0	0	0	0	0	0	0	0	0
Small mammals		8.4	5.7	0	0	0	0	10.0	10.0	25.0	15.0	5.3	5.0	39.9	34.4
Black rat	<i>Rattus rattus</i>	0	0	0	0	0	0	0	0	0	0	5.3	5.0	0	0
Swamp rat	<i>Rattus lutreolus</i>	5.6	5.4	0	0	0	0	10.0	10.0	0	0	0	0	0	0

House mouse	<i>Mus musculus</i>	0	0	0	0	0	0	0	0	12.5	12.5	0	0	0	0
Antechinus	<i>Antechinus</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	13.3	10.4
Long-tailed mouse	<i>Pseudomys higginsii</i>	0	0	0	0	0	0	0	0	0	0	0	0	13.3	12.5
White-footed dunnart	<i>Sminthopsis leucopus</i>	0	0	0	0	0	0	0	0	0	0	0	0	8.0	8.2
Pygmy possum	<i>Cercartetus concinnus</i>	0	0	0	0	0	0	0	0	12.5	2.5	0	0	5.3	3.3
Sugar glider	<i>Petaurus breviceps</i>	2.8	0.3	0	0	0	0	0	0	0	0	0	0	0	0
Birds		41.2	21.2	23.5	7.7	18.2	13.6	20.0	0.5	37.5	17.5	21.1	5.6	17.3	8.4
Reptiles		0	0	0	0	0	0	0	0	0	0	0	0	12.0	2.4
Invertebrates		11.1	1.9	0	0	9.1	1.8	70.0	20.6	12.5	11.3	15.8	2.7	32.0	7.1
No. items		52		20		13		18		11		26		118	
No. scats		36		17		11		10		8		19		75	

2.4.4 Effect of rainfall on prey consumption

Rainfall had a significant effect on the diet composition of quolls but no effect on devils (Table 2.7). The occurrence of large mammals in the diet of quolls was higher, while small mammals and invertebrates were lower with lower rainfall (Table 2.7), representing a decline both from east to west and with rising altitude.

Table 2.7. Generalised linear mixed model (GLMM) estimates and standard errors for the effect of rainfall on diet composition of devils and quolls for each prey category. Site was included as a random factor. Bold numbers indicate statistical significant (p value <0.05).

		Intercept	Rainfall			Site	
		Estimate \pm s.e.	Estimate \pm s.e.	z-value	p-value	Variance	Std
Devils	Large mammals	-1.32 \pm 0.53	-0.13 \pm 0.88	-0.15	0.882	1.05	1.03
	Medium mammals	1.25 \pm 0.56	0.15 \pm 0.92	0.16	0.871	1.16	1.08
	Small mammals	-4.34 \pm 1.66	1.75 \pm 1.99	0.88	0.381	4.45	2.11
	Birds	-1.30 \pm 0.38	-0.10 \pm 0.66	-0.16	0.876	0.56	0.75
	Invertebrates	-4.26 \pm 0.37	1.31 \pm 0.86	1.53	0.126	0	0
	Reptiles	-4.95 \pm 0.58	2.11 \pm 1.38	1.53	0.126	0	0
Quolls	Large mammals	-0.91 \pm 0.18	-0.84 \pm 0.30	-2.78	0.005	0	0
	Medium mammals	-0.24 \pm 0.27	0.04 \pm 0.43	0.09	0.931	0.09	0.29
	Small mammals	-1.68 \pm 0.42	1.55 \pm 0.65	2.39	0.017	0.34	0.59
	Birds	-1.18 \pm 0.21	-0.45 \pm 0.33	-1.36	0.175	0.01	0.12
	Invertebrates	-1.38 \pm 0.21	1.67 \pm 0.42	3.96	<0.001	0	0
	Reptiles	-5.26 \pm 2.79	3.74 \pm 3.18	1.18	0.240	3.03	1.74

2.5 Discussion

Devils and quolls showed high overlap of dietary niche but there was significant partitioning within this, and quolls had a broader niche than devils. Relative to devils, the diet of quolls included more small mammals, reptiles and invertebrates, whereas devils consumed more large and medium-sized mammals. Both species preyed predominately on Tasmanian pademelon, Bennett's wallaby and birds but also consumed a wide range of prey species at lower frequencies, suggesting that they are both opportunistic and flexible foragers. Rainfall, which is confounded with population decline of devils from facial tumour disease, influenced the diet of quolls but not devils. In drier sites, which is also where devils have experienced the greatest population decline, quolls consumed more large mammals than in wetter sites where devil density was still intact. The extensive dietary overlap suggests high potential for competition and aggressive interference over food resources between devils and quolls if resources become limited and for competitive release if devils are lost from the landscape.

2.5.1 Preferred prey species in the diet of devils and quolls across Tasmania

Devils and quolls fed predominately on Tasmanian pademelon and Bennett's wallaby, which are both widespread and abundant in Tasmania (Rounsevell *et al.* 1991). The abundance of these macropods may facilitate coexistence of sympatric devil and quoll populations. Pademelons and wallabies show a preference for agricultural areas and reach their highest abundance where there are high metric values for patchiness with long lengths of edges between pasture, that provides high quality food for herbivores, and remnant native vegetation patches, that provide shelter (Le Mar and McArthur 2005; Wiggins and Bowman 2011). In these agricultural areas, grazing marsupials such as macropods and possums are frequently culled by farmers to reduce competition with domestic livestock. The carcasses are often left for species such as devils and quolls to scavenge on. Modified pasture for grazing livestock is integral to or occurs within 5km of all of our sites except Cradle Mountain, Melaleuca and kunanyi/Mt Wellington. In addition, Bennett's wallabies and pademelon are frequently killed on Tasmanian roads (Hobday and Minstrell 2008) providing carrion for both devils and quolls.

2.5.2 Large mammals in the diet of quolls

The diet of spotted-tailed quolls included large native mammals such as Bennett's wallaby and wombats. Due to the size difference between quolls and these large mammals, it is plausible that the presence of these items in the diet reflects scavenging of carcasses. Bennett's wallabies occurred at a high frequency in the diet of quolls at Arthur River, Freycinet and Meander. Bitumen roads run through these sites and macropods are frequently killed by vehicles, enabling quolls to scavenge on large prey. Similarly, the presence of large livestock, such as cows and sheep, in quoll scats were assumed to represent consumption of carrion. In addition, it is possible that devils hunting large macropods facilitate scavenging opportunities for quolls by opening up the carcass. Yarnell et al. (2013) suggest that brown hyenas (*Parahyaena brunnea*) access scavenging opportunities derived from apex predators such as lions (*Panthera leo*) and wild dogs (*Lycaon pictus*) killing large herbivores.

Another explanation is that these diet records are of juveniles. It is not possible to differentiate whether large-bodied prey taxa in quoll scats come from young or adult animals as quolls do not consume large bones (bones of small mammals and birds are sometimes found in their scats). Devils consume large bones and if these are not digested completely, there can be sizeable bone fragments that can be used to age larger prey. The high proportion of Bennett's wallabies in the scats of quolls could be juveniles, which are vulnerable from when they first start to come out of the pouch, through permanent emergence and independence, and until they grow to a size when they are too large for quolls to easily kill.

2.5.3 Geographic variation in diets

The breadth of dietary niches of devils and quolls varied among sites suggesting that both species are opportunistic and flexible foragers, and consume a wide variety of taxa if their preferred prey species is not available. This finding agrees with studies on the diet of spotted-tailed quolls on mainland Australia which also identified medium-sized mammals (500g-4999g) as the most important prey group and found that quolls consume a wide range of taxa and vary their diet in response to short-term fluctuation in prey abundance (Belcher 1995; Glen and Dickman 2006a; Belcher et al. 2007; Dawson et al. 2007). At the

Epping Forest site in the dry (499mm rainfall) Midlands agricultural region, rabbits were the most important prey item in quoll diets and Tasmanian pademelons were rare. Rabbits are common in this farming landscape and while Bennett's wallabies are present, Tasmanian pademelons, which prefer wetter, denser habitat, are likely to be uncommon.

Pemberton et al. (2008) analysed the frequency of occurrence of prey items in the diet of Tasmanian devils at six sites in Tasmania and found that birds followed by ringtail possums, Tasmanian pademelons and Bennett's wallabies were the most important food items. The higher occurrence of birds in the diet in Pemberton *et al.*'s study may be because half of their six sites were coastal where there is a source of seabirds, compared to only four of thirteen in this study. All of the sites in Pemberton *et al.* (2008) were in the wetter western or southwestern region of Tasmania and this may explain the higher frequency of ringtail possums than in our study. In our study, ringtail possums only occurred at a frequency of 3.6% at Oldina and 21.5% at Cradle Mountain. The high frequency of ringtail possums in Pemberton et al. (2008) relative to our study could be attributed to a difference in prey composition at study sites but still supports our findings that medium-sized mammals are the preferred prey group for devils.

2.5.4 Partitioning of resources

Competition theory predicts that a high dietary overlap will result in some degree of resource partitioning, if prey is limited (Schoener 1986). Our results suggest that devils and quolls partition resources on prey size. Prey size partitioning is expected with the body size differential. Devils are larger and consumed more large mammals (e.g. wombats) and medium- sized mammals (e.g. pademelons), whereas the smaller quolls consumed more small mammals, reptiles and invertebrates. Prey size separation will reduce dietary resource competition to some degree because different prey species will be consumed by devils and quolls.

Vertical partitioning of resources can enable sympatric species to coexist (Emmons 1980; Estrada and Coates-Estrada 1985). For example, Ray and Sunkist (2001) examined dietary overlap between eight sympatric carnivores in central Africa and found that the three species with the highest overlap in diet showed temporal and vertical niche partitioning. Quolls have specialised adaptations for utilising the arboreal niche such as a

clawless hallux on the pes and ridges on the foot pads, which are lacking in devils that are far less adept at climbing trees (Jones 2003). In a study conducted on the mainland of Australia, quolls consumed more arboreal prey despite extensive dietary overlap with sympatric foxes (*Vulpes vulpes*) and wild dogs (*Canis lupus* spp) (Glen and Dickman 2008). An explanation for the lack of partitioning on arboreal prey between quolls and devils in our study could be that there are few arboreal mammal species in Tasmania. Most species of arboreal mammals that occur on the adjacent mainland in Victoria have not occupied Tasmania across the arid Bassian land bridge during the Pleistocene (Keast 1981). Of the two arboreal mammals that are common in Tasmania, brushtail possums forage extensively on the ground and ringtail possums also frequent the ground, where they are available as prey to devils. Vertical partitioning in habitat use does suggest that the arboreal niche could be exploited by quolls to give them a competitive advantage over devils if resources become limited.

2.5.5 Effect of rainfall on diet

Rainfall and the presense of DFTD had no influence on the consumption of the six prey categories for devils across Tasmania. Devils focused on Tasmanian pademelons and Bennett's wallabies across their distributional range. Quolls, however, consumed more large mammals and fewer small mammals and invertebrates at sites with lower rainfall (and, currently, low densities of devils). Rainfall is a strong bottom-up factor influencing the local abundance of medium-sized mammals, the prey species of devils and quolls, in Tasmania from year to year (Hollings *et al.* 2014). Whether it also influences prey abundance across geographic regions has not been assessed and direct assessment of prey abundance at the sites was beyond the scope of this study.

If competition is driving the observed resource partitioning, we could expect quolls to include more medium and large-sized mammals in their diet when devils are at low density as these prey species may be more abundant and/or available because they are not being hunted by devils. Our result, of no differences in devil diet across Tasmania but increased large mammal category and reduced small mammal and invertebrate in quoll diet in eastern Tasmania, could suggest competitive release resulting from the decline of devils. It may, however, represent greater availability of carrion rather than of live prey for quolls in the areas of devil decline. Measurement of prey and carrion abundance and predator density at the same time as assessing dietary composition of devils and quolls across

Tasmania is recommended for future studies to clarify the mechanisms behind the observed resource partitioning.

2.5.6 Intraguild predation

Carnivores that have a high dietary overlap are more likely to encounter each other when foraging because they are hunting the same prey species, which can result in interspecific aggression (Donadio and Buskirk 2006). The chance of intense interspecific aggression including killing is higher when an intermediate body-size difference exists between carnivores (Donadio and Buskirk 2006). Relative to devils, quolls fall into the intermediate size class, which when coupled with the observed high dietary overlap and preference for similar prey, could lead to aggressive encounters. If encounters between devils and quolls result in mortality of quolls, devils could have a suppressive effect on quoll populations. While devils are competitively dominant at carcasses (Jones and Barmuta 1998) and adult female quolls will chase subadult devils away from carcasses where older age may provide more advantage than larger body size (Jones 1995), the extent of intraguild killing remains unknown. Four devil scats at Cradle Mountain contained spotted-tailed quoll fur, but we cannot determine if this was a result of scavenging or intraguild predation. There are anecdotal records of devils killing quolls, as well as a quoll wounding a devil in a conflict over food at this site (M. Jones, pers. comm.). No quoll scats contained devil fur, which suggests that intraguild scavenging and potentially predation is asymmetrical. However, we cannot rule out that our relatively low sample size of quolls meant that we failed to detect intraguild feeding. The frequency of interspecific, intraguild killing may be underestimated in diet studies as animals killed in acts of extreme aggressive interference competition are not always consumed (Palomares and Caro 1999). Intraguild killing could also be overestimated because both devils and quolls scavenge and are susceptible to road mortality (Jones 2000), which provides a source of devil and quoll carcasses for scavenging. All of our sites, except Melaleuca and kunanyi/Wellington Park were within 5km of roads with traffic speed and volume sufficiently high to provide opportunities for road mortality and hence scavenging of devils and quolls.

2.5.7 Intersexual dietary overlap

The high overlap in diet between males and females of both devils and quolls suggests that diet partitioning based on sexual dimorphism does not occur broadly in Tasmania. This is consistent with results of studies on the mainland of Australia on the diet of male and female quolls (Glen and Dickman 2006a; Belcher *et al.* 2007; Dawson *et al.* 2007). Diet overlap between female and male quolls and female quolls and adult devils of either sex was lower at Cradle Mountain than at Arthur River and Freycinet. An explanation for the apparent sex partitioning in prey size for spotted-tailed quolls at the Cradle Mountain site is the small size of the quolls (and devils) in this alpine environment combined with the low abundance and species diversity of smaller medium-sized mammals at the site. While spotted-tailed quolls regularly reach body masses of 4.5kg for males and 2.5kg for females in lowland sites, in alpine environments their maximum body mass is smaller, with male quolls typically 3.5kg and females not usually exceeding 2kg (Jones 1995). Pademelons and brushtail possums are abundant but these species are at the larger end of the medium mammal size spectrum. Ringtail possums are present and are mostly arboreal. Quolls are capable of catching them in trees (Phil Bell, personal communication to M. Jones 1995). Records of smaller medium-sized mammalian species are rare. There are very occasional records of a brown bandicoot or a rabbit (Menna Jones, pers. obs) and there are no other species of bandicoots or potoroos at the site. While adult female spotted-tailed quolls in northwest Tasmania (body mass up to 2.5kg) are capable of killing a pademelon (Jones and Watts 1996), the smaller females in this alpine environment at Cradle Mountain (body mass 1.8-2kg) may be restricted to small mammals such as rodents and antechinus that they can more easily kill.

2.5.8 Conclusions

Interspecific competition occurs when a shared resource is in limited supply and can lead to a reduction in the growth, reproduction or survivorship of one of the competing individuals. Thus, the availability and abundance of prey can potentially influence the strength of competitive interactions between carnivore species and also demographics. However, current competition is not always apparent in sympatric species as niche partitioning may have resulted from past competitive interactions e.g. the ghost of competition past (Connell 1980). Competition has already been minimised among the

Tasmanian marsupial carnivores through character displacement and ecomorphological adaptation to different niches (Jones 1997; Jones 2003). Devils have evolved to exploit the facultative scavenger niche, with strong jaw musculature and robust teeth, while spotted-tailed quolls are arboreally adapted (Jones and Barmuta 2000; Jones 2003). Temporal or spatial partitioning may facilitate coexistence among sympatric carnivores where overlap in diet is high (Breuer 2005; Andheria *et al.* 2007; Lovari *et al.* 2015). Future studies should take abundance and composition of prey species, habitat features and density of competitors into account when attempting to identify interspecific competition.

Chapter 3 Spatial ecology of sympatric Tasmanian devils and spotted-tailed quolls



This chapter is currently in preparation for *Wildlife Research*:

Andersen, G.E., Johnson, C.N., and Jones, M.E. Spatial ecology of sympatric Tasmanian devils and spotted-tailed quolls.

3.1 Abstract

Context. Effective conservation of threatened carnivores requires an understanding of space use patterns. In Tasmania, Australia, the Tasmanian devil (*Sarcophilus harrisii*), is endangered due to a fatal transmissible cancer, Devil Facial Tumour Disease (DFTD). Management approaches aimed at restoring the Tasmanian devil population include translocation of devils back into the wild but little is known about their spatial requirements and those of sympatric spotted-tailed quolls (*Dasyurus maculatus*).

Aims. To gain baseline data of the spatial ecology of Tasmanian devils and spotted-tailed quolls to aid translocation decisions. We chose a study site, not yet affected by DFTD and a time of the year when females of both species were in late lactation, to obtain data on a natural population when energetic demands are at their highest.

Methods. GPS collars were used to investigate space use and movement patterns between devils and quolls and between males and females of each species, in northwest Tasmania, Australia.

Key results. Mean seasonal home-range size of devils was larger than for quolls. Male seasonal home-ranges were larger than females' in devils but not in quolls. There was little spatial segregation of home-range and core-area placement among devils, and between devils and quolls. Females of both species travelled significantly further per night than did males. Devils maintained a high movement speed throughout the night until 4am after which movement speed decreased. Quolls remained active throughout the night but increased their activity around dawn and dusk.

Conclusions. When females of both species are invested in maternal care, the seasonal home-ranges and nightly movement patterns suggest that both devils and quolls need large areas to meet their energetic requirements.

Implications. Translocating devils into areas where spotted-tailed quolls occur is unlikely to affect their home-range placement but fine scale avoidance patterns could occur and future research should investigate these.

3.2 Introduction

Human impacts have contributed to substantial population decline and range contraction of many carnivores (Ripple *et al.* 2014). Furthermore, natural events such as high-mortality disease outbreaks can be catastrophic for carnivore populations, particularly those that are already threatened (Thorne and Williams 1988; Alexander and Appel 1994; RoelkeParker *et al.* 1996; Packer *et al.* 1999; Lachish *et al.* 2007). Translocations are used in conservation to reintroduce species to their former ranges or to augment existing populations (Griffith *et al.* 1989). For translocations of carnivores to be successful, understanding of species-specific area requirements, which influence population dynamics, is fundamental (Harris *et al.* 1990; Morales *et al.* 2010).

The Tasmanian devil (*Sarcophilus harrisii*) is the world's largest marsupial carnivore and co-exists with the second largest carnivorous marsupial the spotted-tailed quoll (*Dasyurus maculatus*) in Tasmania, Australia. Devils are solitary, nocturnal, non-territorial with large overlapping home ranges (1300ha; Pemberton 1990). Female devils den their young in the same den each night, while males alternate between 2-3 dens (Pemberton 1990). Spotted-tailed quolls are also solitary, with males occupying overlapping home ranges (Glen and Dickman 2006b). There is evidence for territoriality in female quolls on mainland Australia (Belcher and Darrant 2004; Claridge *et al.* 2005) but not in Tasmania (Troy 2014). Male quolls and females with young use several dens (Belcher and Durrant 2006; Glen and Dickman 2006b).

Devils, once widespread across Tasmania, are now Endangered (IUCN red list/ Hawkins *et al.* 2008) due to the impacts of a fatal transmissible cancer, Devil Facial Tumour Disease (DFTD) (Hamede *et al.* 2012). The total population has declined by at least 85% in the last 20 years, with local declines in excess of 90% (Hawkins *et al.* 2006). Efforts to conserve Tasmanian devils include translocations to the wild from “insurance” populations held in captivity, to augment or restore wild populations (Huxtable *et al.* 2015). Quolls are listed as near-threatened on the IUCN red list of threatened species (Burnett and Dickman 2008), Vulnerable under federal legislation (EPBC 1999) and Rare under Tasmanian legislation (TSPA 1995).

Interactions between devils and quolls remain largely unknown but interference and exploitation competition is likely to occur, with the devil numerically and behaviourally dominant (Jones and Barmuta 1998; Jones and Barmuta 2000). Devils are larger and

competitively dominant at carcasses and their diet overlaps with that of spotted-tailed quolls (Jones 1995; Jones and Barmuta 1998). Interference competition from devils may cause quolls to spatially or temporally avoid devils. However, knowledge on the spatial ecology of devils and quolls in Tasmania is limited to one study on each species (Pemberton 1990; Troy 2014). Our aim, therefore, is to enhance our knowledge of their interspecific spatial relationships. Furthermore, as translocations and reintroductions are essential tools used to restore endangered species such as the devil, spatial information gained in this study can assist management decisions. It will provide an indication of the number of devils that can be translocated into a given area and the effect this might have on quoll populations. We deployed GPS collars on sympatric devils and quolls at a site in northwest Tasmania that is still free of DFTD, to quantify natural spatial ecology of these sympatric species. More specifically, we aim to (1) quantify home-range size and home-range overlap between and within devils and quolls (2) investigate nightly movement and activity patterns.

3.3 Materials and methods

3.3.1 Study site

The study was conducted in northwest Tasmania, Australia, in a 100 km² of the northern section of the Arthur-Pieman Conservation Area (41°05'S, 144°66'E). The study area encompassed both native and modified vegetation together with a network of roads, consisting of a 12 km section of sealed road running through the centre of the area and gravel, dirt and 4WD secondary roads and tracks. Coastal scrub/heath (*Leptospermum scoparium*, *Acacia longifolia*, *Melaleuca squarrosa* and *Leucopogon collinus*) and moorland (*Gymnoschoenus sphaerocephalus*) dominated the west side of the sealed road, while the east side consisted of a mosaic of forest (*Eucalyptus obliqua*, *Eucalyptus nitida*, *Melaleuca ericifolia* and *Leptospermum lanigerum*) and agricultural land with cattle grazing on pasture. The climate was temperate, with monthly mean temperatures ranging from 9.4-16.1 °C, and mean annual rainfall of 1073mm (Australian Bureau of Meteorology 2016).

3.3.2 Trapping and GPS collaring

Devils and quolls were trapped in PVC pipe traps (diameter 315 mm x length 875 mm; N. Mooney and D. Ralph, unpublished data), baited with meat from local prey species (Bennett's wallaby *Macropus rufogriseus* and pademelon *Thylogale billardierii*). Traps were placed near roads and tracks and were checked for captures at dawn. Upon capture, animals were transferred to a hessian sack without the use of anaesthesia and were weighed, sexed and microchipped for future identification.

Seven devils (three males and four females) and four quolls (two males and two females) were fitted with Global Positioning System (GPS) collars (Quantum 4000E, Telemetry Solutions Ltd, Concord, USA) between November 2012 and February 2013. Twelve devils (six males and six females) and six quolls (five males and one female) were GPS collared between October 2013 and January 2014. Half of the adult quoll population were collared. GPS tracking coincided with the period when devils and quolls are in late lactation with young in dens and includes weaning (devils early February; quolls December). Devil collars weighed 185 g and quoll collars weighed 60 g, less than three percent of the body weight for each species. Corrodible links were used to fasten collars, as these are designed to degrade over time and eventually cause the collar to fall off (Thalmann 2013). In addition, the devil collars were fitted with a programmable timed-release mechanism and the quoll collars were made from hard chrome suede, which is designed to stretch over time and eventually fall off. All animals were monitored regularly (every three weeks) through trapping to ensure correct fit of collars. Data from the night an animal was in a trap was removed from analyses. Because devils are mainly active at night, GPS fixes for both species were acquired every 15 minutes from 2030 to 0630 hours for approximately six weeks.

3.3.3 GPS data screening

Animal locations obtained through Global Positioning System (GPS) contain errors due to missing location fixes or location errors of successfully acquired fixes (Bjorneraas *et al.* 2010). These must be removed. First, we visually screened for GPS errors and spikes using 'adehabitatLT' (Calenge 2006) in R version 3.1.3 (R Development Core Team 2015). Second, because Horizontal Dissolution of Precision (HDOP) is related to location error (D'Eon 2003), we determined an appropriate HDOP threshold to ensure that positional

accuracy was similar to the resolution of the vegetation types in our study site. A low HDOP value represents a higher level of precision as the satellites used to generate the fix are widely dispersed across the sky (Bjorneraas *et al.* 2010). Only GPS fixes with a dilution of precision (HDOP) of <7 were included in analyses. This decision was based on a test collar that was left recording 15min fixes for two days. Horizontal error was determined by calculating Euclidean distances between the recorded location and the true location measured with a handheld GPS unit (Garmin GPSMAP 78, Garmin Ltd, USA) (D'Eon and Delparte 2005).

3.3.4 Home-range estimation

Seasonal home-range sizes were determined using 100 % minimum convex polygons (MCP) (Mohr 1947), to allow comparison with previous studies, and movement-based kernel density estimation methods (MKDE) (Benhamou and Cornelis 2010; Benhamou 2011). Using MKDE, we summarised the utilization distributions of each species and sex, at the level of the home-range (the area containing 95 % of the locations) and core-area (the area containing 50 % of the locations). As MKDE benefits from serial autocorrelated data (Benhamou and Cornelis 2010) we used data at 15min intervals. We conducted MCP estimates on data that were subsampled at two hourly intervals, which reduced autocorrelation but did not entirely remove it. Forays were excluded from the MCP analysis following visual inspection of the data set. We conducted an asymptote analysis (Harris *et al.* 1990; Laver and Kelly 2008) to determine whether sufficient GPS locations had been collected to adequately represent each animal's home range, for both the MCP and the MKDE. This analysis adds GPS points sequentially at 10 % intervals from 10-100 % of the dataset to assess whether an asymptote was reached. We considered an asymptote was reached when adding more locations did not increase area estimates. Home-ranges were calculated using the 'adehabitatHR' package (Calenge 2006) in R version 3.1.3 (R Development Core Team 2015). Data from all animals and seasons were pooled to calculate mean home-range and core-area. Two sample t-tests ($\alpha = 0.05$) of unequal variance were used to test for differences between sex of each species in home-range size, core area size estimates.

Because resources are distributed heterogeneously, animals are likely to use different areas of their home-range with different intensity (Vander Wal and Rodgers

2012). Intensity was measured as the core area (50 % MKDE) divided by home-range (95 % MKDE) expressed as a percentage. Intensity represents the proportion of the home-range area in which animals spend 50 % of their time. Two sample t-tests ($\alpha = 0.05$) of unequal variance were used to test for differences in intensity of use between species and between males and females for each species.

3.3.5 Spatial overlap

Using MKDE, we investigated the degree of home-range and core-area overlap for each combination of species and sex within each year. Data from both years were then pooled to obtain a mean estimate of home-range and core-area overlap. We determined the mean percentage of overlap as (Minta 1992):

$$\left[\left(\frac{\text{area overlap}}{\text{area of animal A}} \right) \times \left(\frac{\text{area overlap}}{\text{area of animal B}} \right) \right]^{0.5}$$

3.3.6 Nightly movements

We quantified activity time from dusk to dawn as this is the period devils and quolls are predominately active. The nightly activity pattern was described for devils and quolls by calculating the average movement speed in 15 minute intervals throughout the night. Mean movement speed was also calculated for each species. Due to numerous unsuccessful fixes, only fixes 15 minutes apart were used in these analyses. Mean distance moved per night was also calculated based on nights that included ≥ 20 fixes to provide a robust estimation. Significant differences between sexes of each species were investigated using a one-way ANOVA.

3.4 Results

3.4.1 Trapping and GPS collaring

Trapping between November 2012 and February 2013 yielded 85 individual devils and 30 individual quolls over 104,440 trap nights. Trapping between October 2013 and January 2014 yielded 57 individual devils and 12 quolls over 23,517 trap nights. One devil was collared in both years and data obtained on it in the second year were not included in

analysis. A total of 24,649 GPS fixes were obtained, 17,837 for devils and 6,812 for quolls. Devils were collared on average for 50 days (range: 40-77 days) and quolls for 28 days (range: 10-49 days). The overall GPS success rate (i.e. the number of successful fixes by an individual GPS collar in proportion to the total number of programmed fixes) was $60 \pm 3\%$ (mean \pm s.e.). Adult male devils weighed 9.22 ± 0.22 kg (mean \pm s.e.) ($n = 43$), adult female devils 6.2 ± 0.20 kg ($n = 57$), adult male quolls 3.4 ± 0.10 kg ($n = 18$) and adult female quolls 2.2 ± 0.09 kg ($n = 9$).

3.4.2 Home-range estimation

Home-ranges reached an asymptote for all individuals. For devils the mean (\pm s.e.) home-range estimate was $2,145 \pm 188$ ha (100 % MCP) or $1,448 \pm 127$ ha (95% MKDE) (Table 3.1). Quolls had a mean home-range size of 528 ± 94 ha (100 % MCP) or 321 ± 41 ha (95 % MKDE) (Table 3.1). Devils had a mean core-area size (50 % MKDE) of 254 ± 25 ha and quolls had a mean core-area of 58 ± 9 ha (Table 3.1). The mean home-range and core-area size of male devils were significantly larger than that for females (95 % MKDE: $t = -2.89$, $df = 10$, $P = 0.016$; 50 % MKDE: $t = -2.4$, $df = 10$, $P = 0.037$). There was no significant difference in home-range or core-area size of male and female quolls (95 % MKDE: $t = -1.04$, $df = 4$, $P = 0.367$; 50 % MKDE: $t = 0.71$, $df = 3$, $P = 0.527$).

Table 3.1. Home-range data from Tasmanian devils and spotted-tailed quolls collared in the Arthur-Pieman Conservation Area, northwest Tasmania, Australia, between November 2012 - February 2013 and October 2013 - January 2014. Mean area in ha \pm s.e. and range for two home-range estimators are given. MCP, minimum convex polygon; MKDE, movement-based kernel density estimation method. N = number of home-ranges.

		N	100 % MCP	95 % MKDE	50 % MKDE
Devils	All	18	2145 ± 188	1448 ± 127	254 ± 25
			(1131 - 3587)	(837 - 2569)	(118 - 472)
	Males	8	2688 ± 265	1807 ± 205	316 ± 42
			(1466 - 3587)	(1017 - 2569)	(170 - 472)
	Females	10	1710 ± 170	1159 ± 90	205 ± 19
			(1131 - 2685)	(837 - 1631)	(118 - 281)
Quolls	All	10	528 ± 94	321 ± 41	58 ± 9
			(110 - 943)	(110 - 978)	(16 - 99)

Males	7	591 ± 118 (214 - 943)	349 ± 47 (173 - 978)	63 ± 10 (33 - 99)
Females	3	379 ± 135 (110 - 525)	255 ± 77 (110 - 373)	47 ± 18 (16 - 79)

The mean intensity of use of home-range for devils (= 17.7 %) was similar to quolls (= 18.0 %) ($t = -0.19$, $df = 16$, $P = 0.856$) (Fig. 3.1). Intensity of core use areas for male-female devils ($t = 0.31$, $df = 16$, $P = 0.761$) and male-females quolls ($t = -0.18$, $df = 7$, $P = 0.863$) was also similar (Fig. 3.1).

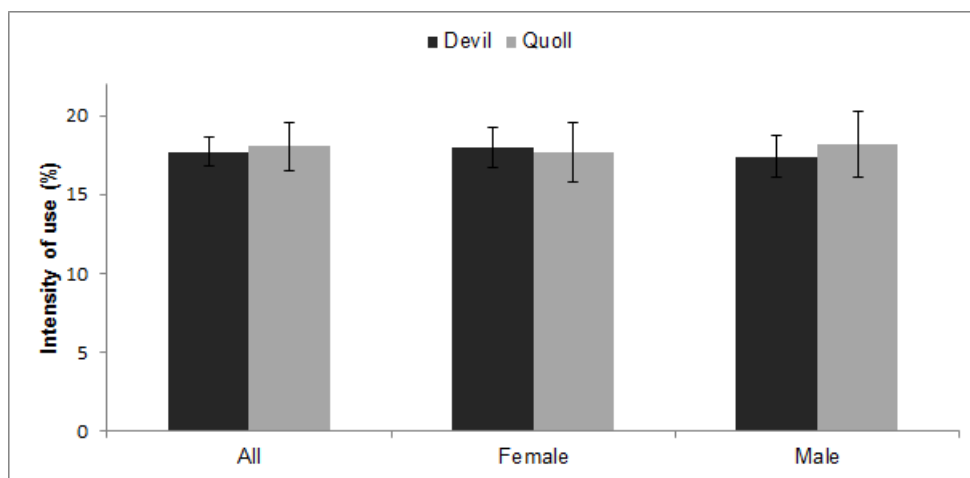


Fig. 3.1. Mean intensity of use (\pm standard error) of home-range areas for Tasmanian devils and spotted-tailed quolls in the Arthur-Pieman Conservation Area, northwest Tasmania, Australia between November 2012 - February 2013 and October 2013 - January 2014. Intensity represents the proportion of the home-range area that devils and quolls spent 50 % of their time in.

3.4.3 Spatial overlap

Home range overlap at the 95 % MKDE utilisation distribution occurred in 78 devil-devil dyads, 81 devil-quoll dyads and 8 quoll-quoll dyads. Overlapping core-areas occurred in 59 devil-devil dyads, 49 devil-quoll dyads and 3 quoll-quoll dyads. Home-range overlap was highest between devils, regardless of sex, than the other dyads (Table 3.2). The mean overlap between devils and quolls was approximately 30 % regardless of sex (Table 3.2). Home-ranges of male quolls overlapped considerably with those of female quolls but showed very little overlap with one another (Table 3.2). Female quolls home-range did not overlap.

Overlap in core-areas was less for all dyads except for the quoll-quoll dyad (Table 3.2). This was a consequence of there being only three quoll dyads with overlapping core-areas and that 90 % of one female quoll's core-area was covered by the core-areas of two males. The highest level of interspecies home-range overlap occurred in the same female quoll whose entire home-range, at 95 % MKDE, was within the home-range of two male devils.

Table 3.2. Mean percent \pm s.e. home-range (95 % MKDE) and core use area (50 % MKDE) overlap for each dyad type for Tasmanian devils (TD) and spotted-tailed quolls (STQ) in the Arthur-Pieman Conservation Area, northwest Tasmania, Australia between November 2012 - February 2013 and October 2013 - January 2014. Range provided in parenthesis. N = number of overlapping home-ranges.

	N	TD - TD	N	TD - STQ	N	STQ - STQ
95 % MKDE						
All	78	41 \pm 3 (0 - 99)	81	29 \pm 2 (0 - 100)	8	19 \pm 6 (0 - 82)
Females	18	37 \pm 6 (0 - 79)	11	37 \pm 6 (0 - 98)	0	
Males	16	40 \pm 5 (0 - 82)	29	30 \pm 4 (0 - 98)	5	9 \pm 3 (0 - 35)
Females-Males	44	42 \pm 4 (0 - 99)	41	28 \pm 5 (0 - 100)	3	36 \pm 13 (0 - 82)
50 % MKDE						
All	59	23 \pm 3 (0 - 96)	49	19 \pm 3 (0 - 100)	3	47 \pm 13 (0 - 93)
Females	12	23 \pm 8 (0 - 90)	7	22 \pm 9 (0 - 93)	0	
Males	13	19 \pm 6 (0 - 77)	20	16 \pm 4 (0 - 91)	1	28 \pm 4 (0 - 32)
Females-Males	34	26 \pm 4 (0 - 96)	22	20 \pm 4 (0 - 100)	2	57 \pm 18 (0 - 93)

3.4.4 Nightly movements

Devils maintained a high movement speed from just after sunset until four am, when movement slowed (Fig. 3.2). Quolls remained active throughout the night but with increased activity around dawn and dusk (Fig. 3.2). Devils moved with an average speed of 21.8 m/min and quolls 7.1 m/min.

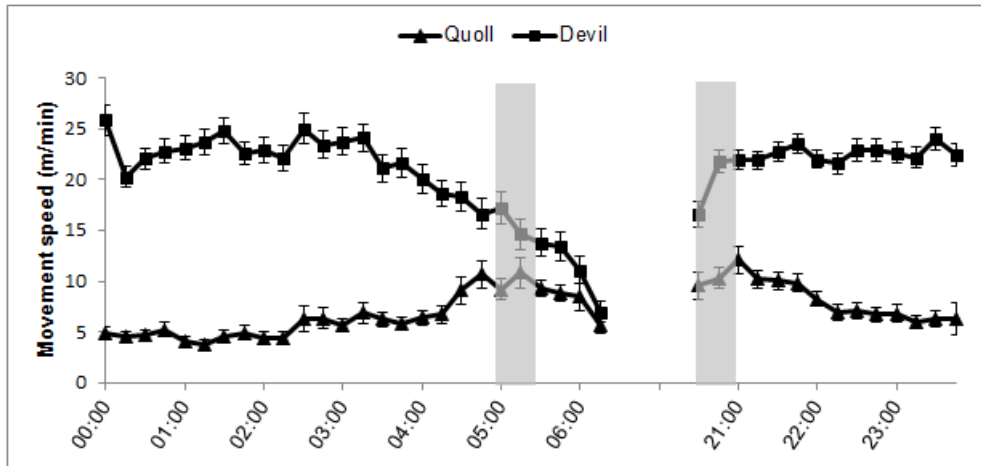


Fig 3.2. Mean (\pm s.e.) movement speed of Tasmanian devils ($n = 13,519$ fixes) and spotted-tailed quolls ($n = 5523$ fixes) in the Arthur-Pieman Conservation Area, northwest Tasmania, Australia between November 2012 - February 2013 and October 2013 - January 2014. Grey rectangles represent dusk and dawn.

Total distance moved per night by devils varied from 214 m to 22,700 m, the mean (\pm s.e.) being significantly greater for females than males (females $9,479 \pm 296$ m; males $7,950 \pm 261$ m, $F = 18.89$, $P < 0.05$). Quolls travelled between 270 m and 8,100 m per night and females moved significantly further than males (females 3716 ± 177.2 m and males 2958.5 ± 164.7 m, $F = 9.5$, $P < 0.05$).

3.5 Discussion

This is the first study to use GPS collars to investigate space use and movement patterns of sympatric Tasmanian devils and spotted-tailed quolls. Devils displayed intersexual difference in home-range size and distance moved each night, with larger male home-ranges but greater female nightly movements. In contrast, there was no intersexual difference in quoll home-range size but female quolls moved further than males. There was little spatial segregation of home-range and core-area placement between devils and quolls

and among devils. Both species remained active throughout the night but displayed different activity patterns.

Tasmanian devils had larger home-range sizes than spotted-tailed quolls, as expected from their larger body size and larger prey size, which consists of medium to larger-sized mammals up to three times their body weight (Jones and Barmuta 1998). Devil home-range, at 100 % MCP, was larger than previously recorded (1300 ha; Pemberton 1990), but comparisons between studies are difficult due to different methodology. VHF-collaring, as used by Pemberton (1990), yields less accurate data than the modern GPS-tracking technology (Hulbert and French 2001) and the lower temporal resolution of data may have underestimated home-range size. Food availability is an important determinant of home-range size in other carnivores (Hayward *et al.* 2009). It is therefore plausible that the difference in home-range size could be attributed to a difference in prey availability.

Spotted-tailed quoll home-range, at 100 % MCP, was within the range reported in studies from other regions of Australia (Belcher and Darrant 2004; Claridge *et al.* 2005; Glen and Dickman 2006b). In contrast to these studies, which found that male quoll home-range was significantly larger than females and that male home-ranges overlapped extensively with both other males and with females, our study found no difference in home-range size between the sexes and very little overlap between males. The lack of difference in home-range size between male and female quolls should be interpreted with caution due to the low sample size of female quolls. However, these differences could be attributed to the different time of year that this and the previous studies were conducted. The previous studies took place during or immediately after the mating season, when males may range widely to access multiple females. Our study was conducted when females were in late lactation and had high energetic and so hunting requirements. As quolls are solitary and lack paternal care (Jones *et al.* 2001), male quolls would be expected to avoid contact with one another outside the mating season when they are more likely to risk injury to gain access to females.

Our results on home-range overlap among quolls should be interpreted with caution due to the low sample size. The female-male quoll overlap was based on a sample size of three. One female quoll's home-range was almost entirely encompassed by two male quolls, which resulted in an extremely high percent female-male overlap. Another female quoll's home-range overlapped only slightly with a male quoll's. Similarly our female-

female home-range analysis was based on three females and we found no home-range overlap. Previous studies on spotted-tailed quolls also found no overlap among females and attributed this to territoriality (Belcher and Darrant 2004; Claridge *et al.* 2005; Glen and Dickman 2006b). In contrast, a study approximately 60km north of our study site found a high degree of overlap among females (Troy 2014). Thus, we cannot definitively conclude that Tasmanian female quolls show little overlap in home-range.

Female devils and quolls moved significantly further than males each night, although there was no difference in intensity of home-range use between the sexes of either species, and female devils had smaller home-ranges than males. These patterns can probably be attributed in part to the timing of the study in late lactation when females are provisioning young in the den. Lactation is energetically costly and females may increase their foraging movements (Lindstedt *et al.* 1986) to obtain enough food. In the latter stages of the study, they may also have been bringing food back to the den for their offspring. At the same time they are restricted in how far they can travel from the den as they have to return to the same den and probably during the night's foraging as well as at the end of the night. Different energy requirements in sexually dimorphic species (Harestad and Bunnell 1979) could also explain the smaller home-ranges in female than in male devils.

Prey abundance is a major determinant of spatial organisation of carnivores (Herfindal *et al.* 2005), and probably influences the space use patterns of devils and quolls. For example, when resource availability is either extremely low or high, home-ranges are less likely to be defended, leading to more overlap of ranges (Maher and Lott 2000). Devil home-ranges and core-areas overlapped extensively regardless of sex, which could be a result of high prey abundance, which in turn facilitates a high density of carnivores. Our study site encompassed some farmland, which is associated with a higher abundance of macropods, the preferred prey of devils and quolls (Jones and Barmuta 1998). The high abundance of macropods could facilitate overlapping home-ranges. Despite this, intensity of use of home-ranges for both devils and quolls regardless of sex was low, which suggests that they both range widely in search of food. While devils and quolls can overlap almost complete in space use and coexist there may be partitioning in other habitat types i.e. Jones and Barmuta (2000) found habitat partitioning at Cradle Mountain.

Devils and quolls exhibit different activity patterns during the night. Devils were active from dusk until 4am while quolls were increasingly active in the early and latter

parts of the night. It is plausible that quolls minimise competition and the chance of agonistic interactions with devils by being active earlier in the night before devils emerge, then rest throughout the middle of the night, becoming active again in the hours around dawn when devils have decreased their activity. The different hunting modes of the two species may also contribute to differences in their activity patterns. Devils are pounce-pursuit predators (Jones 2003) capable of short fast pursuits that hunt using a moving search (Pemberton 1990). Their hunting strategy may be to cover sufficient distance in a night to find food and then return to a den. A study conducted during summer and winter in a subalpine environment showed that devils were active for about eight hours per night and then returned to the den, irrespective of night length which changed from eight to 15 hours between summer and winter (Jones *et al.* 1997). In contrast to devils, quolls have limb ratios indicative of a slow-running, ambush predator of closed habitats (Jones and Stoddart 1998; Jones 2003). Quolls could leave their den sites at dusk and travel to optimal foraging areas, where they slow down and forage during the night. This sit-and-wait strategy could be reflected in the slow movement speed during the middle parts of the night. Overall movement speeds were substantially higher for devils than for quolls, as expected from their larger home-range size, larger body size and hunting style. In addition, the majority of collared females of both species had young in a den and may have returned to them earlier in the night than they would return to a den if they did not have young.

Spatial avoidance of a dominant competitor by a subordinate is a common result of interactions among carnivores (Palomares and Caro 1999). However, there was little spatial segregation at the home-range scale between devils and quolls. Nor did we observe fine-scale patterns of avoidance in core-area placement. The maternal den of a female quoll was observed only 400m away from the maternal den of a female devil. Furthermore, it is likely that spatial overlap between species is underestimated because we collared only a small proportion of the devils and quolls that lived in the study area. Our results do suggest, however, that reintroducing devils into areas where spotted-tailed quolls occur will not affect their home-range placement. Fine-scale patterns of avoidance may occur though and future research should investigate these.

Our study provides important information on Tasmanian devil and Tasmanian spotted-tailed quoll spatial and movement ecology. The data provided here should help managers make informed decisions on the number of Tasmanian devils that can be released into a given area. Translocation of devils with young is highly unlikely, however,

the home-range sizes described in this study indicate the home-range size that is needed during lactation. During the period of the year when females of both species are invested in maternal care, the large home-ranges and nightly movement patterns suggest that both species need large areas to meet their energetic requirements. If devil translocations are attempted in areas smaller than observed home-range sizes, prey availability could become a limiting factor. Further research into spatial use at other times of the year, and in areas with differing abundance of these predators, will provide a more complete insight into Tasmanian devil and spotted-tailed quoll spatial organisation and movement patterns.

Chapter 4 Anthropogenic habitat modification enhances traveling and hunting opportunities for a carnivore community



This chapter is in review in *Journal of Applied Ecology*:

Andersen, G.E., Johnson, C.N., Barmuta, L.A., and Jones, M.E. Anthropogenic habitat modification enhances traveling and hunting opportunities for two medium-sized carnivores

4.1 Abstract

1. Many carnivores are threatened by habitat loss and fragmentation. These changes also create linear features and habitat edges that can provide opportunities for hunting and travel. Whether carnivores benefit from these features may depend on the intensity of other threats, such as persecution. To understand the significance of anthropogenic linear features in the ecology of carnivores, we need fine-scaled studies to show how individual animals use them.

2. We studied two threatened medium-sized carnivores, the Tasmanian devil (*Sarcophilus harrisii*) and spotted-tailed quoll (*Dasyurus maculatus*) in a mixed landscape of conservation and agricultural land. Using GPS tracking, we compared their use of intact habitat *versus* linear features such as fence lines, roads and pasture/forest edges.

3. Both species selectively used anthropogenic linear features, preferring the pasture/cover interface for foraging and roads for movement and foraging. Devils often travelled along fence lines, while quolls showed little preference for them. Otherwise, they concentrated their foraging in forest rather than areas cleared for pasture.

4. *Synthesis and applications.* Anthropogenic linear features improve habitat quality for devils and spotted-tailed quolls, and could increase abundance provided that sufficient intact forest remains to sustain prey. Management of these and probably many other species of carnivores should focus on controlling mortality factors associated with human use of landscapes.

4.2 Introduction

Carnivores are vulnerable to habitat loss and fragmentation because of their low population densities and large area requirements, and because they are often persecuted by humans (Purvis *et al.* 2000; Woodroffe 2000). Anthropogenic landscape alteration creates linear features, such as the ecotone between native vegetation and livestock pasture, roads, fences, and power lines, which can have complex effects on carnivores. Roads may impede movement, increase mortality from vehicle collisions, increase hunting and poaching by providing access to previously inaccessible habitats, and cause stress due to noise and visual stimuli (Fahrig and Rytwinski 2009; Parris and Schneider 2009; Benitez-Lopez *et al.* 2010). Fences can also obstruct movement (Newmark 2008; Cozzi *et al.* 2013).

On the other hand, linear features may provide some benefits. Roads and tracks may facilitate faster travel, enabling carnivores to cover more ground in less time when seeking food (Frey and Conover 2006). Roads, fences and power lines might also provide opportunities for hunting and scavenging, because they create edges and barriers to trap prey and furnish carcasses of animals that have died in collisions with vehicles or power lines (Knight and Kawashima 1993; Lambertucci *et al.* 2009). Roads and tracks also afford predators with quiet avenues of movement as leaf litter does not alert prey as much as it does on the forest floor. Agricultural landscapes with remnant patches of native vegetation create edges that are often rich in small vertebrates and can therefore concentrate prey for medium-sized carnivores (Austen *et al.* 2001; Michel *et al.* 2006; Salek *et al.* 2010; Cervinka *et al.* 2011; Cervinka *et al.* 2013). Many carnivore species that have become invasive outside their native ranges flourish in human-altered habitats. This is true of red foxes (*Vulpes vulpes*) and feral cats (*Felis catus*), and is also the case for some predators in their native range, including red foxes, raccoons (*Procyon lotor*), grey foxes (*Urocyon cinereoargenteus*) and opossums (*Didelphis virginiana*) (Crooks 2002; Bateman and Fleming 2012).

Understanding how anthropogenic landscapes, and particularly the linear features they often contain, affect movement, foraging efficiency and ultimately survival is especially important for threatened and declining species. Of the world's largest mammalian carnivores, 59% are threatened with extinction (Ripple *et al.* 2016). To evaluate the significance of linear features in the ecology of such species, we need detailed behavioural studies showing the extent to which they exploit or avoid them.

We examined the habitat use and fine-scaled movement of two medium-sized marsupial carnivores in their native range in a mixed conservation and agricultural landscape in Tasmania, Australia. The Tasmanian devil (*Sarcophilus harrisii*) is a specialist scavenger and pounce-pursuit predator that weighs 5-14kg (Jones 2008) and has large home ranges (2145ha; G. Andersen, unpublished data). The spotted-tailed quoll (*Dasyurus maculatus*) is an arboreal specialist predator that weighs 0.9-5kg (Belcher 2008) with smaller home ranges (528ha; G. Andersen, unpublished data). Both are diet generalists but primarily feed on mammals (Jones and Barmuta 1998). At our study site in northwest Tasmania, Australia, the Tasmanian devil is not yet affected by Devil Facial Tumour Disease (DFTD), which has caused severe population decline elsewhere in its range (McCallum *et al.* 2009). We asked the following questions: (1) how do these species

utilise landscapes modified by agricultural land use? (2) to what extent do they use edges between pasture and natural vegetation? And, (3) how do roads and tracks affect movement?

4.3 Material and methods

4.3.1 Study area

The study area covered about 100 km² of the northern part of the Arthur-Pieman Conservation Area, northwest Tasmania, Australia (Fig. 4.1). It encompassed native and modified vegetation, and a network of roads consisting of a 12 km section of sealed road running through the centre of the area and gravel, dirt and 4WD minor roads and tracks. Areas to the west of the sealed road were dominated by coastal scrub/heath (*Leptospermum scoparium*, *Acacia longifolia*, *Melaleuca squarrosa* and *Leucopogon collinus*) and moorland (*Gymnoschoenus sphaerocephalus*). The east side of the sealed road consisted of a mosaic of forest (*Eucalyptus obliqua*, *Eucalyptus nitida*, *Melaleuca ericifolia* and *Leptospermum lanigerum*) and agricultural land with cattle grazing on pasture. The climate is temperate, with monthly mean temperatures ranging from 9.4-16.1°C, and mean annual rainfall of 1069mm (Australian Bureau of Meteorology 2016).

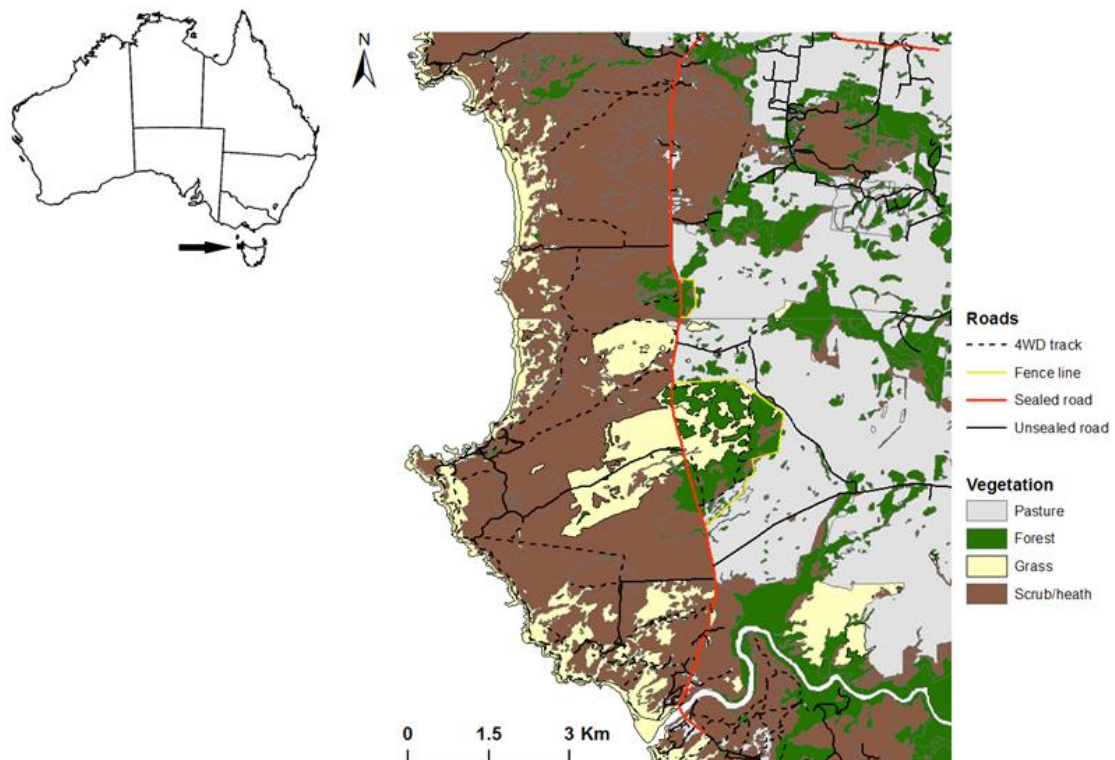


Fig 4.1. The study area in northwest Tasmania, Australia. Vegetation and road types are displayed.

4.3.2 GPS telemetry

Animals were trapped in PVC pipe traps (diameter 315mm × length 875mm) and fitted with GPS collars (Quantum 4000E, Telemetry Solutions Ltd, Concord, USA) from November 2012–February 2013 and October 2013–January 2014. These periods covered times when both species are in late lactation with young in dens and when they are weaned (devils early February; quolls December). Collars weighed 185g (devils) and 60g (quolls), less than 3% of body weight for each species. Collars were fastened with corrodible links which degrade over time and eventually allow the collar to fall off (Thalmann 2013). Collar schedules were set to collect simultaneous fixes of both species. Because devils are mainly active at night, GPS fixes for both species were acquired every 15min from 2030 to 0630 hours for approximately 8 weeks.

4.3.3 Habitat covariates

A vegetation and road map of the study site was created in ArcGIS 10.2 (ESRI, Redlands, California, USA) using the Tasmanian vegetation mapping spatial database TASVEG 3.0 (Department of Primary Industries 2013) and LIST Transport (Department of Primary Industries 2009) and verified through high resolution (1:2000) digital orthophotographs (Department of Primary Industries, Parks, Water and Environment, Tasmania, Australia).

We combined structurally similar vegetation communities into four categories and categorized roads and tracks according to structure and amount of traffic (Table 4.1). We created a 20m buffer either side of a road or track and categorised steps that fell within this buffer to be in the vicinity of and therefore potentially influenced by the road. Similarly, we created a 20m buffer either side of an interface between vegetation and pasture ('pasture/cover') and either side of wildlife-proof fences ('fence') to account for any influence of ecotones. We used steps 'outside' an ecotone or road type as a reference (Table 4.1), as we aimed to characterize changes in habitat selection or movement rate near these features to habitat selection/movement rate away from them.

Table 4.1. Description of the habitat covariates used in analyses of anthropogenic habitat use of Tasmanian devils and spotted-tailed quolls in Tasmania, Australia.

Covariates	Variable	Description
Vegetation type (Veg)	Pasture	Grass paddocks with cattle
	Forest	<i>Eucalyptus obliqua</i> , <i>E. nitida</i> , <i>Melaleuca ericifolia</i> and <i>M. squarrosa</i> swamp forest
	Scrub/heath	<i>Leptospermum lanigerum</i> , coastal heathland, <i>Acacia longifolia</i> and <i>M. squarrosa</i> scrub
Road type (Road)	Grass	Native grassland, buttongrass moorland and wetlands
	Outside	Steps away from a road
	Sealed	The main road that runs through the centre of the study site.
	Unsealed	Receives moderate amount of traffic
Ecotone type (Ecotone)	4WD	Receives limited or no traffic
	Outside	Steps away from an ecotone
	Pasture/cover	Interface between vegetation and pasture
	Fence	Wildlife-proof fences that were placed on ecotones between forest and pasture.

4.3.4 Habitat selection

We used step selection functions (SSF) (Fortin *et al.* 2005; Thurfjell *et al.* 2014) to examine habitat selection for devils and quolls. For each observed step, 15 random steps were generated from the empirical step length and turning angle distributions within each animal's 100% MKDE home range polygon to compare the habitat or feature selected by the animal to a range of 'available' habitats/features. These polygons did not include the ocean, so no random fixes were located at implausible locations.

Models were created using case-control logistic regression models in R version 3.1.3 (R Development Core Team 2015). The animal's selection is measured as an odds ratio representing the magnitude of change in the odds selection for each unit of the predictor variable. Devil and quoll individual ID was considered as a random effect in models, using the R library 'survival' (Therneau 2015). We included vegetation type, road type, ecotone type and distance to the nearest core area polygon edge (' D_{core} ') as parameters in the model selection analysis. The animal's selection of vegetation type in successive GPS fixes may be dependent on the last vegetation type it was in. Therefore, we fitted a binary 'carry-over' variable ('Veg same'), which described whether the vegetation type was equal to the previous fix. We tested for collinearity among explanatory variables using chi-squared tests. An information theoretic framework was used to rank competing models based on Akaike's information criterion corrected for small sample sizes (AICc) (Burnham and Anderson 2002); models within a $\Delta AICc$ of 2 were considered the most

plausible, with substantial empirical support. In addition, we used Akaike weights (ω_i) to gauge the relative importance of variables that influence habitat selection.

4.3.5 Effect of habitat on movement rate and turn angles

We constructed separate generalized linear mixed models (GLMMs) for each of the three habitat covariates described in Table 4.1 for devils and quolls. Movement between two successive locations within a trajectory was defined as a step and was computed in metres per minute. For all analyses, we log-transformed movement rate (m/min) to meet the assumptions of normality and fitted it as the response term. Long periods of rest (>6 hours without movement) were excluded from analysis. Devil and quoll individual ID was included as a random variable to account for repeated observations of the same individual. In the devil and quoll model containing ecotone type, we combined forest, grass and scrub/heath into a category called ‘cover’ to contrast movement in the vegetation side of an ecotone to movement in the pasture side of an ecotone. Vegetation type (‘cover’ or ‘pasture’), ecotone type and their interaction were included as fixed factors. The devil road type model included vegetation type, road type and their interaction as fixed factors. The quoll road type model only included road type, as there were not enough steps in some vegetation types near roads to include vegetation type in the model. Only steps that had both locations within an ecotone, road type or vegetation type were used in all models. Statistical analyses for movement rates were undertaken using the ‘nlme’ package (Pinheiro *et al.* 2015) in R version 3.1.3 (R Development Core Team 2015). Parameter estimates were averaged across the final model set and the relative importance of predictor variables was assessed by summing Akaike weights across all models in which the variable appeared (Burnham and Anderson 2002).

We examined the turning angle of steps within a vegetation type, road type and ecotone type using circular statistics (Batschelet 1981) using the ‘circular’ package (Agostinelli and Lund 2013) in R version 3.1.3 (R Core Team 2015). We also examined the turning angle of steps within the cover and pasture side of the pasture/cover ecotone. Turn angles were calculated as the clockwise angle relative to the movement trajectory. We computed the mean turning angle (μ), mean vector length (r) and standard error (s) for the distribution of turning angles. The mean vector (r) is a measure of directionality for circular data that ranges from 0 (angles are distributed randomly) to 1 (all angles are

identical). We tested for directionality of movement within each ecotone type, road type and vegetation type using Kuiper's test of uniformity (Batschelet 1981).

4.4 Results

4.4.1 Collared animals

We GPS-collared 7 devils and 4 quolls between November 2012 and February 2013, and 12 devils and 6 quolls between October 2013 and January 2014. One devil was collared in both years and data obtained in the second year were not included in analyses. A total of 24 649 GPS fixes were obtained 17 837 for devils and 6812 for quolls. The overall GPS success rate (i.e. the number of successful fixes by an individual GPS collar in proportion to the total number of programmed fixes) was $60 \pm 3\%$

4.4.2 Habitat Selection

The best model of habitat selection in devils included all covariates except for Veg same ($\omega_i = 73\%$). The second most parsimonious model was the full model ($\Delta AIC = 1.92$; $\omega_i = 27\%$). Model-averaged parameter estimates revealed that devils were slightly more likely to select forest and scrub/heath than pasture but this was not significant (Table 4.2). They were ten times more likely to be near a fence and almost 3 times more likely to be near a pasture/cover ecotone than outside an ecotone and showed a strong positive selection for all road types (Table 4.2). They were almost 9 times more likely to be near a sealed road, 6 times more likely to be near an unsealed road and 3 times more likely to be near a 4WD track than away from a road (Table 4.2). In addition, devils selected to be close to their core area (Table 4.2).

The most parsimonious model for habitat selection of quolls was the full model. The second best alternative model performed poorly in comparison with a ΔAIC of 14.48 for the model with all covariates except for Veg same. Quolls were slightly more likely to select forest and grass than pasture but this was not significant (Table 4.2). They were twice as likely to be near a fence and a pasture/cover ecotone than away from an ecotone (Table 4.2). Quolls exhibited positive selection for sealed and unsealed roads compared to

being away from roads (Table 4.2), and showed a strong selection to be near their core area (Table 4.2).

Table 4.2. Statistics of the top ranked model of Tasmanian devil (n=18) and spotted-tailed quoll (n=10) habitat selection in Tasmania, Australia.

Covariates	Tasmanian devils			Spotted-tailed quolls		
	Odds ratio	95% CI		Odds ratio	95% CI	
		Lower	Upper		Lower	Upper
Veg _{Forest}	1.21	0.92	1.59	1.16	0.53	2.54
Veg _{Grass}	0.84	0.65	1.09	1.53	0.68	3.44
Veg _{Scrub/heath}	1.12	0.87	1.43	0.89	0.40	1.95
Road _{Sealed}	8.51	7.10	10.17	1.60	1.14	2.23
Road _{4WD}	2.93	2.41	3.56	0.96	0.71	1.27
Road _{Unsealed}	6.22	4.80	8.04	2.18	1.29	3.65
Ecotone _{Fence}	10.06	7.92	12.69	1.92	0.99	3.69
Ecotone _{Pasture/cover}	2.64	2.21	3.13	1.84	1.07	3.12
Veg same _{Yes}	1.00	0.88	1.13	1.15	0.93	1.41
D_{core}	0.99	0.99	0.99	0.99	0.99	0.99

4.4.3 Effect of habitat on movement rate and turn angles

Devils and quolls moved more slowly in forest, grass and scrub/heath than in pasture (Fig 4.2 and Table 4.3).

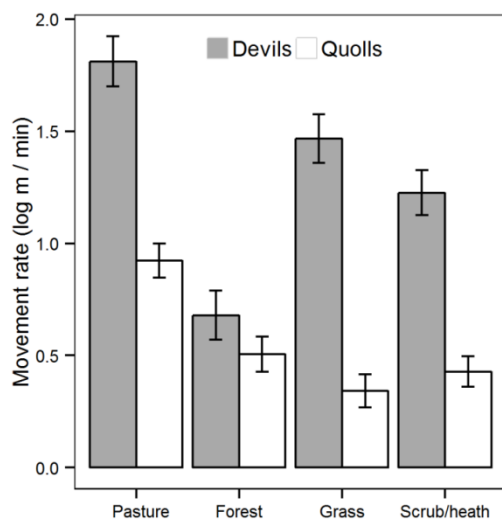


Fig 4.2. Mean (\pm standard error) movement rate for devils (n=18 devils, n=11487 steps) and quolls (n=10 quolls, n=5282 steps) in different types of vegetation.

Table 4.3. Model averaged results of GLMM analyses for movement rate (log m/min) in Tasmanian devils and spotted-tailed quolls in Tasmania, Australia. RI= relative importance of variables.

	Fixed effects	Devils		Quolls	
		Estimate \pm SE	RI	Estimate \pm SE	RI
Vegetation type	Intercept	1.811 \pm 0.111		0.922 \pm 0.075	
	Veg		1		1
	Forest	-1.132 \pm 0.071		-0.417 \pm 0.075	
	Scrub/heath	-0.585 \pm 0.061		-0.495 \pm 0.068	
	Grass	-0.344 \pm 0.072		-0.581 \pm 0.068	
Road type	Intercept	1.761 \pm 0.100		0.704 \pm 0.090	
	Road		1		1
	4WD	-2.876 \pm 0.467		-0.493 \pm 0.164	
	Sealed	-0.806 \pm 0.347		0.549 \pm 0.161	
	Unsealed	-0.607 \pm 0.234		-0.262 \pm 0.108	
	Veg		1		na
	Forest	-1.415 \pm 0.080			
	Scrub/heath	-1.196 \pm 0.069			
	Grass	-0.651 \pm 0.082			
	Road * Veg		1		na
	4WD*Forest	2.475 \pm 0.527			
	Sealed*Forest	1.318 \pm 0.387			
	Unsealed*Forest	2.715 \pm 0.911			
	4WD*Grass	3.225 \pm 0.524			
	Sealed*Grass	1.245 \pm 0.418			
	Unsealed*Grass	1.434 \pm 0.388			
	4WD*Scrub/heath	4.243 \pm 0.482			
	Sealed*Scrub/heath	1.185 \pm 0.365			
	Unsealed*Scrub/heath	3.176 \pm 0.275			
Ecotone type	Intercept	1.551 \pm 0.139		1.104 \pm 0.125	
	Ecotone		1		1
	Pasture/cover	-0.649 \pm 0.124		-1.209 \pm 0.171	
	Fence	0.011 \pm 0.114		0.269 \pm 0.610	
	Veg		0.27		1
	Cover	-0.008 \pm 0.069		-0.599 \pm 0.072	
	Ecotone * Veg		0		1
	Pasture/cover*cover			0.654 \pm 0.214	
	Fence*cover			-0.569 \pm 0.677	
	Random effect (ID)	Variance		Variance	
Vegetation type		0.41		0.17	
Road type		0.34		0.20	
Ecotone type		0.49		0.24	

The full model was the top model for movement rate for devils and quolls near roads (Table 4.3). Road type had a relative importance of 1 for both species. Vegetation type and the interaction term had a relative importance of 1 for devils (Table 4.3). Devils moved more quickly along all road types when the adjacent vegetation was forest, grass or scrub/heath compared to movement in these vegetation types away from roads (Fig 4.3a). When pasture was adjacent to any road or track, devils moved more slowly than when they were moving through pasture away from roads (Fig 4.3a). Quolls moved slower when they were near 4WD tracks and unsealed roads but faster near the sealed road compared to movement away from roads (Fig 4.3b).

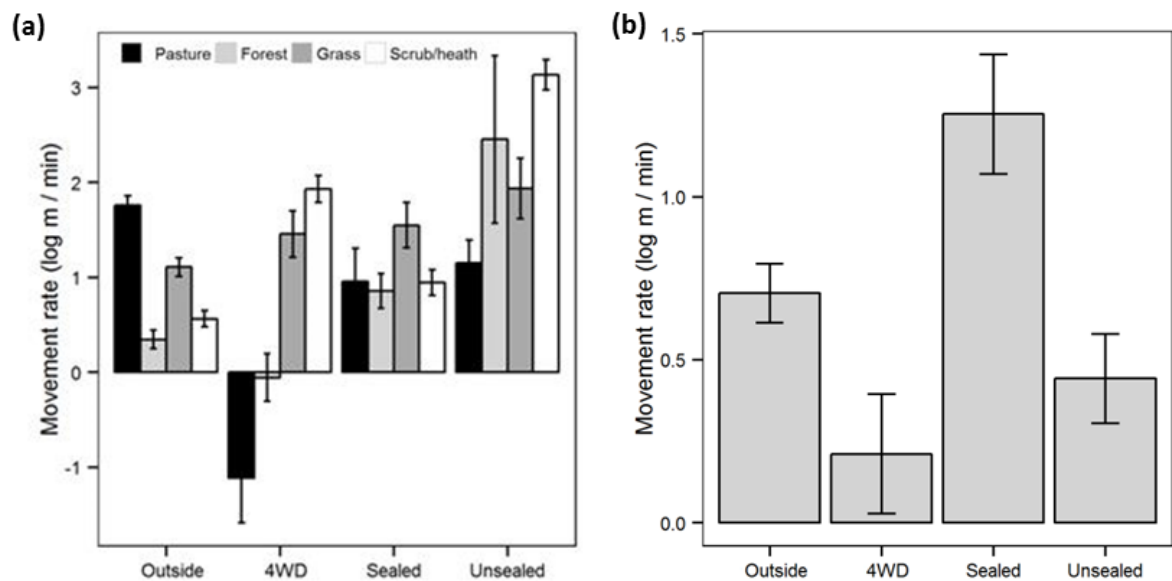


Fig 4.3. Mean (\pm standard error) movement rate for (a) devils (n=18 devils, n=9095 steps) and (b) quolls (n=10 quolls, n=5547 steps) near roads compared to movement outside them.

The final model set for movement rate in an ecotone included two models for devils and the full model for quolls. Ecotone type had a relative importance of 1 for both species, whereas vegetation type had a relative importance of 0.27 for devils and 1 for quolls (Table 4.3). The interaction between ecotone and vegetation had a relative importance of 1 for quolls (Table 4.3). Both species moved slower near a pasture/cover ecotone compared to when they were moving in the landscape away from ecotones (Fig 4.4). There was no difference in movement rate of devils and quolls near fences compared to movement away from any ecotone (Fig 4.4). Devils moved slightly slower along the cover side than the pasture side of ecotones (Table 4.3). Quolls moved slower in cover compared to pasture when moving away from any ecotone and slower along the cover side of a fence (Fig 4.4b and Table 4.3).

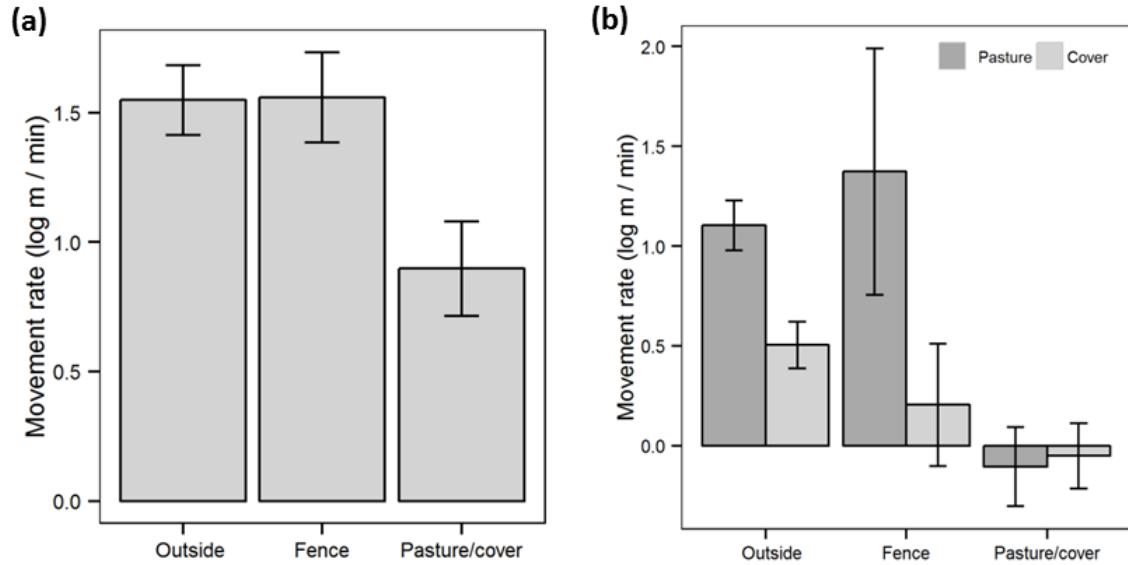


Fig 4.4. Mean (\pm standard error) movement rate for (a) devils (n=14 devils, n=10501 steps) and (b) quolls (n=5 quolls, n=3300 steps) near ecotones compared to movement outside them.

There was a wide distribution of turning angles for both species as demonstrated in the mean vector length (r) that ranged from 0.02–0.47 and the standard error of mean(s) that ranged from 1.82–141.95° (Table 4.4). Devils exhibited significant directional movement near all road and ecotone types and away from these features (Table 4.4). They exhibited tortuous movement when they were moving in the cover side of an ecotone (Table 4.4). In contrast, quolls exhibited directional movement only near sealed roads and when they were moving outside of an ecotone and road (Table 4.4). Their movement was tortuous along fences, and in a pasture/cover ecotone, regardless of whether they were moving in the cover or pasture side (Table 4.4). They also exhibited tortuous movement along unsealed and 4WD tracks (Table 4.4). Both species exhibited directional movement in pasture (Table 4.4). Devils exhibited directional movement in grass and scrub/heath, quolls in grass (Table 4.4). Devil movement was tortuous in forest, quolls in forest and scrub/heath (Table 4.4).

Table 4.4. Summary statistics of Kuiper’s test for turn angle distribution near each vegetation, road and ecotone type for Tasmanian devils and spotted-tailed quolls. Bold numbers indicates significant results ($p < 0.05$).

		n	Mean turn angle (μ)	Mean vector length (r)	Standard error (s)	k	P
Devils	Vegetation						
	Pasture	1539	13.27°	0.57	3.77°	7.97	<0.05
	Forest	1909	251.77°	0.04	21.87°	2.85	>0.15
	Grass	2003	0.01°	0.22	3.96°	7.54	<0.05
	Scrub/heath	6036	356.68°	0.20	2.60°	13.22	<0.05
	Road						
	Outside	7731	355.19°	0.09	4.88°	12.45	<0.05
	Sealed	586	355.65°	0.23	7.05°	10.14	<0.05
	Unsealed	322	0.95°	0.47	4.53°	7.57	<0.05
	4WD	456	356.89°	0.30	6.09°	7.74	<0.05
	Ecotone						
	Outside	9904	1.18°	0.22	1.82°	17.38	<0.05
	Fence	325	5.84°	0.20	11.22°	3.26	<0.05
	Pasture/cover	272	352.35°	0.12	20.77°	2.03	<0.05
	Cover	127	354.34°	0.08	46.06°	1.40	>0.15
	Pasture	144	351.46°	0.15	21.86°	2.03	<0.05
Quolls	Vegetation						
	Pasture	1440	1.79°	0.35	4.16°	6.94	<0.05
	Forest	949	147.94°	0.03	48.30°	2.02	>0.15
	Grass	1085	191.80°	0.47	17.17°	3.48	<0.05
	Scrub/heath	1808	186.44°	0.03	29.16°	3.54	>0.15
	Road						
	Outside	5122	354.69°	0.04	13.08°	5.38	<0.05
	Sealed	97	1.12°	0.34	11.64°	2.75	<0.05
	Unsealed	232	352.35°	0.10	25.73°	2.37	>0.15
	4WD	96	112.13°	0.10	41.13°	1.32	>0.15
	Ecotone						
	Outside	3035	354.51°	0.05	15.93°	3.82	<0.05
	Fence	33	347.49°	0.03	2.8°	0.66	>0.15
	Pasture/cover	232	5.60°	0.02	141.95°	1.24	>0.15
	Cover	145	24.01°	0.07	50.24°	1.36	>0.15
	Pasture	86	217.80°	0.07	65.28°	0.99	>0.15

4.5 Discussion

Our results provide a clear example of medium-sized carnivores favouring landscape features created by humans. Devils and quolls can be regarded as generalist carnivores exhibiting habitat plasticity and the ability to use edge habitats, traits that facilitate adaptation to fragmented landscapes (McKinney 2002; Cervinka *et al.* 2011). Despite differing ecomorphological specialisations, we demonstrate that both a pounce-pursuit predator that is a specialised scavenger (the devil) and an arboreal ambush predator (spotted-tailed quoll) can respond to anthropogenic modification of intact landscapes in ways that enhance movement and hunting opportunities. They evidently used the

pasture/cover interface for foraging, and roads and fence lines (devils only) for movement and foraging.

The creation of additional linear features in landscapes may enhance what are already natural behaviours. Natural linear features occur in the form of animal trails, creek lines, and edges between closed and open vegetation types. Carnivores, including devils and quolls, use these to hunt, to move through vegetation (for example, following trails created by wombats (*Vombatus ursinus*) and macropods, M Jones, *pers. obs.*), and to position latrines in areas of high animal traffic (Ruibal *et al.* 2010). Human-altered landscapes and the linear features they contain are likely to benefit many species of medium-sized carnivores, including devils and quolls, by improving prey acquisition, either by enhancing opportunities for hunting or for travel to hunting areas (Hebblewhite and Merrill 2008; Martin *et al.* 2010; Knopff *et al.* 2014a).

The capacity of carnivores to respond positively to fragmentation is influenced not only by landscape structure but indirectly by the responses of prey species to fragmentation and the increased length of edges or ecotones between native vegetation and pasture (Mortelliti and Boitani 2008). On several continents, including Australia, vertebrate prey reach high population densities in fragmented landscapes with a diversity of habitat types (Austen *et al.* 2001; Michel *et al.* 2006; Salek *et al.* 2010; Cervinka *et al.* 2011; Cervinka *et al.* 2013). Many species, particularly medium-sized herbivores that are often the major prey for medium-sized carnivores, favour edges where they can take refuge in intact native vegetation during the day and emerging through the cover-pasture ecotone to forage on pasture at night (Le Mar and McArthur 2005). Edges thus provide carnivores with a rich prey source (Austen *et al.* 2001; Michel *et al.* 2006; Salek *et al.* 2010) and prey individuals are especially vulnerable to predation as they cross the ecotone twice daily (Nielsen 2009). This high abundance and concentration of prey could support higher densities of medium-sized carnivores in fragmented agricultural landscapes. This is clearly the case in our study system, where Tasmanian pademelons (*Thylogale billardierii*), which are major prey species of devils and quolls (G Andersen, unpublished data), emerge from the forest edge at night to feed on pasture (Le Mar and McArthur 2005). While devils and quolls use both native and anthropogenic vegetation types at night when foraging, slow and tortuous movements in native forest vegetation, especially near edges, indicate foraging; faster, straight movements across pasture suggest direct travel.

Roads are highly attractive to carnivores (May and Norton 1996; Barrientos and Bolonio 2009; Beatty *et al.* 2014) because they offer food, faster travel and sites for olfactory communication, even though vehicle-strike causes significant mortality. Roads provide carcasses of animals killed by vehicles, as well as concentrations of herbivores attracted to roadside verges. The linear path and edges between the road and the surrounding vegetation creates possibilities for ambushing prey. Reflecting their specialist scavenger niche, devils show stronger preference than quolls for sealed roads, on which there is significant road mortality of prey species (Hobday and Minstrell 2008). In contrast, quolls, which are ambush predators, show strong selection for unsealed roads, and their slow and tortuous movement patterns on unsealed roads and 4WD tracks indicate hunting. Unsealed roads, including 4WD tracks, create a linear open space which acts as a barrier to the movement of small mammals (Rico *et al.* 2007; Ford and Fahrig 2008; McGregor *et al.* 2008) which may be vulnerable to predators if they linger in the adjacent vegetation.

Roads provide a linear corridor that could increase the distance travelled and extent of foraging by predators in a night. Commuting along roads to foraging areas is documented in other medium-sized carnivores, such as red foxes, raccoons and striped skunks (*Mephitis mephitis*) (Frey and Conover 2006) and may explain road use by devils and quolls. Roads also offer prominent open locations for chemical communication and many carnivores, including wolves (*Canis lupus*) (Barja *et al.* 2004), coyotes (*Canis latrans*) (Barja and List 2014) and black-backed jackals (*Canis mesomelas*) (Hayward and Hayward 2010), as well devils and quolls, deposit faeces and scent mark with para-anal or para-cloacal gland secretions on roads. Devils deposit faeces on all road types at the study site, and quolls deposit faeces more frequently on maintained roads than on overgrown logging tracks or within the adjacent forest (Burnett 2001).

Fences constitute a physical barrier which carnivores can exploit to trap prey, a strategy used, for example, by African wild dogs (*Lycaon pictus*) (Davies-Mostert *et al.* 2013). Again, the differences in ecomorphology and hunting mode between devils and quolls are reflected in their use of fence lines. The ambush predator, the quoll, did not use fence lines. Devils, however, travelled extensively along fence lines and their low turning angles indicate directional travel. They may be using the same hunting strategy as African wild dogs, running along fences to flush macropods towards the fence line, where they can more easily be captured. As the fences at our study site are designed to prevent macropods from moving onto pasture to graze at night, they are built around patches of forest in which

macropods rest and devils den. Constructed of 150 mm x 80 mm wire mesh with an electric wire at ground level, they are impenetrable to macropods and devils alike, unless breached by animals such as wombats digging under the fence. It is, therefore, plausible that devils are traveling along fence lines looking for a way through.

While we have demonstrated the positive response of devils and quolls to landscape fragmentation, both fences and roads also have negative effects on carnivores and other wildlife. Fences block movement of wildlife and contribute to habitat fragmentation (Newmark 2008; Gates *et al.* 2012; Cozzi *et al.* 2013). Understanding how fences affect movements of carnivores and other wildlife, and working with landowners to develop structures to facilitate movement of key species through fences, is important to ensure connectivity among populations. The impact of roads on wildlife is of global concern (Laurance *et al.* 2015) and many carnivores are highly susceptible to mortality from vehicles (Cervinka *et al.* 2015). Devils and quolls are both on the IUCN Red List, devils as Endangered (Hawkins *et al.* 2008) and spotted-tailed quolls Near Threatened (Burnett and Dickman 2008). Road mortality is a demonstrated cause of local population decline (Jones 2000). Potential measures to reduce road death include wildlife crossing structures (Grilo *et al.* 2015), and virtual fences, consisting of flashing and sound alarm units at 100m intervals, triggered by the headlights of approaching vehicles, show promise in reducing road mortality of wildlife (Potts 2015).

Medium-sized carnivores, more than large carnivores, are thought to be better able to adapt to anthropogenic landscape alteration and fragmentation, probably because of their smaller size and area requirements and generalist ecologies. Our study demonstrates that two species of marsupial medium-sized carnivores with contrasting ecomorphological specialisations and hunting modes can adapt to moderate landscape modification in their native range in Tasmania, Australia. Such adaptability is well known in successful invaders such as red foxes. Our results confirm that such adaptability is taxonomically and geographically widespread. However, agents of mortality for carnivores abound in anthropogenic landscapes, from collisions with vehicles to persecution by humans and attacks by dogs (Dobrovolski *et al.* 2013) and restrictions on movement from fences (Gates *et al.* 2012). Carnivores also need species-specific minimum areas of structurally complex vegetation for den sites and for refuge. Retaining linear remnants and small patches of native vegetation in agricultural landscapes is important to facilitate animal movement through the matrix (Taylor *et al.* 1993). Identifying thresholds in the degree of

anthropogenic landscape modification that carnivore species can benefit from and persist within, with respect to denning and foraging habitat, and ensuring that these are not exceeded, will aid the ongoing conservation of carnivores in these habitats.

Chapter 5 Sympatric predator odour reveals a competitive relationship in size-structured mammalian carnivores



This chapter is published in *Behavioral Ecology and Sociobiology*, 70(11), 1831-1841.

Andersen, G. E., Johnson, C. N., Jones, M. E., 2016, Sympatric predator odour reveals a competitive relationship in size-structured mammalian carnivores.

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Appendix 5.1. Top ranking models with $\Delta AICc < 2$ for Tasmanian devil behavioural variables are presented. $\Delta AICc$ is the difference in AICc values between each model and the lowest ranking model and ω_i is AIC weight.

	Model rank	Lure age	Scat age	Basal	Site	Treatment	Vis25	AICc	$\Delta AICc$	ω_i
Scent marking	1		✓	✓	✓	✓	✓	334.5	0.00	1
Investigation	1	✓		✓	✓	✓		383.6	0.00	0.684
	2			✓	✓	✓		385.1	1.54	0.316
Vigilance	1	✓		✓	✓	✓	✓	1245.3	0.00	0.308
	2	✓		✓		✓	✓	1246.1	0.85	0.202
	3	✓		✓	✓	✓		1246.2	0.87	0.199
	4	✓				✓	✓	1246.5	1.17	0.172
	5	✓	✓	✓	✓	✓	✓	1247.2	1.90	0.119
Time spent at camera traps	1	✓	✓	✓	✓	✓		1596.6	0.00	0.572
	2	✓	✓	✓	✓	✓	✓	1598.5	1.94	0.216
	3	✓	✓		✓	✓		1598.6	1.99	0.212
Maintenance	1							208.2	0.00	0.187
	2				✓			209.0	0.77	0.127
	3						✓	209.1	0.88	0.120
	4		✓					209.1	0.93	0.117
	5		✓				✓	209.5	1.28	0.099
	6		✓		✓			209.5	1.29	0.098
	7			✓				209.5	1.29	0.098
	8	✓						209.9	1.75	0.078
	9		✓	✓				210.0	1.80	0.076

Appendix 5.2. Top ranking models with $\Delta AICc < 2$ for spotted-tailed quoll behavioural variables are presented. $\Delta AICc$ is the difference in AICc values between each model and the lowest ranking model and ω_i is AIC weight.

	Model rank	Lure age	Scat age	Basal	Site	Treatment	Vis25	AICc	$\Delta AICc$	ω_i
Scent marking	1	✓						122.5	0.00	0.260
	2							123.3	0.76	1.178
	3	✓			✓			123.8	1.30	0.136
	4	✓	✓					124.0	1.53	0.121
	5	✓		✓				124.3	1.78	0.107
	6			✓				124.4	1.89	0.101
	7	✓					✓	124.5	1.96	0.098
Investigation	1							132.2	0.00	0.420
	2	✓						133.7	1.39	0.209
	3				✓			133.8	1.51	0.197
	4		✓					134.1	1.77	0.173
Vigilance	1					✓	✓	277.7	0.00	0.464
	2			✓		✓	✓	279.5	1.82	0.186
	3				✓	✓	✓	279.6	1.95	0.175
	4	✓				✓	✓	279.6	1.95	0.175
Time spent at camera traps	1	✓		✓		✓		399.3	0.00	0.367
	2	✓		✓		✓	✓	400.0	0.71	0.257
	3	✓				✓		400.1	0.84	0.241
	4	✓			✓	✓		401.3	2.00	0.135

Chapter 6 General discussion

This thesis assessed the feeding ecology, movement behaviour, habitat utilisation and interactions of two sympatric marsupial carnivores, the Tasmanian devil and the spotted-tailed quoll, with the broad goal of investigating the ecological relationship of these two species and providing a stronger scientific foundation for the management and conservation of both species in the wild. In this final Chapter, I first provide a brief overview of my main findings. Then, I discuss the potential for competition between devils and quolls based on previous knowledge and knowledge I gained through this thesis. I also discuss the mechanisms which could facilitate coexistence. Finally, I emphasize that there are still many gaps in our knowledge and that more research is needed to better understand coexistence between devils and quolls.

6.1 Summary of main findings

First, I determined diet composition and overlap across the geographic range of devils and quolls in Tasmania to examine the potential for competition (Chapter 2). Both species prey predominately on Tasmanian pademelon, Bennett's wallaby and birds but also consume a wide range of prey species at lower frequencies, suggesting that they are both opportunistic and flexible foragers. I found a high dietary overlap between devils and quolls, which suggests the potential for competition and aggressive interference, if resources are scarce. Devils consume more large mammals (e.g. wombats) and medium- sized mammals (e.g. pademelons), whereas quolls consume more small mammals, reptiles and invertebrates suggesting that partitioning of resources based on prey size occurs.

Second, I investigated whether there was temporal separation or spatial separation at the home-range level between devils and quolls (Chapter 3). I found little spatial segregation of home-range and core-area placement. Mean home-range size of devils was larger than for quolls. Male home-ranges were larger than females' in devils but not in quolls. Devils and quolls exhibited different activity patterns during the night. Devils were active from dusk until 4am while quolls were most active in the early and latter parts of the

night. This pattern of activity could allow quolls to avoid agonistic encounters with devils, but could also reflect the different hunting modes of the two species.

Third, I investigated the selection of habitat types and environmental features by both devils and quolls in the same landscape (Chapter 4). I examined habitat use in a conservation area, which consisted of native vegetation, both forest and low heathland/grassland/moorland and a network of unsealed roads and 4WD tracks and in an agricultural landscape, which consisted of a mosaic of forest and pasture. I found that both species responded positively to this moderate degree of anthropogenic modification of intact habitats which enhanced their natural movement and facilitated prey acquisition. Devils and quolls can be regarded as generalist mesocarnivores exhibiting habitat plasticity and ability to use edge habitats. They used the pasture/cover interface for foraging and roads for movement and foraging. Devils utilised fence lines, while quolls showed little preference for them. Macropods are the preferred prey species of devils and quolls (Chapter 2) and reach higher densities in fragmented areas, using forest cover for daytime refuge and grassland/pasture for foraging at night. Roads and edges facilitate hunting by devils and quolls by providing a focus where they can intercept prey. Higher densities of prey and habitat structure which facilitates hunting presumably enable devils and quolls to survive in healthy numbers in these mosaics of intact and modified habitats. However, living in these landscapes makes them susceptible to human persecution and collision with vehicles. Human tolerance and mitigation measures to reduce the effect of road kill combined with maintaining connectivity in the agricultural matrix should be the focus of management strategies in these habitats. In addition, there is likely to be a threshold of fragmentation beyond which devils and quolls may not be able to exist.

Fourth, I used behavioural responses of the two sympatric carnivores to one other's odour to help understand their behavioural interactions and test mechanisms of competitive interaction (Chapter 5). The larger predator, the devil, was as vigilant at quoll odour as at control camera traps and did not avoid quoll odours. This suggests that devils don't fear encountering quolls. We would expect devils to be dominant during interspecific encounters and not engage in costly fear-induced behaviours. The smaller predator, the quoll, increased its vigilance near devil odour compared to control camera traps but did not avoid it. Quolls could be eavesdropping on signals in the devil odour to acquire information on resources or to evaluate risk, while the heightened vigilance could ensure a quick response should a threat materialise. Behavioural responses exhibited by devils and

quolls are indicative of a dominant predator-mesopredator relationship and suggest the potential for interspecific competition. However, the ability of devils to function as a top predator and suppress quoll populations remains unknown.

6.2 The potential for competition and mechanisms for coexistence

6.2.1 The ghost of competition past

In many systems worldwide, sympatric carnivore species have coexisted for sufficiently long periods that they have evolved divergent ecomorphologies that reduce intraguild competition and predation. As a result, current competition can be difficult to observe as niche partitioning may have resulted from past competitive interactions, an effect described by Connell (1980) as “the ghost of competition past”. Tasmanian devils and spotted-tailed quolls have coevolved as part of a marsupial guild of predators and in isolation from placental analogues. This coevolution has presumably resulted in ecomorphological adaptation for the two taxa that reduces but does not eliminate niche overlap and resource exploitation.

Character divergence in body size and/or dental morphology can arise to mediate competitive interactions among sympatric carnivores (Davies *et al.* 2007). Body size is an important predictor of competitive ability among carnivore species (Donadio and Buskirk 2006). Devils are larger than quolls and competitively dominant at carcasses (Jones and Barmuta 1998). Dental morphology is indicative of diet and the trophic structures proximal to prey killing, such as canine tooth size, scale with prey size (Dayan *et al.* 1989). Divergence in dentition and competitive character displacement in canine size has been documented within guilds of canids (Dayan *et al.* 1992; Van Valkenburgh and Wayne 1994), mustelids (Dayan *et al.* 1989; Dayan and Simberloff 1994) and felids (Dayan *et al.* 1990). Character displacement in the strength of the canine teeth and size of the temporalis muscle that determines jaw closing strength, both related to prey size, has occurred in the Tasmanian carnivore guild (Jones 1997). Devils have evolved jaw musculature and robust teeth associated with bone crushing (Jones 2003; Attard *et al.* 2011) and exploit the facultative scavenger niche. Spotted-tailed quolls lack specialisations for consuming the hard parts of carcasses. Quolls have specialised adaptations for arboreal use of habitat such as a clawless hallux on the pes and ridges on the foot pads, which are lacking in devils that

are far less adept at climbing trees (Jones 2003). This may facilitate the coexistence of quolls with other carnivores, such as devils but also including feral cats. A review on intraguild interactions in American carnivores found that members of the Mustelidae family may reduce competition by being arboreal (Hunter and Caro 2008). Therefore, competition between devils and quolls has already been minimised through character displacement and ecomorphological adaptation to different niches.

6.2.2 Dietary breadth and overlap

Devils and quolls had a very high diet overlap (Pianka index: 0.92), which suggests the potential for competition and aggressive interference over food resources. Previous studies that used Pianka's index to estimate diet overlap within carnivore guilds found that species with the highest diet overlap showed temporal or spatial separation (Ray and Sunquist 2001; Vieira and Port 2007; Lovari *et al.* 2015). However, high dietary overlap may result in competition only when resources are scarce (Schoener 1983).

Even if resources are limited, there are ways quolls may facilitate their coexistence with devils. First, while devils and quolls both preferred large and medium-sized mammals, quolls consumed more small mammals, reptiles and invertebrates than devils. Therefore, it is plausible that despite a similar diet, quolls could reduce their niche overlap with devils by preying on smaller prey. Second, vertical partitioning of prey species may also facilitate coexistence in this species that spends 25-50% of its movement distance above the ground on logs and in trees (Jones and Barmuta 2000; Burnett 2001). While my diet study found that quolls consumed marginally more arboreal prey species than devils, studies on the Australian mainland quoll show that they regularly incorporate arboreal prey into their diet (Glen and Dickman 2006a; Jarman *et al.* 2007). This suggests that increasing their consumption of arboreal prey is a niche quolls could exploit to give them a competitive advantage over devils when resources are scarce.

6.2.3 Spatial and temporal partitioning

The potential for competition and risk of intraguild predation, between sympatric carnivores using similar resources, is largely determined by the extent of spatial overlap (Kitchen *et al.* 1999; Palomares and Caro 1999). To minimize competition and aggressive

encounters, the subordinate species can avoid establishing its home-range within a dominant competitor's (Case and Gilpin 1974; Atwood and Gese 2010). For example, bobcats (*Lynx rufus*) had a high home-range overlap with coyotes (*Canis latrans*), but their core-areas did not overlap (Thornton *et al.* 2004). However, I found little spatial segregation between devils and quolls at the home-range and core-area level (Chapter 3). Both devils and quolls used similar habitat types and features (Chapter 4). The overlap in home-range and habitat use is likely driven by the distribution and acquisition of similar resources such as prey. Macropods reach high abundance in fragmented landscapes, which in turn could facilitate higher densities of carnivores. If a subordinate species was to completely avoid a larger more dominant species, it could result in a costly loss of feeding opportunities. A high spatial overlap does not preclude the possibility that animals avoid direct encounters. Quolls may instead assess the level of risk when in the vicinity of a devil and adjust their behaviour accordingly. The heightened vigilance quolls exhibited when near a devil odour (Chapter 5), provides support for this. Utilising the arboreal niche would allow a quoll to escape a devil and this has been observed in the wild (Menna Jones, pers.comm.). Unfortunately, GPS collars do not allow us to determine whether the animal is on or above the ground.

If sympatric carnivores have a high spatial overlap, they may also reduce the probability of aggressive encounter by being active at different times of the day. Temporal partitioning has been found in other sympatric carnivores (Di Bitetti *et al.* 2009; Harrington *et al.* 2009; Hayward and Slotow 2009; Lucherini *et al.* 2009). Devils and quolls exhibited different activity patterns during the night (Chapter 3). Devils were predominately nocturnal and decreased their activity after 4am (Chapter 3). Quolls were also active throughout the night but activity peaked around dawn and dusk (Chapter 3). Reasons for the difference in activity times are discussed in Chapter 3, but could relate to an attempt to minimise competition by being active when devils aren't or to a difference in hunting modes and the availability of prey under each mode (e.g. the timing of prey activity and availability in arboreal habitats and on ecotones). As I was not able to conclusively relate the different activity times to avoidance behaviours, future studies should investigate this, at different sites across Tasmanian and with different densities of devils and quolls. Collars fitted with motion sensors to record activity data would help determine at which time of the day and in which habitats each species hunts, moves and/or rests in.

6.2.4 Intraguild predation

The outcome of direct encounters between devils and quolls has not been formally documented (but see Jones (1995)), but it probably overall involves a greater risk of injury for the smaller quoll than for the devil. In Chapter 2, I found that four devil scats, at Cradle Mountain, contained spotted-tailed quoll fur but I am not able to determine whether this reflects intraguild predation or scavenging by devils. None of the quoll scats contained devil fur, which suggests that intraguild predation or scavenging is asymmetrical. However, this could also be the result of a low sample size for quolls. There are anecdotal records of devils killing quolls, as well as a quoll wounding a devil in a conflict over food at Cradle Mountain (Jones 1995). The ability of quolls to climb trees might alleviate the severity of direct aggressive encounters and spotted-tailed quolls have been observed sitting on tree branches above a carcass where devils are feeding (Menna Jones, pers. comm.). *Antechinus agilis* climbs to avoid direct encounters with the dominant *A. swainsonii* (Dickman 1991) and American mustelids may utilise the arboreal niche to avoid competition (Hunter and Caro 2008).

Understanding the extent and dynamics of intraguild predation between devils and quolls would help understand the potential for competition and what effect it could have on each species. As both devils and quolls scavenge dietary studies are not useful for determining intraguild predation. Instead, direct observations of aggressive encounters or dead quolls with clear evidence of having been killed by devils are needed.

6.2.5 Scavenging opportunities

Interspecific interactions are not always negative and can benefit either one or both species. A facultative scavenger or opportunistic predator may benefit from being sympatric with an efficient hunter, despite the risk of interference competition (Creel *et al.* 2001). Coyotes (*Canis latrans*) follow wolves (*Canis lupus*) and scavenge at their kills, which suggests that the increased foraging opportunity outweighs the risk of intraguild predation (Paquet 1992). Wolverines (*Gulo gulo*), a facultative scavenger, may benefit from scavenging on reindeer that have been killed by Eurasian lynx (*Lynx lynx*) (Mattisson *et al.* 2010).

Many interactions between carnivores occur around carcasses, which can be an important resource in addition to live prey. Carcasses are potential foci for intense contest

competition between devils and quolls with devils more dominant and readily displacing quolls from a carcass, although an adult quoll (even a smaller female) can displace a subadult devil (Jones 1995; Jones and Barmuta 1998). Both devils and quolls hunt, kill and scavenge and could benefit from each other's leftovers. If quolls kill prey too large to consume quickly they risk kleptoparasitism from devils. In other systems, dominant competitors kill or steal prey from subordinate ones, but the subordinate predator may also benefit by scavenging carcasses killed by the dominant predator. Spotted-hyenas (*Crocuta crocuta*) can scavenge from lions (*Panthera leo*) but also lose food to lions (Watts and Holekamp 2008).

6.2.6 Bottom-up process

Ecosystems can be strongly influenced by bottom-up process (e.g. prey availability and abundance and rainfall, which may reduce the influence of top-down forces (Oksanen and Oksanen 2000). Carnivore densities generally reflect the abundance of prey (Fuller and Sievert 2001); a relationship which has been found in leopards (*Panthera pardus*) (Stander *et al.* 1997), tigers (*Panthera tigris*) (Karanth *et al.* 2004) and gray wolves (*Canis lupus*) (Fuller and Sievert 2001). Prey availability and abundance are likely to influence the strength of interspecific competition and dietary overlap among sympatric predators (Holt and Polis 1997; Elmhagen and Rushton 2007). Devils and quolls fed predominately on Tasmanian pademelon and Bennett's wallaby (Chapter 2), which are both widespread and abundant in Tasmania. Therefore, it is plausible that the high abundance of prey in productive environments, such as the mesic, warmer northwest corner of Tasmania and in native vegetation – agricultural mosaic landscapes, facilitates co-existence between devils and quolls and minimizes competition in non-extreme environmental (climatic) conditions when bottom-up influences are strong relative to top-down forces. In these conditions, exploitation competition may not occur. I did not take the availability and distribution of prey into account when assessing dietary overlap and habitat use. Future studies would benefit from incorporating prey availability and distribution.

6.2.7 Conclusions

Currently, interspecific competition is not the main factor driving devil and quoll populations at my study site. There are two plausible explanations for this: First, prior ecomorphological divergence and character displacement could have caused sufficient divergence of traits to remove much of the potential for competition. Second, resource abundance was not a limiting factor at my study site during the years of my study and therefore did not induce competitive behaviour. A study by Jones and Barmuta (2000) found that at the time of the year when dietary overlap was greatest between devils and quolls, habitats were partitioned to reduce competition. Quolls were more arboreal and the diet of adult male quolls contained a much higher proportion of arboreal prey than that of adult devils (Jones and Barmuta 2000). This supports the second scenario, and in times of resource shortage competition is likely to occur between devils and quolls.

Competition for food, both exploitative (diet overlap) and interference (dominance at carcasses), from devils has been thought to contribute to low spotted-tailed quoll population densities (Jones 1995; Jones and Barmuta 1998), in addition to female territoriality in spotted-tailed quolls which naturally limits density. At my study site, but also at all sites surveyed across Tasmania, regardless of whether the devil population was affected by DFTD, quolls were not as abundant as devils (G. Andersen, unpublished data; M. Jones, unpublished data; Jones and Barmuta 1998). Due to the potential for interspecific competition and the observed difference in abundance, it has been hypothesized that the population decline of the devil will result in a mesopredator release of quolls (Jones *et al.* 2007). However, in fragmented areas such as my study site, Tasmanian pademelons and Bennett's wallabies, which are the preferred prey species of devils and quolls, both reach high population densities. A high abundance of prey may have lowered the necessity for competition driven changes in behaviours. When resources are abundant, losing devils from an ecosystem may not result in a mesopredator release of quolls. The extensive resource overlap, however, suggests that competition could occur if resources become scarce. In this case, losing devils from a system might result in a mesopredator release of quolls.

The effects of one predator are unlikely to operate in isolation and will usually influence or be influenced by sympatric predators. Loss of a dominant predator from the system may directly or indirectly lead to an increased abundance of another and the effects upon prey species may be ultimately negative (Ritchie and Johnson 2009). As the devil

population is declining due to a fatal transmissible cancer, it is important to understand the impacts this could have on not only quoll populations but on feral cats as well and the mechanisms by which these impacts occur. Future research should continue to focus on understanding interactions between Tasmania's carnivores with varying degrees of fragmentation, prey abundance and carnivore densities. In particular, there is a need to examine the spatio-temporal relationships among devils, quolls and cats at different sites and habitats across Tasmania.

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