The Web of Death: Scavenger Communities and Interactions on Carrion in Australian Landscapes

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Dedicated to Joan Evelyn Spencer

(12 December 1928 – 11 January 2022)

"Nothing is lost, nothing is wasted, nothing really dies"

—Densey Clyne, Australian naturalist (1989)

DECLARATION

I hereby declare that this submission is my own work and that, to the best of my knowledge and belief, it contains no material previously published or written by another person nor material which to a substantial extent has been accepted for the award of any other degree or diploma of the University or other institute of higher learning, except where due acknowledgement has been made in the text.

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Published papers included in this thesis:

Spencer, E. E., and T. M. Newsome. 2021. Dingoes dining with death. Australian Zoologist 41: 433–51.

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E. Rhodes Jr, A. Ordiz, C. Wikenros, B. Zimmermann, P. Wabakken, C. C. Wilmers, J. A. Smith, C. J. Kendall, D. Ogada, E. Frehner, M. L. Allen, H. U. Wittmer, J. R. A. Butler, J. T. du Toit, A. Margalida, P. Oliva-Vidal, D. Wilson, K. Jerina, M. Krofel, R. Kostecke, R. Inger, E. Per, Y. Ayhan, H. Ulusoy, D. Vural, A. Inagaki, S. Koike, A. Samson, P. L. Perrig, E. Spencer, T. M. Newsome, M. Heurich, J. D. Anadón, E. R. Buechley, and J. A. Sánchez-Zapata. 2020. Network structure of vertebrate scavenger assemblages at the global scale: drivers and ecosystem functioning implications. Ecography 43:1143–1155.

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ABSTRACT

Carrion is a nutrient-rich resource that attracts a diverse community of organisms, from insects and vertebrates to microbes. These organisms engage in a series of complex interactions, as they compete for a shared resource that is generally ephemeral and patchy in distribution. Carrion consumers may also interact with surrounding ecosystems, as they contribute to nutrient cycling and dispersal, and to carrion removal, which can limit potential disease spread. Further, as most animals that interact with carrion also take on predatory roles, carrion may impact local environments by enhancing or redirecting predation or fear effects. These interactions are largely shaped by the ecosystem context in which the carcass is situated. Yet there remains a paucity of data on the different environmental drivers affecting carrion ecology generally, especially in Australian environments.

This thesis addressed this gap by exploring key aspects of the carrion community in Australia. It applies a large-scale standardised survey of the vertebrates and insects associated with over 120 experimentally positioned kangaroo carcasses in three distinct biogeographic regions across Australia. These bioregions included a sub-alpine and montane forest and grassland site in Kosciuszko National Park (Alpine bioregion), a temperate forest and grassland site in the Blue Mountains (Forest bioregion), and the arid sand dunes and gidgee forests of the Simpson Desert (Desert bioregion).

In my first two experimental chapters, I explore the composition of carrion-associated insect (Chapter 2) and vertebrate (Chapter 3) communities in each of the three bioregions and in relation to two key environmental variables: season and habitat. My findings revealed a substantial diversity of taxa directly associating with carrion, including several invasive predators: red foxes (*Vulpes vulpes*), feral pigs (*Sus scrofa*), European wasps (*Vespula germanica*), and feral cats (*Felis catus*). Across bioregions there was clear variation in carrion communities, with corvids (*Corvus* spp.), wedge-tailed eagles (*Aquila audax*), red foxes, and ants associating with carcasses more frequently in the Desert bioregion, and dingoes (*Canis dingo*), beetles, flies, and wasps associating with carcasses more frequently in the Alpine and Forest bioregions. Across the three bioregions, insects were generally most abundant at carcasses in warm seasons, while vertebrates used more carcasses in cooler seasons. Similarly,

several insect taxa associated more strongly with carcasses in closed habitat compared to open habitats, while open habitat was a stronger predictor of vertebrate, and particularly avian, carcass use.

In Chapter 4, I examined the effects of carcass use by Australia's largest terrestrial apex predator, the dingo, and also considered how season and habitat variables influence the persistence of animal remains. I showed that season played a strong role in carrion removal, and that carcasses always decomposed fastest in warmer seasons. I further showed that dingo scavenging may contribute to substantial carcass removal in certain contexts. Indeed, decreased carcass persistence in the Forest bioregion was evident in the cool season, when dingo scavenging occurred during the first two weeks of monitoring.

I then assessed how carrion communities interact with surrounding ecosystems by shaping predation impacts and pollination services. In Chapter 5, I showed that vertebrate scavenging, particularly by red foxes, may increase predation rates on some native ground nesting birds. I showed that carcasses attracted foxes, which led to nests experiencing higher predation risk. In Chapter 6, I showed that wasps swarmed carcasses in large numbers during the autumn study period, in the Alpine bioregion. I showed that these wasps killed and mutilated native blowflies (Diptera: Calliphoridae) and also appeared to interfere with dingoes feeding on carcasses. I concluded that European wasps may alter the way energy flows through scavenging food webs, which could have cascading impacts on ecosystem dynamics and services, especially as wasps appeared to negatively influence important native/long established scavengers including blowflies and dingoes.

Overall, this work comprises the largest replicated carrion ecology experiment to date on mainland Australia. The findings reveal novel insights into the structure and function of carrion communities across a range of bioregions. They also highlight the context dependency of carrion communities and their various interactions. I suggest that future work focuses on enhancing the spatial, temporal, and taxonomic scales upon which carrion research is focused, and support the development of global, standardised carcass monitoring surveys to build a more in-depth understanding of the factors that influence carrion community dynamics and ecosystem processes linked to decomposition.

DATA AND THESIS CONTEXT

For clarity, and to illustrate the substantial field effort that was carried out during my studies, a note must be made on the data collected as part of this PhD. I surveyed 252 carcasses, each for at least 1-month (but some for up to and beyond several years). This included 140 eastern grey kangaroo (*Macropus giganteus*) carcasses in the Wolgan Valley, Blue Mountains (later referred to as the Forest bioregion) across 6 different time periods (including 3 "warm" seasons and 3 "cool" seasons). It also included 40 eastern-grey kangaroo carcasses and 10 deer (*Dama dama*) carcasses in Kosciuszko National Park (later referred to as the Alpine bioregion) across 3 different time periods (including 1 "warm" and 2 "cool" seasons). Finally, it included 80 red kangaroo (*Osphranter rufus*) carcasses and 2 feral camel (*Camelus dromedarius*) carcasses in the Simpson Desert (later referred to as the Desert bioregion) across 4 different time periods (including 2 "warm" and 2 "cool" seasons). All carcasses used remote wildlife cameras to monitor visitation by vertebrate species, and 220 carcasses were additionally sampled for insect visitors.

Some of the data I collected has been explored and published in other research pieces. My PhD thesis specifically includes data from 160 carcasses, including 80 kangaroo carcasses from the Forest bioregion, 40 kangaroo carcasses from the Alpine bioregion and 40 carcasses from the Desert bioregion. The first two experimental chapters (Chapter 2 and 3) included data from 40 kangaroo carcasses in each bioregion (total of 120 carcasses). The third experimental chapter (Chapter 4) also included data from 40 kangaroo carcasses in each bioregion (total of 120 carcasses), however the dataset for the 40 kangaroo carcasses in the Forest bioregion differs from the dataset used in Chapters 2 and 3. This difference occurred, as Chapter 4 was published earlier and included data where no insect surveys had taken place. I made the decision to make Chapters 2 and 3 (which have not yet been published) more comparable, by only including carcasses that had surveyed insect visitors. The final two experimental chapters included a subsection of data from Chapters 2, 3 and 4, including the 40 kangaroo carcasses in the Desert region (Chapter 5), and 20 kangaroo carcasses from the cool season in the Alpine bioregion (Chapter 6).

This thesis is set out as a series of papers, an option available at The University of Sydney. Individual chapters have been written for publication and have either been submitted or are being prepared for submission to journals. This means that there may be some repetition within chapters and journal-specific formatting. Further, the term "we" is sometimes used to reflect the contribution of my collaborators, although I have been the driving force behind the conception, planning, and execution of all surveys, analyses, writing, and interpretations. Chapters that have been a published or accepted to peer-reviewed journals are indicated at the beginning of each chapter. My co-authors on these papers, and my contributions are also listed. I am first author on all of the published and submitted papers and my contribution to these papers was in each case very substantial, and included conceptualisation of ideas, engagement in fieldwork, completion of data manipulations and analyses, and writing and editing drafts of all the chapters. Dr Thomas Newsome (lead project supervisor), Dr Philip Barton, Professor Chris Dickman, and Dr Aaron Greenville provided supervision of the project, including discussions on initial concepts, design, and analyses of data, and improved earlier versions of the chapters.

As supervisors of this PhD thesis, we concur with the statements above Ms Spencer's contributions.

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A huge thank you also goes to my partner **Guillaume Tutton**, who put up with everything from extended trips away in the field, to maggots somehow appearing in my hair. I met Guillaume at the very start of my thesis. Apart from providing endless encouragement, over the past few years he has also visited and helped with fieldwork in all three of the regions I studied. He helped me haul around carcasses for a month in the Simpson Desert, he rescued my fieldtrip when our car broke down and we were delayed in the Wolgan Valley (more than once), and he made sure we spent Christmas together each year, even if it meant traveling down to meet me in the middle of Kosciuszko National Park. I also thank my other partner in crime;

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impacting access to fieldwork sites, to the pandemic putting a stopper on everything from fieldwork to lab access (and general sanity). Despite my personal hardships, there have been so many more people out there doing it tougher. Especially those working on the front lines of these disaster events. I would therefore like to finish by acknowledging the hard work and bravery of the **many firefighters, nurses** and **other emergency personnel** who not only provided incredible support in saving houses and lives through these events, but also helped 'reopen' fieldwork sites (and society in general) to greatly benefit students like me.

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GLOSSARY

Abiotic factors: a non-living part of the environment like temperature or season that influences or impacts an ecosystem and its organisms.

Apex predator: also known as a "top predator", it is a predator at the top of a food chain, without any natural predators (Wallach et al. 2015).

Apex scavenger: highly efficient scavengers, also referred to as dominant scavengers. Can include obligate scavengers such as vultures, as well as apex predators like the Tasmanian devil (*Sarcophilus harrisii*).

Carrion: referring to decomposing dead animal biomass.

Cull: the lethal control of animals, which may target perceived pest or invasive species such as the red fox (*Vulpes vulpes*), and feral pigs (*Sus scrofa*), or overabundant native species such as the eastern grey kangaroo (*Macropus giganteus*).

Decomposition: the process of an organic body being broken down into simpler parts especially by the action of living things including bacteria.

Facultative scavenger: animals that acquire their food through scavenging, in addition to other methods, especially predation.

Generalists: organisms that can subsist off a variety of food types, in a range of habitats and biomes.

Mesopredators: medium-sized animals that are considered middle trophic level predators, which both engages in predation and is preyed upon (e.g. by apex predators) (Prugh et al. 2019).

Necrobiome: the organisms that associate with decomposing necromass, including the complex and dynamic interactions they share (Benbow et al. 2019).

Necrobiota: the animal and microbial life that associates with necromass, in a particular region, habitat, or geological period.

Necromass: decomposing dead organic matter that arises from a variety of sources including plant and animal material, microbial detritus, and waste products such as animal dung.

Necrophage: organisms that acquire nutrients via the consumption of decomposing animal biomass, including carrion.

Obligate scavenger: animals that acquire their food solely through scavenging animal remains.

Specialist: organisms that have stricter diets and habitat requirements, sometimes subsisting off one food type.

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CHAPTER 1
GENERAL INTRODUCTION

Feral deer (*Dama dama*) carcass in the process of being swallowed by the undergrowth. Photograph by Emma Spencer.

1.1 Overview

The organisms that associate with decomposing necromass (i.e. dead organic matter), including the complex and dynamic interactions they share, are collectively referred to as the "necrobiome" (sensu Benbow et al. 2019). In this thesis I explore various aspects of the necrobiome, focusing specifically on the terrestrial insect and vertebrate biota that associate with animal carrion in Australia. I investigate various environmental factors that drive insect and vertebrate community structure and their use of carrion, as well as carrion persistence rates. I then go on to explore some of the ways that carrion communities interact with surrounding ecosystems, such as via predation on rare ground nesting birds and on flies involved in important pollinator services. In this general introduction, I begin by providing an overview of carrion as a nutrient-rich type of necromass and continue by outlining key members of the necrobiome community that commonly associate with carrion. I then delve into interactions relating to the decomposition of carrion in terrestrial ecosystems. This includes interactions that take place between organisms within the necrobiome community, interactions that occur between necrobiome community members and the carrion resource itself, and interactions that occur between the external ecosystem and the necrobiome community and carrion resource. I also identify important environmental factors, including human activities, which drive these interactions. Finally, I introduce carrion ecology in Australia and then highlight key research gaps in the literature, also providing an overview of my thesis objectives and design.

1.2 Carrion as a nutrient-rich type of necromass

All living things eventually die. Some organisms succumb to predation, or are killed by grazing herbivores, but many others perish as a result of disease, parasites, injury, exposure, or malnourishment (Young 1994, DeVault et al. 2003). Whatever the cause of death, unless an organism is consumed entirely, their remains will begin to decompose and will enter the pool of dead and decaying organic matter known as "necromass" (Benbow et al. 2019). Necromass arises from a variety of sources including plant and animal material, as well as much smaller organic matter such as microbial detritus, but it can also include waste products such as animal dung. It forms a substantive part of the total available consumable material in ecosystems. In some systems, for example, up to 90% of all plant matter enters the necromass pool, with only 10% of live biomass consumed by herbivores (Swift et al. 1979, Gessner et al. 2010). Similarly, larger vertebrate species such as Serengeti wildebeest (*Connochaetes taurinus*), European bison (*Bison bonasus*) and moose (*Alces alces*), may contribute predominantly to the

necromass pool because predation is not typically the primary cause of death (e.g. 79% of European bison die from disease in the Białowieża Primeval Forest, Poland) (Okarma et al. 1995, Mduma et al. 1999).

Estimates suggest that approximately 99% of necromass in terrestrial ecosystems is comprised of plant material, and other types of decaying organic matter including faecal waste (Swift et al. 1979). Compared to plant necromass, animal necromass, or carrion, is usually a temporally and spatially patchy resource that represents only a small part of the total decomposing matter present in ecosystems (Swift et al. 1979, Parmenter and MacMahon 2009). The relative rarity of carrion as a resource perhaps explains why there is such a bias in the literature towards understanding the decomposition processes of plant-derived organic materials and faecal matter (Carter et al. 2007), although carrion can still be present at high densities in some conditions and environments. For example, during extreme weather events such as severe winters and heat waves carrion density may be elevated as many animals succumb to food and water shortages or extreme temperatures (Barrett 1982, Merone et al. 2020). Similarly, mass mortality events leading to increased carrion density in the landscape may also occur due to particularly virulent diseases (Robinson et al. 2019), or biological phenomena such as annual mass migration events of Serengeti wildebeest (Subalusky et al. 2017) and Pacific salmon in North American rivers (Hocking and Reimchen 2006) and following resource pulses (Yang 2004).

Even when rare in the environment, however, carrion provides a cost-effective resource that is high in important and often limiting nutrients. Indeed, carrion is one of the most nutrient-rich forms of necromass present in ecosystems (Carter et al. 2007). Compared with other forms of necromass such as dead plant matter, carrion is characterised by higher nitrogen levels and a lower carbon:nitrogen (C:N) ratio, and it also contains higher quantities of other key macronutrients such as phosphorus (Swift et al. 1979, Moore et al. 2004). Its nutrient-rich quality, paired with the fact that a dead animal is also generally easier to handle than live prey as it cannot flee or engage defensively with predators (Pereira et al. 2014), makes carrion a highly attractive resource that is used by a wide variety of organisms.

1.3 Organisms that associate with carrion

Carrion attracts a suite of organisms from several biological kingdoms. Animals are the largest visitors in terms of size, with vertebrates such as mammals and birds, and arthropods like flies, beetles and mites often associating with carrion (DeVault et al. 2003, Barton et al. 2013a).

Carrion can also host species-rich microbial communities, including bacteria, fungi, archaea, and protists (Barton et al. 2013a).

1.3.1 Microbial communities

Carrion resources can host incredibly diverse microbial communities comprising thousands of taxa (Pechal et al. 2013, Crippen et al. 2016). These communities can be found on carrion and around the carcass, for example, within soil substrates. On carrion, microbes can colonise a wide range of substrates in and outside of the dead animal including all internal organs, hair, skin, and bone (Barton and Bump 2019). Bacteria are often associated with the gut inside carcasses, or the mucous membrane of a cavity (e.g. the mouth), with common aerobic taxa from the Firmicutes and Bacteroidetes phyla, and anaerobic bacteria including *Lactobacillus*, *Streptococcus*, and *Staphylococcus* (Forbes and Carter 2016). Fungi on the other hand are typically more abundant on the surface or soil surrounding carcasses and are usually present at later decomposition stages when nutrients from the carcass flush into the surrounding environment (Tibbett and Carter 2003). The microbial communities characterising carcasses typically originate from the carcass itself (e.g. from the gut of the live animal) or from the surrounding soil environment but can also be introduced by other organisms that visit the carcass, such as scavengers (Vicente and VerCauteren 2019).

1.3.2 Insect communities

Insects associate with carrion resources for varied reasons. Some insect taxa act as decomposers and scavengers throughout their entire life cycle, or alternatively may scavenge only at certain life stages (Benbow et al. 2019). Other insects interact with carcasses as predators of other adult insects, larvae, and eggs present on the resource, or will also feed on dung and other animal waste products in addition to carrion resources (Benbow et al. 2019). Targeted insect necrophagy may also occur upon the carcass itself, as some species prefer certain parts of animal carcasses such as the skin or bones (Benbow et al. 2019). Many insects, particularly fly species, also use carrion to complete their breeding cycle, ovipositing eggs on the carcass so that the resultant larvae have easy access to nutrient-rich food resources (Kuusela and Hanski 1982).

The most commonly reported insects on carrion are from fly and beetle families (Barton et al. 2013a). These groups are not only often the most abundant species recorded on carcasses, especially in terms of the larval masses that are generated, but they are also commonly the

focus of studies due to their importance in ascertaining time of death for crime scene investigation (Greenberg 1991, Bala 2015). Of the flies, larger families like the blowflies (Diptera: Calliphoridae), house flies (Diptera: Muscidae) and flesh flies (Diptera: Sarcophagidae) are present in virtually every terrestrial habitat on the planet and are among some of the most abundant organisms to colonise animal remains. Fly larvae in particular are responsible for rapid decomposition of carcasses, with 'maggot masses', or hundreds or thousands of larvae, aggregating on carcasses (Rivers et al. 2011). Flies are often the first to arrive at carcass sites as they are typically abundant in the environment, are capable of significant dispersal, and can detect minute traces of decomposition odour in air currents (Norris 1965). Beetles typically arrive on carcasses following flies. They are generally slower to disperse but are also more species-rich and typically associated with later stages of decomposition, as they fulfil roles as generalist predators or specialise on components of the carcass less attractive to most other species (Braack 1987, Barton et al. 2013b). For example, some family groups such as clown beetles (Family: Histeridae) or carrion beetles (Family: Silphidae), will visit animal remains to feed on eggs and insect larvae, but also consume carrion as adults or as larvae (Charabidze et al. 2021). Some beetles, such as skin or hide beetles (Coleoptera: Dermestidae), are more often associated with later decomposition periods as they specialise on skin and cartilage from bones (Goff 2009).

Apart from flies and beetles, many other insects associate with carrion and contribute to decomposition processes. Ants, for example, directly influence decomposition by feeding on carcasses and by depredating carrion-feeding invertebrates but may also alter carrion microhabitat by constructing nests under or around carcasses (Eubanks et al. 2018). Wasps (e.g. *Vespula germanica*) may associate with carrion to depredate other insects, as well as their eggs and larvae (Archer and Elgar 2003). Other insects such as bees and butterflies may visit carcasses to gather moisture and minerals from animal remains (Hamer et al. 2006, Baz et al. 2010). Finally, a quick mention must also be given to mites. While not insects, mites are commonly found on carrion and are often phoretic, using other insects such as flies and beetles to disperse from one carcass to the next (Braig and Perotti 2009).

1.3.3 Vertebrate communities

All carnivorous vertebrates are capable of scavenging (DeVault et al. 2003). While some subsist entirely on carrion resources, others are more flexible in their diet. Amongst vertebrates, these two different types of scavengers are typically grouped as "obligate scavengers", or those

species that rely almost entirely on decaying animal matter to survive, and "facultative scavengers", or species that supplement their diet with carrion to varying degrees.

Few vertebrate species are considered obligate scavengers, but those that exist have evolved specific traits that support efficient carcass detection and consumption. The relative rarity of carrion in the landscape means that these species generally exhibit efficient dispersal and can travel long distances in a cost-effective manner to search for these resources. Indeed, vultures (Families: Accipitridae and Cathartidae), which, with their large wingspan and soaring flight, can cover great distances with relatively little energy expenditure in search of carrion resources (Ruxton and Houston 2004, Duriez et al. 2014). Some vulture species use their excellent eyesight or even their sense of smell to detect distant carcasses or carcasses hidden underneath dense vegetation (Houston 1986). They also have a range of anatomical and physiological adaptations to reduce their chances of picking up diseases from carcasses. For example, their bare head and neck reduces the amount of food and bacteria they hold on their feathers and facial skin, and the large intestine hosts a range of microbial taxa that play a protective role against harmful microbes (Zepeda Mendoza et al. 2018). As with most specialists, however, obligate scavengers including vultures can be rare in some environments and are typically vulnerable to change and disturbance (Ogada et al. 2012).

On the other hand, most carnivorous, and many omnivorous vertebrates will consume carrion alongside other food resources. Most of these animals also play dual roles as predators-scavengers (DeVault et al. 2003). These facultative scavengers can supplement a substantial part of their diet with carrion. For example, some species like the brown hyena (*Hyaena brunnea*) may rely on scavenging for almost all of their dietary intake (Mills 1990). Other species, such as cheetahs (*Acinonyx jubatus*), feed on carrion only when their preferred prey types are scarce (Skinner and Chimimba 2005). For facultative scavengers, however, carrion can be a resource that shifts in importance over time and across different conditions. During winter, for example, almost half of the diet of red foxes (*Vulpes vulpes*) in Norway comprised ungulate carrion, which is thought to stabilise their populations during this time (Needham et al. 2014). Similarly, coyotes (*Canis latrans*) can depend highly on winter scavenging, with supplemental elk carrion contributing to greater litter sizes and pup survival (Crabtree and Sheldon 1999). Unexpected scavengers, including herbivorous animals like the snowshoe hare (*Lepus americanus*), may also arise during periods of low food resources (Peers et al. 2018). Finally, some vertebrates may interact with carrion for purposes other than to use it as a food resource. For example, birds have been recorded collecting fur and hair off animal carcasses to

insulate their nests (Tóth 2008). Similarly, herbivores may also associate with carcass sites as the decomposition process increases plant biomass and foraging opportunities in the immediate area (van Klink et al. 2020).

1.4 Ecological interactions relating to carrion

The carrion necrobiome provides an arena for a series of direct and indirect interactions that fall within three main groups: 1. necrobiome community interactions, which occur between species that associate with carrion resources, 2. carrion interactions, which occur between carrion-associated species and carrion resources and 3. ecosystem interactions, which involve the interactions between the surrounding environment, and the necrobiome community and carrion resources (Figure 1.1) (Benbow et al. 2013, 2019). These interactions may influence the community structure of organisms within the necrobiome, as well as important ecological processes such as decomposition and nutrient transfer (Benbow et al. 2016).

1.4.1 Necrobiome community interactions

The interactions that species share may involve positive, negative, or neutral outcomes for the interacting species (Haskell 1947). These interactions can occur between individuals of the same species (intraspecific) or different species (inter-specific) and can involve individuals from different trophic levels through to different classes and kingdoms.

Competition is generally considered as the most important interaction between species that coexist on carcasses. Indeed, the premise of most forensic investigations associated with carrion is that intense competition occurs between insect species, leading to predictable trends of 'succession' in different species over time (Carter et al. 2007). Species compete on carrion by consuming and monopolising this resource and making it unavailable or inaccessible to other species. For example, blowfly (Diptera: Calliphoridae) larvae outcompete colonising flesh fly (Diptera: Sarcophagidae) larvae by rapidly monopolising and consuming carrion resources (Denno and Cothran 1976). Vertebrate and insect scavengers will also compete heavily for carcass resources, with studies indicating that avoidance of certain carcasses by vertebrate scavengers enables more diverse colonisation of insects on the resource (Munoz-Lozano et al. 2019). Among vertebrate scavengers, the presence of dominant (e.g. efficient or large) scavengers on carrion resource may also reduce the availability of carrion resources to other less dominant (e.g. less efficient or smaller) scavengers. For example, apex predators may inhibit carcass access to smaller vertebrates that avoid the resource out of fear (Hill et al. 2018,
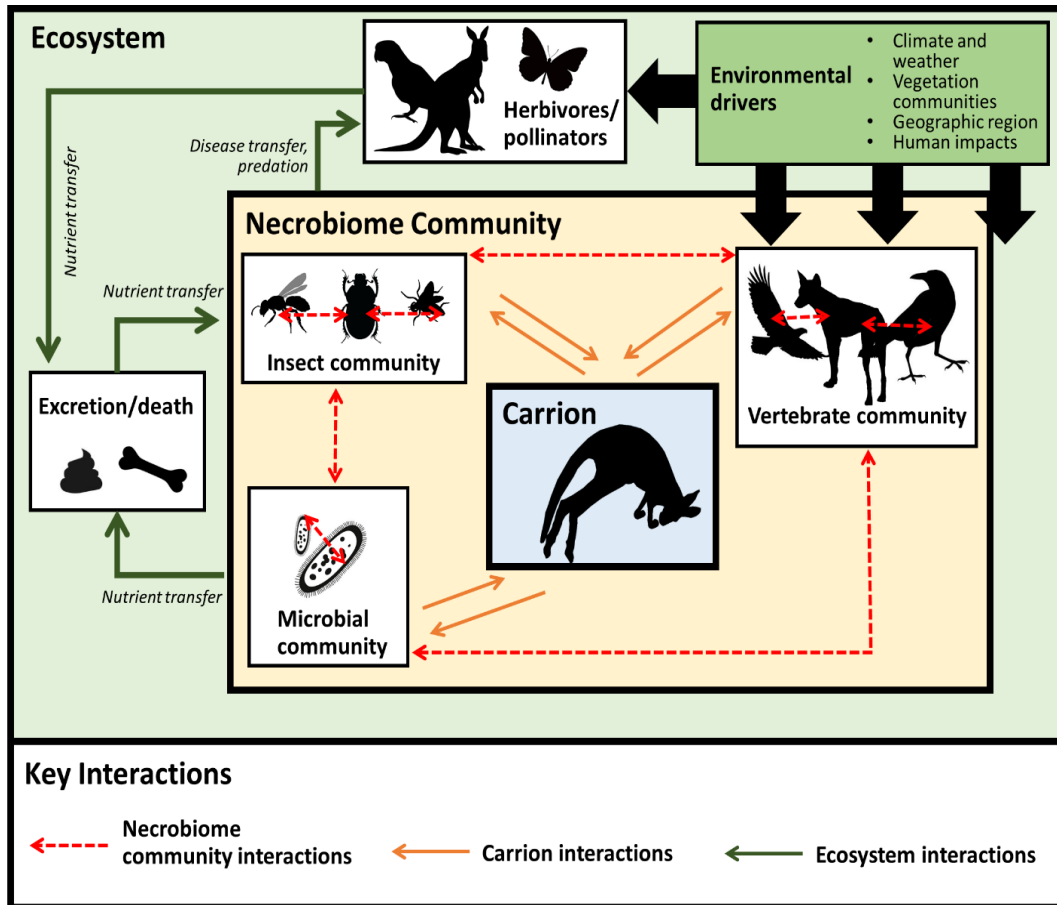
Figure 1.1. Key interactions that necrobiome communities share with carrion, and the surrounding ecosystem, including environmental drivers that shape these interactions. These interactions can be categorised into three main groups: necrobiome community interactions, which occur between species that associate with carrion resources, carrion interactions, which occur between carrion-associated species and carrion resources and ecosystem interactions, which involve the interactions between the surrounding environment, and the necrobiome community and carrion resources. Necrobiome community interactions (dashed red arrows) primarily comprise competitive and predatory relationships but can also include mutualistic and facilitatory interactions. Carrion interactions (orange arrows) include both the effects that the necrobiome community can have on carcasses (e.g. via carrion removal), but also the effects that carcasses can have on the necrobiome community (e.g. as a source of sustenance). Ecosystem interactions (green arrows) can include the effects that carrion and the necrobiome community can have on pollinators and herbivores (e.g. via predation by facultative predators, and by disease transfer), and by energy dispersal and nutrient cycling (e.g. via excretion of scats or faeces and by dying, which herbivores and pollinators also contribute to). Excretion products and the dead bodies of necrobiome community members will also feed back into the necrobiome, as they represent new sources of necromass. Finally, environmental drivers or factors that influence the necrobiome can include climate and weather, vegetation communities or habitat, geographic region, and human impacts such as species introductions and climate change.

Cunningham et al. 2018). Similarly, vultures form intra- and interspecific hierarchies based on age and size classes, using aggression and intimidation to restrict competing species' access to carrion (Moreno-Opo et al. 2020). Organisms may also compete through use of toxic chemicals to deter other species from the carrion resource. These interactions often occur between species in different biological kingdoms. For instance, blowflies secrete antimicrobial compounds (Čeřovskỳ et al. 2010) that may affect the microbial community on carrion.

Predation is another interaction that structures carrion communities. Many species are attracted to carrion because of the availability of prey on or around that resource. The consumptive effects of predators can directly impact the dynamics of carrion communities. Indeed, predation by red imported fire ants *Solenopsis invicta* (Hymenoptera: Formicidae) on fly eggs and larvae can slow colonisation of carrion by blowflies (De Jong et al. 2021). Predators may also have non-consumptive effects on carrion communities. For example, in the presence the facultative predator *Chrysomya rufifacies* (Diptera: Calliphoridae), *Cochliomyia macellaria* (Diptera: Calliphoridae) may avoid ovipositing on carrion at earlier stages of the decomposition process to avoid predation (Brundage et al. 2014). Other interactions such as parasitism, mutualism and facilitation are also commonly observed in carrion communities. For example, phoretic mites interact with carcasses by parasitising insects that associate with carrion resources. While some of these relationships can be negative, especially if mites are present on the host in excessive numbers, mites can also interact mutualistically with their hosts. Indeed, mite species *Poecilochirus carabi* can enhance the reproductive success of their host *Nicrophorus vespilloides*, by consuming the eggs of competing blowfly species (Sun and Kilner 2020). Facilitative interactions, on the other hand, can take place when carrion use by one species enables its use by others. Hyaenas, for example, can tear through tough skin of large carcasses, providing access to the resource for other scavengers such as griffon vultures *Gyps africanus* and *G. ruppellii* (Houston 1974). Further, discovery of animal carcasses by certain animals may also be facilitated by avian scavengers. Indeed, vultures can locate carrion by following other vultures or eagles to carrion that is hidden or hard to detect (Kane et al. 2014).

1.4.2 Carrion interactions

The decomposition and removal of carrion from environments is in part directed by intrinsic chemical processes including autolysis and putrefaction (Carter et al. 2007). Carrion decomposition is also driven by extrinsic biological drivers, and specifically the consumptive interactions between necrophagous organisms and the resource (Barton and Bump 2019). For

example, insect communities (and particularly fly larvae) interact directly with carcasses via consumption of the resource and can dramatically accelerate the decomposition process (Payne 1965, Pechal et al. 2014). Vertebrates also play important roles in the breakdown of carrion, and their interaction with larger carcasses in particular produces some of the greatest rates of carrion removal from environments (DeVault et al. 2003, Wilson and Wolkovich 2011). In contrast to small necrophagous insects, vertebrate scavengers are capable of dispersing carcass material across landscapes, as they disarticulate and move partially consumed remains. Carrion interactions can also be indirect. For instance, predatory insects, such as ants that prey upon fly larvae and eggs, may slow rates of carrion decomposition as they suppress abundant carrion-consuming larval populations (Paula et al. 2016).

Carrion-consumer interactions also include the effects that carrion has on the consumer organisms. These interactions are largely positive, as carrion resources often provide an important and sometimes essential energy and nutrient source that contributes to fitness and reproductive success. Animal populations that use carrion as a primary source of food (e.g. obligate scavengers), for example, fulfil their entire energy and nutrient requirements via carrion consumption. If carrion resources are sparse in the environment, this can have profound, negative impacts on certain animal populations, such as vultures (Families: Accipitridae and Cathartidae) and burying beetles (*Nicrophorus* spp.) (Sikes and Raithel 2002, Ogada et al. 2012). Consumptive interactions between facultative scavengers and carrion may also be important for these species during certain conditions. For example, during winter carrion consumption can stabilise red fox (*Vulpes vulpes*) populations (Needham et al. 2014) and supplemental elk carrion can contribute to greater litter sizes and pup survival in coyotes (*Canis latrans*) (Crabtree and Sheldon 1999).

1.4.3 Ecosystem interactions

Necrobiome communities, and carrion resources, interact with surrounding ecosystems through a variety of processes. For example, carcasses left to rot may become hubs for disease, as bacteria multiply on the resource and spread throughout systems infecting animals, including livestock and humans. Disease spread from decaying carcasses has been documented, with scavenger-carcass interactions potentially responsible for propagating diseases such as chronic wasting disease across environments (Jennelle et al. 2009). On the other hand, scavengers could also limit the capacity for disease to take hold, and to spread, as these organisms assist in the break-down of carrion resources as "waste removalists" (Vicente and VerCauteren 2019).

Vultures, for example, have been linked with healthier environments, as they protect humans, livestock and wildlife from disease by removing carcasses (Markandya et al. 2008). Similarly, invertebrate scavenging can also prevent disease spread with, for example, scavenging of the larval carcasses of long-toed salamanders (*Ambystoma macrodactylum*) by water beetles (Family: Dytiscidae) preventing the spread of frog virus 3 (Genus: *Ranavirus*, Family: Iridoviridae) (Sage et al. 2019).

Scavenger interactions with carrion also affect ecosystems by altering energy dispersal and nutrient cycling (Pereira et al. 2014). Energy dispersal may be substantial, with some estimates suggesting that 124-fold more energy may be transferred per vertebrate scavenging link than via the predation link in some food webs (Wilson and Wolkovich 2011). By consuming carcasses, scavengers help to "free up" energy and nutrients from the system. They distribute this energy and nutrients across systems, via their faeces, and by dying and being consumed by other predators or scavengers. The nutrients in carrion are dispersed at different speeds and to different extents, largely dependent on the scavengers that feed on the remains. Vertebrate scavengers, for example, are typically responsible for wider dispersal of nutrients and energy from carcasses than insects as they are capable of movement over greater distances (Payne and Moore 2006, Barton et al. 2013a). By dispersing nutrients across multiple trophic levels, scavengers also interact with ecosystems by providing stability to food-webs. Facultative scavengers, and apex predators in particular, play an especially important role in the stabilisation of food webs, as they interact with detrital channels not only via scavenging, but also by producing faeces and through leaving remnants of their prey behind for scavengers to consume (Wilson and Wolkovich 2011).

Carrion may also affect important ecosystem services such as pollination, as species that use carrion may also function as pollinators. For example, blow flies (Diptera: Calliphoridae) that associate with carrion, are also known to play valuable roles as pollinators of some plants, and can increase seed yields even beyond that of honey-bee pollination (Heath 1982). Similarly, pollinators may be attracted to the nitrogen-rich vegetation growth that often occurs around carrion sites (Barton et al. 2013b). This means that carrion could indirectly effect pollinator services by increasing populations of organisms that take on a dual role as scavengers and pollinators, or by redirecting pollination services to areas surrounding carrion resources (Cusser et al. 2021). Finally, by elevating predator numbers or activity, carrion can also influence the predation impacts experienced by local animal communities in the environment surrounding carrion resources. For example, a mass die-off of reindeer in Norway following a

lightning strike increased corvid (common raven *Corvus corax* and hooded crow *C. cornix*) activity and led to locally reduced rodent activity (Frank et al. 2020). Similarly, hunter-provided ungulate carcasses increased red fox activity, while reducing the local activity of brown hares (*Lepus europaeus*) and red squirrels (*Sciurus vulgaris*) (Cortés-Avizanda et al. 2009).

1.5 Environmental drivers of carrion communities

The interactions between members of the necrobiome community and the degree to which these community members interact with carrion and surrounding ecosystems are influenced by a complex interplay of environmental factors, or drivers (Figure 1.1).

1.5.1 Climate and weather

Abiotic factors relating to climate and weather such as temperature, humidity and rainfall are key drivers shaping how organisms associated with carcasses interact with each other, and with carrion resources. Warmer and wetter conditions positively correlate with increased insect and particularly maggot activity, as well as microbial presence on carcasses (Archer 2004). These increased activity levels not only influence carrion mass loss rates, but also how other carrion consumers interact with carcasses. For example, greater microbial presence can enhance odour propagation from carcass sites, which could increase discovery rates of the resource by animals that rely on scent to locate food, such as Turkey Vultures (*Cathartes aura*) (Houston 1986). Higher microbial and insect activity may also increase the competition experienced by vertebrate scavengers. Indeed, this is why more carcasses are often consumed by vertebrates during cooler months (DeVault et al. 2003). Scavenging by some vertebrate species and colonisation by insects could alternatively be impacted negatively by high temperatures, and more generally, by temperature and other environmental extremes. Hot and dry conditions can desiccate, and cold temperatures can freeze carcasses, potentially limiting accessibility to the carcass meat and increasing carcass persistence times (Selva et al. 2003, Santos et al. 2011). Sunlight exposure and whether a carcass is positioned in shade or in direct sun may also influence colonisation of insects on carcasses and carcass decomposition (Probst et al. 2020). Further, high rainfall and heavy winds may also impact scavenger community composition by impeding dispersal and therefore colonisation of carcasses by animals associated with carrion, such as blowflies (George et al. 2013).

1.5.2 Vegetation communities

Different vegetation communities, or habitats, may also affect variation in carrion community structure as well as carrion decomposition. Species density in certain areas often depends on their habitat preferences or requirements, such as for foraging or breeding, which could then influence their chance of encountering carcasses in specific habitats (Hager et al. 2012). For example, certain blowfly species have difference preferences for open areas, dense cover, or intermediate coverage with scrub and sparse trees present (Macleod and Donnelly 1957). Different habitat characteristics such as vegetation cover can also influence scavenger communities at carcasses by favouring the detection of carcasses by species that rely on sight to locate food resources (Fernández-Juricic et al. 2004). For example, many Old-World vultures (Family: Accipitridae) tend to be associated with carrion in open habitat, as they find carcasses exclusively by sight (Ogada et al. 2012). Predation risk may also influence habitat use and therefore scavenging activity, as some species will avoid feeding at food resources that are positioned in "risky" habitats such as open fields (Wikenros et al. 2014). It has also been suggested that habitat could play a more important role in shaping generalist insect communities at carrion, such as ants and beetles, compared to specialist flighted insects such as flies (Barton and Evans 2017).

1.5.3 Geographic region

One of the more important drivers influencing carrion insect communities is geographic region. Climate, habitat, vegetation, and soil type all vary among regions, and together influence the necrobiome community at carrion sites (Anderson 2010, Barton et al. 2013a, Olea et al. 2019). Scavenger pools are ultimately drawn from the species present in the surrounding environment, which may vary widely across different locations and particularly across different continents. In some locations, obligate scavengers like vultures may characterise scavenger communities, while in others, facultative scavengers such as red foxes and Virginia opossums (*Didelphis virginiana*) may be dominant (Mateo-Tomás et al. 2015). The species pool will not only contribute different scavenger guilds, but also different carcass types, and sizes. For instance, larger carcasses such as elephants and wildebeest are widely present in African environments, while urbanised areas in the UK may be characterised by smaller carcasses of birds and rodents (Mateo-Tomás et al. 2015). Scavenger communities and carcass decomposition are often shaped by carcass type (or species) and carcass size (Mateo-Tomás et al. 2015, Moleón et al. 2015, Olson et al. 2016). Thus, large ungulate carcasses are often associated with a greater

diversity and abundance of scavengers compared to smaller carcasses such as mice or chickens, and they decompose faster than smaller carcasses too (Moleón et al. 2015, Olson et al. 2016, Turner et al. 2017). Certain carcass types may also be avoided by scavengers due to food preferences but also disease associations. For instance, scavengers may avoid or delay scavenging on the dead bodies of carnivorous species compared to herbivorous species, potentially because carnivore carcasses are more likely to spread disease among scavenger populations (Moleón et al. 2017).

The effects of seasonality and habitat on carrion communities may also differ according to biogeographic region. For example, in temperate bioregions most insect activity is suppressed in winter, whereas in warmer tropical bioregions insects are generally active throughout the year (Wolda 1988). More generally, in bioregions that experience extreme climatic conditions, such as tundra, alpine areas and deserts, carcasses are more likely to host lower scavenger species richness (Mateo-Tomás et al. 2015). On the other hand, in productive environments closer to the equator, where average temperatures are warm and conditions often wetter, and where species diversity and population densities of arthropods are frequently much larger (Stork 1988), abundant carrion assemblages and high rates of carrion decomposition may occur. Plant communities and vegetation complexity also differ across bioregions, which may alter how easily carcasses are discovered and who discovers them too. For example, preference for dense forest versus open pasture habitats for certain blowflies such as *Lucilia* spp. differs across Europe and North American regions (Anderson 2010).

1.5.4 Human factors

Anthropogenic impacts have been identified as a key driver of scavenger communities, particularly vertebrate scavenger communities (Sebastián-González et al. 2019). Humans dramatically influence biodiversity across the planet, which in turn affects the pool of species from which scavenging communities can draw. Indeed, some of the only obligate vertebrate scavengers – vultures – are experiencing global declines due to human persecution and poisoning, as well as human interference with carrion production in the environment (Ogada et al. 2012). In India, for example, declines of more than 95% of *Gyps* spp. vulture populations have been recorded, largely due to the usage of the veterinary drug diclofenac to treat farm animals (Wani et al. 2019). There have also been declines in insect carrion specialists, such as the American burying beetle (*Nicrophorus americanus*), possibly due to a range of human factors such as pesticide use, artificial lighting, and habitat loss (Sikes and Raithel 2002).

Changes in vegetation structure by humans may also influence carrion communities, with distinct differences existing between urban and rural habitats in terms of carrion insect and vertebrate communities and corresponding rates of carrion decomposition (Kavazos and Wallman 2012, Huijbers et al. 2013). The human-driven decline of apex predators across the planet may also influence scavenger assemblages, as well as rates of carcass removal. In urban areas, for example, where apex predators have been largely removed, scavenger assemblages are dominated by mesopredators and generalists (Inger et al. 2016). Locations that lack or have lower numbers of these dominant scavengers could see increased use of carrion by mesopredators and generalists, which may then influence the persistence of carrion in the environment. Further, the loss of apex predators such as wolves may also influence spatial and temporal distribution of carcasses, which could have flow-on effects to smaller scavenger species, like coyotes (Switalski 2003).

Humans also influence scavenging communities via the introduction of exotic animals. These animals can interact and outcompete native scavengers, but also produce novel sources of carrion that may be used differently by native scavengers (Abernethy et al. 2016). For example, introduction of large ungulates such as cattle and deer produce large carcasses that potentially persist in landscapes for long periods. Larger carcass sizes could influence not only the community of animals that scavenge the resource, but also the length of time at which a carcass is present in the environment (Hewadikaram and Goff 1991, Moleón et al. 2015). While this could have positive effects such as providing greater nutrient sources for native animals, some research suggests that carcasses of invasive species can be disproportionally fed on by other invasive species (Abernethy et al. 2016). Further, carcasses that persist for longer periods may be more likely to spread disease into the environment. Humans are further altering the input of carcasses into systems via climate change, which is driving more frequent mass mortality events (Fey et al. 2015), as well as through practices such as hunting and farming (Mateo-Tomás et al. 2015).

1.6 Carrion ecology in Australia

The carrion ecology of Australia is an important subject of research for several reasons. Australia is one of only two continents in the world where obligate vertebrate carrion consumers are absent (the other being Antarctica). Instead, it is home to a variety of native carnivorous species that may supplement their diets with carrion.

Of native Australian vertebrates, numerous species have been observed scavenging to different degrees. Some, like the Tasmanian devil (*Sarcophilus harrisii*), scavenge prolifically and play an important role in the removal of carrion from systems (Cunningham et al. 2018). The use of carrion by other predators such as the wedge-tailed eagle (*Aquila audax*), dingo (*Canis dingo*) and quolls (*Dasyurus* spp.) is less clear, although scavenging by a range of Australian predatory birds including eagles has been shown to play an important role in carcass break-down in pastoral environments (Peisley et al. 2017), and dingoes have also been observed frequenting ungulate carcasses (Forsyth et al. 2014) as well as stranded sea life (Behrendorff et al. 2018), even cannibalising their own during dry periods (Allen 2010). Generalists such as the forest raven (*Corvus tasmanicus*), Australian raven (*C. coronoides*) and little crow (*C. bennetti*) and reptiles including goannas (*Varanus* spp.) have also been identified as frequent scavengers (Read and Wilson 2004, Rees et al. 2015, 2020, Fielding et al. 2021). While reptiles appear in scavenger studies to a far lesser extent than mammals and birds (Mateo-Tomás et al. 2015), they may prove to be important carcass consumers in Australia due to their high relative diversity and abundance across the country, particularly in desert areas (Vitt et al. 2003).

Australia's often-warm climate also provides ideal conditions for many necrophagous insects. Flies have been studied extensively in Australia, although mostly under a forensic entomological lens. Common families at decaying carrion reflect global trends and include flesh flies (Diptera: Sarcophagidae), house flies (Diptera: Muscidae) and especially blowflies (Diptera: Calliphoridae) (Archer and Elgar 2003, Voss et al. 2009). Also following global trends, beetles tend to form the most diverse communities of insects that associate with carrion in Australia. For example, 88 beetle species from 28 different families were collected from 18 eastern grey kangaroo (*Macropus giganteus*) carcasses (Barton et al. 2014). Ants have also been recognised as potentially important members of carrion necrobiome communities in Australia. Large numbers of meat ants (*Iridomyrmex* spp.) have been observed on carcasses from rabbits to kangaroos and may either inhibit carrion decomposition via predation on fly larvae or could enhance it by feeding on the carrion resource (Read and Wilson 2004, Barton and Evans 2017). Ant species diversity associated with carcasses can be high and comparable to beetle species diversity in some areas. For example, 34 different ant species (compared to 15 fly and 35 beetle species) were collected on 18 rabbit (*Oryctolagus cuniculus*) carcasses in a woodland area outside of Canberra, south-eastern Australia (Barton and Evans 2017).

Another important aspect is the community of invasive species in Australian systems. In Australia, invasive species are abundant across many parts of the country and so scavenging

by invasive vertebrate and insect species may also be frequent. Red foxes frequent carcasses in multiple biomes across the continent and may outcompete native scavengers in some environments and under some conditions (Read and Wilson 2004, Brown et al. 2015). Feral cats (*Felis catus*) have also been recorded scavenging, especially where larger predators that scavenge are absent or in low numbers (Cunningham et al. 2018). Further, invasive insects such as fire ants (*Solenopsis invicta*) and European wasps (*Vespula germanica*) may also scavenge carcasses where they are present in Australia. Studies in North America have shown the high impacts that these species can have in shaping insect and vertebrate scavenger communities (e.g. through deterrence and predation) and corresponding rates of decomposition (Stoker et al. 1995, Turner et al. 2021). These species may impact other native animals that use carrion via competition for the resource and predation of other necrobiome community members, but they may also impact other species not associated with carrion, especially if these resources enable them to increase or sustain their numbers. Invasive predators in Australia cause disproportionately high impacts on native species (Doherty et al. 2016) and so it is important that we understand how carrion affects how they influence species – particularly those that are rare or endangered, or otherwise take part in centrally important ecosystem services such as pollination.

Carrion can be produced in high densities across Australia, both as a result of the many extreme environmental conditions that characterise this country and due to a variety of human practices. Australia is the driest inhabited continent in the world, with 70% of the land being either arid or semi-arid. Droughts are common, and water shortages, heatwaves and fires frequently cause mass mortality events. The 1982–83 drought killed approximately 14,500 kangaroos in Kinchega National Park, with kangaroo mortality reported to have been similar across other parts of eastern Australia during this time (Robertson 1986). Heatwaves have also been responsible for much carcass production, especially among smaller passerine birds and bat species. In 2014, for example, more than 100,000 bats died during hot temperatures experienced across Queensland and New South Wales (O'Shea et al. 2016). Similarly, flood and fire events also produce mass carcass loads. In 2019, for example, floods produced an estimated 625,000 cattle and 48,000 sheep carcasses (Cowan et al. 2019) and the 2019–20 megafires across eastern Australia were estimated to have killed or displaced nearly 3 billion animals (van Eeden et al. 2020), with a proportion of these animals left to rot in the environment as carcasses (Jolly et al. 2022).

In terms of anthropogenic contributions to carcass density, vehicular collision contributes to many of the more visible animal carcasses in Australia. Almost 4 carcasses per 10 kilometres of road may be encountered in some states, such as Tasmania (Hobday and Minstrell 2008), and it is also likely that these numbers are underestimated as some carcasses are removed from the environment by scavengers before they can be counted (Santos et al. 2011). Culling can also produce high densities of carcasses and is used regularly in managing native and invasive species in Australia. Introduced herbivores including pigs, deer, rabbits, and camels are removed in the tens of thousands each year via shooting, poison baiting and the release of disease. For example, following the release of rabbit haemorrhagic disease (RHD) into Flinders Ranges National Park, South Australia, above-ground counts revealed approximately 1 million rabbit carcasses, with many more carcasses likely located underground and more than 30 million rabbits suspected to have died due to the disease in adjacent areas (Mutze et al. 1998). Similarly, three aerial culls of camel populations in the Northern Territory produced upwards of 6,500 carcasses (Hart et al. 2016). With each carcass containing between 125 – 400 kilograms of meat (Kadim et al. 2008), these culls could represent a significant source of food for a variety of animals. Native animals, especially macropods, are also regularly culled for their impacts on vegetation in agricultural and conservation settings. In New South Wales, for example, hundreds of thousands of kangaroos are culled by commercial harvesters and via non-commercial culls (Lunney et al. 2018). Carcasses produced in these quantities are likely to influence more than just scavenging communities, affecting broader ecosystem function and structure too (Barton et al. 2019).

Some carcasses in Australia are collected and buried (e.g. roadkill in urban areas) or are removed from the environment for human consumption (e.g. if animas are culled by commercial harvesters) (Read and Wilson 2004, Dunne and Doran 2021). For the most part, however, carrion management in Australia is rare, and carcasses are typically left to lay, sometimes in excessive numbers. This could have important implications for animals – especially invasive species – that benefit from carrion resources and the corresponding ways in which they interact with surrounding environments (e.g. via predation) (Read and Wilson 2004). A final important management consideration that relates to carrion ecology in Australia, is the persecution of apex predators in this country. Populations of Australia's largest terrestrial apex predator, the dingo (*Canis dingo*) is often controlled via lethal methods (e.g. hunting, baiting, and trapping), as they can have detrimental impacts on livestock (Allen and West 2013). These predators are, however, important trophic regulators in Australian ecosystems

(Glen et al. 2007). Further, as the largest terrestrial carnivore in Australia that is also known to scavenge, they may also play important roles as carrion "removalists" (Forsyth et al. 2014, Behrendorff et al. 2018). Apex predator control may therefore have important effects on carrion persistence in Australian environments. Their removal could also impact carrion use by invasive mesopredators (Olson et al. 2012), which could have flow-on negative impacts to surrounding ecosystems.

1.7 Gaps and significance in carrion research

Despite the importance of carrion to a wide variety of species, many aspects regarding the decomposition of this resource, and the animal communities that engage in scavenging behaviour, have been ignored. For example, scavengers and other detritivores have poor representation in food-web ecology, where it has been estimated that vertebrate scavenging is underrepresented 16-fold in conventional food-webs (Wilson and Wolkovich 2011). Attention has instead focused on the decomposition processes of other forms of necromass, such as plant-derived organic materials and faecal matter, and much of the research into animal carrion has been related to forensic taphonomy and the description of post-mortem intervals (Carter et al. 2007). Further, research on carrion necrobiome communities in Australia is limited, especially compared with northern American, European, and African locations (Sebastián-González et al. 2020). Developing research in Australia will help contribute to general understanding of the necrobiome. The gaps in research on carrion and scavenger communities have probably arisen in part because of our natural aversion to decaying matter. Negative connotations related to "scavengers" are common in popular media, with these animals typically portrayed as harbingers of death and disease (DeVault et al. 2003). Otherwise, carrion has been considered a rare and inconsequential resource, and scavenging as a feeding behaviour exhibited only by a small collection of animal species. Here, I describe four key gaps in carrion research, which will be addressed within this thesis.

1.7.1 Incorporating ecosystem context into carrion research

While studies on scavenger communities and carrion use are increasingly incorporating one or some abiotic and biotic factors, they seldom explore these factors in the context of multiple spatial and temporal scales (but see: Pardo-Barquín et al. 2019). Further, most studies are restricted to single regions (e.g. DeVault et al. 2004; Selva et al. 2005) and have typically also been designed with different methods, making it difficult to compare results (but see: Mateo-

Tomás et al. 2015, Sebastián-González et al. 2019). It is important to undertake studies using standardised methods to explore the impact of different factors on scavenging in different regions, not only because of the potential for wide variability in the conditions experienced and animal assemblages present at these locations, but because of the impact that using different survey methods might have on the results (e.g. different carcass types; Moleón et al. 2015). In these studies, it is also important that a variety of systems are sampled, such that different climates, habitats and species communities are incorporated. Additionally, as most studies are biased towards temperate environments (Barton et al. 2013a), environments that experience greater climatic extremes should be prioritised. Deserts and alpine systems, for example, are often resource-limited and may experience large carcass production events, for example, due to drought or following snowfall.

1.7.2 Increasing taxonomic breadth in carrion surveys

Understanding the various interactions that form among species in the necrobiome is critical and requires further examination. The best way to build this knowledge is to broaden the taxonomic breadth of studies (Barton et al. 2013a, Benbow et al. 2019). Most carrion research focuses only on a small component of the necrobiome community. For example, many entomological studies consider only certain insects, such as specific fly and beetle species that are forensically significant (Lefebvre and Gaudry 2009). Further, there are few studies that simultaneously investigate both the vertebrate and insect species associated with carrion, especially in Australia (but see: Read and Wilson 2004). Expanding the focus of entomological studies is important, as there are many insects (e.g. ants and wasps) that probably contribute to carrion decomposition processes and may shape other aspects of the necrobiome via competition and predation interactions (Archer and Elgar 2003, Eubanks et al. 2018). Sampling both vertebrates and insects around carrion is important because both contribute to central processes such as carcass removal, and because each group generally also interacts with the other in some form (Barton et al. 2013a). This may include direct interactions, as some insects, such as fire ants, may deter vertebrate use of carrion (Turner et al. 2021). It could also include indirect competitive interactions, as species from each group influence carcass removal and therefore the amount of resource available to the other group (DeVault et al. 2004).

1.7.3 Studying the necrobiome when invasive predators are present

While it is well appreciated that invasive or introduced species could have dramatic effects on carrion-centred webs (Wilson and Wolkovich 2011), few empirical studies examine these effects in great detail (but see: Abernethy et al. 2016, Bingham et al. 2018, Brown et al. 2015, Turner et al. 2021). It is crucial that we build knowledge of the impacts of invasive species on carrion necrobiomes. Studies should include investigations into the competitive and predatory interactions they share with co-occurring necrobiome community members, as well as the direct and indirect interactions they may have with carrion (e.g. by reducing or increasing decomposition rates). Finally, there also needs to be a focus on understanding of the ways in which invasive species function within the necrobiome and interact with surrounding ecosystems. Predation impacts, especially on endangered or rare species, or impacts to important ecosystem services such as pollination, should be the primary focus of this research.

1.7.4 Addressing the northern hemisphere bias

There is a focus in the literature on northern hemisphere systems, as well as systems where obligate scavengers are present (Barton et al. 2013a). As geographic region can be a major driver in scavenger communities, it is critical that more research is conducted on other continents. It is also important that more research is focused on areas where facultative scavengers dominate scavenger communities. In the past, most vertebrate scavenging research has focused on obligate scavenging communities. Facultative scavenger communities were probably ignored partly because they weren't seen as important, and also because the decline of obligate scavengers such as vultures was seen as an important conservation issue (DeVault et al. 2003, Ogada et al. 2012). Facultative scavengers can be highly efficient carrion consumers, and they also engage in other foraging strategies such as predation (DeVault et al. 2003). This raises important questions on the role of vertebrate scavengers in carrion removal (e.g. is carrion removal comparable between systems dominated by facultative scavengers compared with systems dominated by obligate scavengers?), as well as on the impacts that carrion may have on herbivores, or other potential prey animals, in surrounding ecosystems (e.g. can carrion resources have indirect impacts on rare or endangered animal species that don't associate with the resource?).

By conducting necrobiome community surveys in Australia, several other more specific research gaps can be addressed too. Research on carrion necrobiome communities in Australia is limited, especially compared with northern American, European, and African locations (Sebastián-González et al. 2020). Therefore, developing research in Australia will contribute

to general understanding of the necrobiome. Gaps in management in Australia can also be addressed. For example, little is known on how the lack of management of animal remains (i.e. the decision to leave and let lay animal carcasses) might be having on surrounding ecosystems. Carrion in Australia is produced from a variety of anthropogenic and natural sources, and carrion production is high at times. Understanding could also be developed around how species interact with carrion produced via anthropogenic sources such as via the lethal control of kangaroos. Of particular importance is the interactions that invasive predators such as the red fox, feral cat, or European wasp, may have with carrion. If these species use this resource frequently, this could have implications for the impact they have on native ecosystems (e.g. via predation). Finally, filling gaps in understanding around the importance of scavenging by apex predators in Australia could also help develop a more complete story of the potentially crucial roles they play in Australian systems. Apex predator populations are declining due to persecution by humans across the world, including in Australia (Ripple et al. 2014). Despite this, we know little of the role they play in scavenging, including how their decline or loss in systems alters carrion removal and other important ecosystem services. In Australia, there is a good breath of knowledge on the important ecosystem role that the Tasmanian devil plays as a scavenger and predator (e.g. Hollings et al. 2014, Cunningham et al. 2018), but much less is understood of the potentially important role that apex predators, and particularly dingoes, play on the mainland.

1.8 Thesis aims

The primary aim of this thesis is to build understanding of the interactions that occur between necrobiome communities and surrounding ecosystems in Australia. I address three specific aims:

1. To characterise the structure and composition of insect and vertebrate necrobiota across a range of different seasons and habitats, in the context of three diverse but contrasting bioregions (Chapters 2 and 3);
2. To investigate how the dingo, an important apex predator on mainland Australia, contributes to the removal of animal remains with respect to season, habitat, and bioregion (Chapter 4);
3. To explore some of the ways in which necrobiome communities, particularly those with invasive facultative scavengers, influence ecosystems. This includes via predation

interactions with ground nesting birds in the Simpson Desert and with blowflies in Kosciuszko National Park (Chapters 5 and 6).

1.9 Overview of thesis

In this chapter (Chapter 1), I provide a general introduction to the core subject of my thesis, the carrion necrobiome. As part of this chapter, I highlight four key gaps in carrion research, which I go on to address through my experimental thesis chapters (Chapters 2 – 6). I address the first gap (***Incorporating ecosystem context in carrion research***) by implementing a large-scale empirical survey of large animal carcasses (~30 kg) across three distinct bioregions and by also incorporating additional environmental factors including season and habitat. These bioregions represent temperate, sub-alpine and desert environments, also fulfilling an important gap in carrion research around studies in ecosystems with more extreme climatic conditions. While season and habitat have been previously explored in single systems, my work is the first to consider the role they play in shaping carrion communities and decomposition across a range of very different ecosystems. To address the second gap (***Increasing taxonomic breadth and comparisons in carrion surveys***), I simultaneously survey insect and vertebrate communities on and around animal carcasses. In my insect surveys I also include less commonly examined groups, including ants and wasps. To address the third (***Studying the necrobiome when invasive predators are present***) and fourth (***Addressing the northern hemisphere bias***) gaps, I base my carrion surveys in Australia. Studies investigating the necrobiome in Australia are limited, and this country is characterised by an abundance of invasive species that are known to associate with carrion.

The five experimental chapters of this thesis (Chapters 2 – 6) are based around standardised large-scale empirical surveys of carcasses across the three bioregions. The initial three experimental chapters (Chapter 2 – 4) use data from all three systems, while the latter two chapters (Chapters 5 and 6) present case studies involving more detailed experiments in single bioregions. In Chapters 2 and 3, I explore the structure and composition of carrion-associated insect (Chapter 2) and vertebrate (Chapter 3) communities across three broadly contrasting bioregions, while also accounting for the effects of different environmental variables, season, and habitat (Aim 1). I then continue the multi-system investigation in Chapter 4, where I go on to examine the effects of carcass use by an important Australian apex predator, the dingo, as well as the effects of different environmental variables on the decomposition of animal remains (Aim 2).

In the remaining two experimental chapters, I explore interactions between necrobiome communities, carrion resources, and surrounding ecosystems, developing complex scavenger webs (Aim 3). In Chapter 5, I investigate how vertebrate scavenging, particularly by red foxes (*Vulpes vulpes*) in the Simpson Desert, may change the ways in which these predators interact with native ground nesting birds via nest predation. In Chapter 6, I examine the potential impacts that carcass use by an introduced wasp species, *Vespula germanica*, had on a scavenger community in the Australian Alps. Specific focus is provided on the relationship between these invader wasps and native scavenging blowflies, which engage in important scavenging and pollination activities. Finally, in Chapter 7 I provide a general discussion and conclusions acquired from my work. I outline how my findings have contributed new knowledge on carrion communities in Australia and the role that environmental drivers play in shaping these communities across local and regional scales. I then go on to identify and discuss key management implications and outline potential next steps for carrion ecology research.

1.10 Acknowledgements

1.11 References

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CHAPTER 2

DRIVERS OF CARRION INSECT COMMUNITIES IN THREE CONTRASTING BIOREGIONS

Carrion beetles (Coleoptera: Silphidae) and blowflies (Diptera: Calliphoridae) pictured on the decomposing remains of an eastern grey kangaroo (*Macropus giganteus*) in Kosciuszko National Park (the Alpine bioregion). Photograph by Emma Spencer.

2.1 Abstract

Insects form abundant and diverse communities around carrion and play a central role in the decomposition of dead organic material. Their association with carrion may vary widely according to a range of environmental factors such as season and habitat, and biogeographic region. Despite this, large-scale and well-replicated studies exploring variation in carrion insect assemblages according to different environmental factors are rare, and there are none that compare multiple bioregions. In this study, we used a standardised sampling protocol and relatively large (~30 kg) experimentally positioned animal carcasses to examine carrion-associated insect communities in three contrasting desert, sub-alpine and temperate bioregions, while also accounting for the effects of season and habitat. We found that different insect groups characterised each bioregion, with beetles and flies most abundant and family-rich in the cooler temperate and sub-alpine bioregions, and ants frequenting carcasses in highest numbers in the desert bioregion. We also found that warmer seasons supported the most abundant and diverse insect communities in the temperate and sub-alpine bioregions, but that carcasses in the desert bioregion attracted more beetles and flies in the cooler season. Closed habitats were also more likely to host greater numbers of staphylinids, chloropids, and phorids, although habitat appeared to be less important in shaping carrion insect communities than season and bioregion. This study has important implications for understanding the drivers of carrion insect community structure within and among bioregions and the critical ecological role that they play as decomposers. It also highlights the importance of conducting large-scale standardised studies to reveal the different effects of local and regional drivers of carrion insect communities.

2.2 Introduction

Dead and decaying animal biomass, or carrion, is a nutrient-rich resource that is used by a range of organisms across every ecosystem on the planet (Barton et al. 2013). In terrestrial ecosystems, insects often form abundant and diverse communities around vertebrate carrion (Braack 1987). Insects consume carrion as a source of food, but also use it to complete their breeding cycles, and some insects associate with carrion to hunt for prey or to parasitise other insects (Barton et al. 2013). Insect communities are particularly effective at removing soft tissues on animal remains and thus play a central role in the decomposition of dead organic material (Payne 1965, Pechal et al. 2014). By facilitating the decomposition process, insects contribute to important ecosystem functions such as nutrient cycling and energy dispersal

(Swift et al. 1979), and their removal of animal remains may also reduce the potential for disease spillover (Sage et al. 2019). Studying the insect communities that associate with carrion, including the drivers that influence their structure and composition, is crucial to understanding this central ecological process (Barton and Evans 2017, Benbow et al. 2019).

From forensic studies, it is known that insects colonise and consume decomposing carcasses in a predictable sequence (Lefebvre and Gaudry 2009). These successional patterns are driven primarily by intense competition between the insects present on the carcass, and the decomposition stage of the carcass resource itself (Payne 1965). Carrion insect communities are also shaped by a variety of extrinsic environmental factors (Anderson 2010, Olea et al. 2019). The prevailing climatic conditions around an animal carcass, for example, can influence insects by suppressing or increasing their activity. Indeed, both temperature and rainfall influence carcass use by insects, particularly as higher temperatures and moist conditions accelerate larval activity (Archer 2004).

Across seasons, weather conditions including temperature, rainfall, and humidity all shift, which can affect insect colonisation (de Faria et al. 2018). Seasonality may therefore play a crucial role in influencing carrion-associated insect communities. The relative abundance of key carrion colonisers changes across the year (Anderson 2010), and some carrion species are only active in certain seasons as they diapause over winter or aestivate during summer. Many *Calliphora* spp. may, for example, be present only in warm weather, while other species (e.g. *Catoposchema tasmaniae*: Leiodidae and species of Phoridae) have been recorded more commonly in cool seasons (Schroeder et al. 2003, Archer and Elgar 2003). Insects better adapted to extreme heat or cold may appear in higher numbers across certain seasons too, as they gain a competitive advantage over other less hardy species. Thermophilic ants, for example, are able to outcompete other ants by foraging in the hottest parts of the day, during the middle of summer (Roeder et al. 2018). While there are some exceptions, insect abundance and diversity are generally lower in the cooler months of the year when their activity is lower (e.g. Archer & Elgar 2003, Johnson 1975).

Many insects also have specific habitat preferences, so differences in habitat may drive variation in carrion insect community structure and composition (Barton et al. 2009). For example, distinct differences exist between urban and rural habitats in terms of carrion insect communities (Kavazos and Wallman 2012). Species that can associate with humans tend to be found on carrion in more urban habitats (Anderson 2010). Habitat fragmentation also

influences insect communities, with species richness and abundance of beetles reduced in fragmented forests, and with flies more abundant in these areas (Gibbs and Stanton 2001). Similarly, some insect species are more often associated with open habitats that are exposed to the sun, while others select closed, shaded or forested areas (Anderson 2010). Associations with open and closed habitats may reflect differences in sunlight and heat as, for example, carcasses exposed to direct sunlight may be warmer, encouraging increased larval activity (Joy et al. 2006). Some associations may also reflect differences in vegetation preferences. For example, certain blowfly species have different preferences for open areas, dense cover, or intermediate coverage with scrub and sparse trees present (Macleod and Donnelly 1957). A recent study by Barton and Evans (2017) also indicated that habitat could play an important role in shaping generalist insect communities at carrion, such as ants and beetles, but a lesser role in influencing more specialist flighted insects such as flies.

Perhaps one of the most important drivers influencing carrion insect communities is geographic region, or the biogeoclimatic zone where the carcass is situated. Climate, habitat, vegetation, and soil type all vary among landscapes, regions, and continents, leading to changes in carrion insect assemblages (Anderson 2010, Barton et al. 2013, Olea et al. 2019). The decomposition of remains also varies widely across bioregions (Anderson 2010), which may then influence the insects that colonise the carcass. Insect species involved in decomposition vary from region to region, but broad insect groups, such as ants, while relatively ubiquitous, may also vary in their association with carrion across different geographic ranges (Eubanks et al. 2018). Similarly, biogeographic differences in carrion insect communities may also be shaped by the vertebrate scavenger guild present. Vertebrate scavenging can increase rates of decomposition and consequent insect colonisation (Munoz-Lozano et al. 2019). Further, vertebrate scavenger communities, and their scavenging efficiency, has been shown to vary widely across different locations (DeVault et al. 2003, Mateo-Tomás et al. 2015). Importantly, the effects of seasonality and habitat on insect communities may also differ according to bioregion. For example, in temperate bioregions most insect activity is suppressed in winter, whereas in warmer tropical bioregions insects are generally active throughout the year (Wolda 1988). Further, preferences for dense forest and open pasture habitats may differ for certain blowflies such as *Lucilia* spp. across Europe and North American bioregions (Anderson 2010).

Studies on carrion-associated insect communities have focused primarily on documenting species visitation patterns, usually for potential forensic applications (Tomberlin et al. 2011). There is far less research on the ecology of these communities, although there are several

foundational (Fuller 1934, Bornemissza 1957, Payne 1965, Coe 1978, Schoenly and Reid 1987, Braack 1987) and more recent (Barton et al. 2013, Barton and Evans 2017) studies that do focus on this subject. As in most community studies, however, the ecological surveys conducted are typically not directly comparable; they have sampled different subsets of the fauna at different temporal and spatial scales and have used different methods. Further, some of these studies have also been limited in other aspects such as replication, or are restricted to surveys of particular environments, such as temperate forest habitats (Barton et al. 2013). These limitations not only restrict our ability to draw generalised conclusions and contribute to overarching understanding of carrion communities and decomposition processes (e.g. the necrobiome framework; Benbow et al. 2019), but have perhaps also introduced a foundational bias in how we understand carrion insect communities (Anderson 2010). It is important we address this bias, as it influences not only the assumptions we make about the role of carrion in supporting insect biodiversity, but also our understanding of how different insects contribute to important ecological processes like decomposition.

In this study we use a standardised sampling protocol and relatively large (~30 kg) experimentally positioned vertebrate animal carcasses to examine the communities of insects associating with carrion in three disparate bioregions, while also accounting for seasonal and habitat effects. We address the following overarching questions: (i) how do carrion insect communities differ across contrasting bioregions, and (ii) do the effects of season and habitat on insect communities vary across these bioregions? We surveyed insects at kangaroo carcasses in desert, sub-alpine and temperate bioregions in Australia, and replicated our surveys within each bioregion in warmer and cooler temperatures, and in open and closed (treed) habitat. We expected marked differences in the abundance, composition, and diversity of insects across bioregions, as they differ dramatically in terms of vegetation, productivity, climate, and scavenger guilds. However, we also anticipated that insect communities would be most comparable between the temperate and sub-alpine bioregions, as these locations probably share greatest similarity in terms of habitat and climatic conditions. We also expected that there would be bioregional and local trends for warmer seasons to host greater abundances and richness of insects. Finally, we anticipated variation in the effect of habitat on different insect taxa. Specifically, we predicted that habitat would have a weaker effect on more mobile insects such as vagile flies, whereas ground-active beetles and ants would show greater habitat preferences (e.g. as for Barton and Evans 2017). Our study is the first to examine insect assemblages associated with vertebrate carrion at large spatial scales across multiple

bioregions, seasons, and habitats in a standardised way, and thus contributes new insights into the drivers of insect diversity and heterogeneity around carrion in ecosystems.

2.3 Materials and Methods

2.3.1 Study bioregions

Fieldwork was conducted in three contrasting biogeographic regions in Australia: (i) the Wolgan Valley, Newnes, eastern New South Wales (hereafter the Forest bioregion; 33°14'S, 150°10'E; 50 km^2; 540–680 m a.s.l), (ii) the Snowy and Botherum Plains in Kosciuszko National Park, southern New South Wales (hereafter the Alpine bioregion; 36°14'S, 148°32'E; 70 km^2; 1305–1540 m a.s.l) and (iii) Ethabuka Reserve in the Simpson Desert, western Queensland (hereafter the Desert bioregion; 23°51'S, 138°28'E; 80 km^2; 65–120 m a.s.l) (Figure 2.1).

The Forest bioregion lies on the edge of the Greater Blue Mountains National Park and contains a mix of temperate open woodland and grassland habitats, with various *Eucalyptus* species (e.g. *E. viminalis* and *E. haemastoma*) and a mix of native (e.g. *Austrodanthonia* sp. and *Themeda triandra*) and introduced (e.g. *Microlaena stipoides*) grasses. The climate is temperate, with average maximum temperatures of 27°C recorded in January and 11°C in July (nearest station 30 km away at Lithgow, records from 1878 - 2020; Bureau of Meteorology 2020)

The Alpine bioregion is situated in the eastern section of Kosciuszko National Park and contains sub-alpine and montane forests and open grasslands. The dominant vegetation in the open grasslands is snow grass (*Poa* sp.), with non-native grass species including *Anthoxanthum odoratum* also abundant. Snow gums (*Eucalyptus pauciflora*) are the most common tree species in the sub-alpine and montane forests. The average maximum temperature ranges from 23°C in January to –6°C in July (nearest station 20 km away at Perisher Valley, records from 2010 - 2020; Bureau of Meteorology 2020).

The Desert bioregion is located on the edge of the Simpson Desert and is a conservation property managed by Bush Heritage Australia. The Simpson Desert is a hot desert, characterised by long, parallel sand dunes (Purdie 1984) and the prevailing habitat is hummock grassland dominated by hard spinifex (*Triodia basedowii*) (Wardle et al. 2015). There are differences in vegetation between the sand dune crests and the inter-dune valleys, with the crests lacking tree cover and the valleys host to stands of gidgee trees (*Acacia georginae*). The
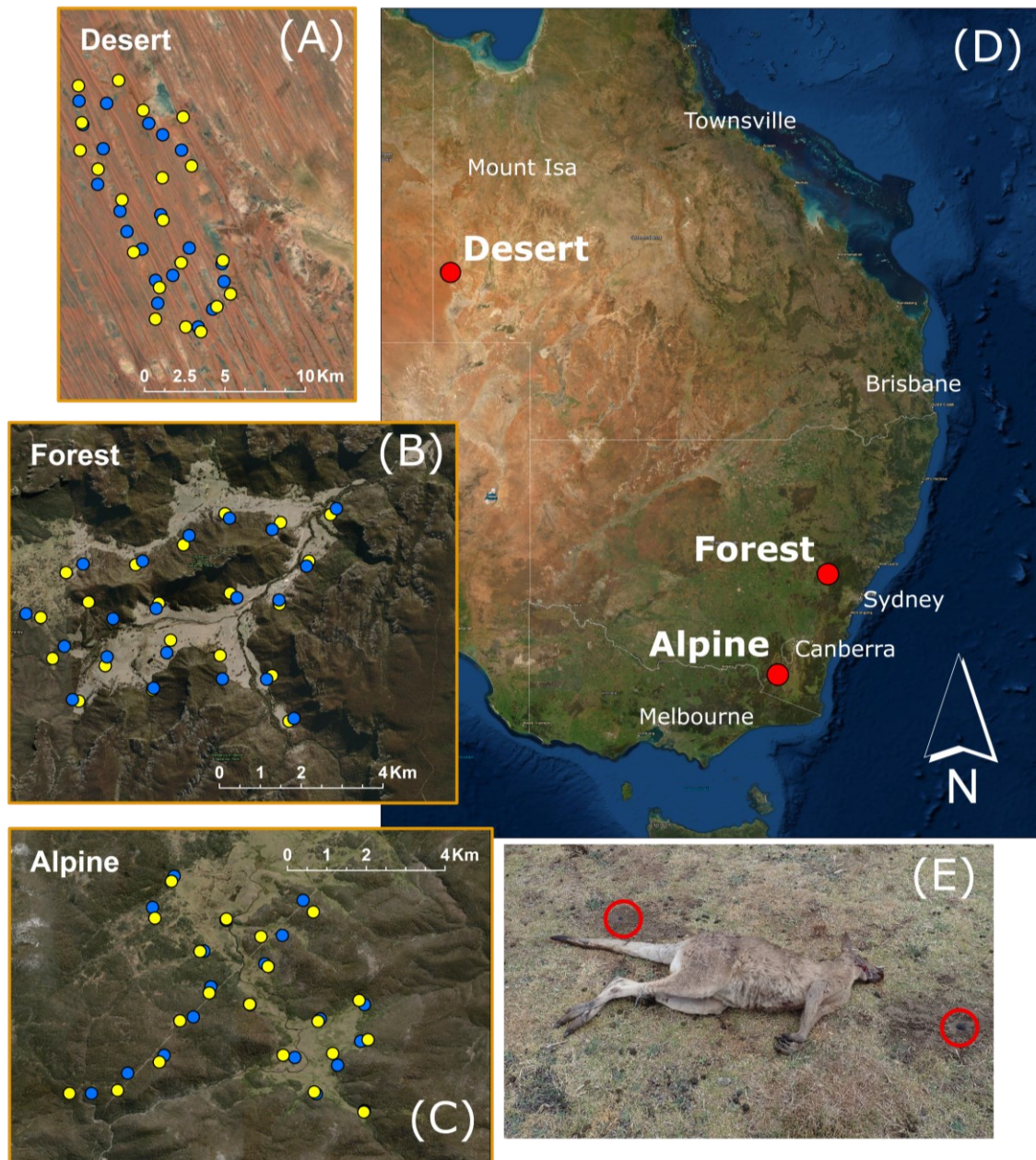
Figure 2.1 Study area map and carcass site set-up (n = 120); satellite images show carcass site spatial spread in the Desert bioregion (A), at Ethabuka Reserve in the Simpson Desert, western Queensland, the Forest bioregion (B), in the Wolgan Valley, in the Blue Mountains, central NSW, and the Alpine bioregion (C), at the Snowy and Botherum Plains in National Park, south-eastern NSW. Yellow dots signify carcasses positioned in the warm seasons (n = 20/bioregion), while blue dots signify carcasses positioned in the cool seasons (n = 20/bioregion). The location of the three study sites in Australia are shown in (D). (E) provides an example carcass site set-up with the two insect pitfall traps (circled in red) positioned at the front and rear of the staked kangaroo carcass.

climate is arid, with the hottest month, January, averaging maxima of 40°C and the coolest month, June, averaging maxima of 23°C (nearest station 100 km away at Bedourie, records from 1988 - 2020; Bureau of Meteorology 2020).

At each location, 40 sites were selected to distribute animal carcasses. These sites were further divided across seasons, such that 20 carcasses were surveyed in a "warm" season and 20 in a "cool" season. Specifically, in the Forest bioregion carcasses were positioned in summer (warm season; January – February 2019) and winter (cool season; July – August 2019), in the Alpine bioregion carcasses were positioned in summer (December – January 2018) and in autumn (March – April 2018), and in the Desert bioregion carcasses were positioned in spring (October – November 2018) and winter (June – July 2018). Carcass sites were further selected to represent two distinct habitat types in each bioregion, with half placed in 'open' and half placed in 'closed' canopy habitats during each survey. In the Forest and Alpine bioregions, this included an even mix of grassland (open) and woodland (closed) habitats. In the Desert site, this included an even mix of dune crest (open) and valley (closed) habitats. Open canopy habitats lacked canopy cover and were at least 50 m from any densely forested or vegetated land. Closed canopy habitats had more than 20% canopy cover. We tried to ensure that these closed canopy sites were at least 50 m from any open space; however, this was not possible in the Desert bioregion due to the low density of trees. Within each bioregion and season, carcasses were separated by a minimum distance of 1 km to mitigate scent travel between carcasses. Carcass sites between seasons were separated by at least 200 m (Figure 2.1), and placements were unlikely to have had any marked effect on each other because the time between study seasons was more than 4 months and only bones remained at old carcass sites.

2.3.2 Carcasses and insect sampling

We sourced dead, adult eastern grey kangaroos (*Macropus giganteus*; Forest and Alpine bioregion) or dead adult red kangaroos (*Osphranter rufus;* Desert bioregion) from nearby management culls. All kangaroo carcasses were intact, generally only with a single bullet wound to the head. Carcasses displaying evidence of disease (e.g. heavy parasite loads) were not used. Each carcass was weighed (precision: ± 50 g) and placed into the field without freezing within 24 hours (warm period) or 36 hours (cool period) of collection. As carcass size can influence insect colonization (Moretti et al. 2008) and was not a variable of interest in this study, we tried to preferentially select dead kangaroos that weighed between 20 – 30 kg. Carcasses were left accessible to scavenging by vertebrates, and to prevent complete removal

of the carcasses, each carcass was secured to the ground by a wire attaching the neck and Achilles tendon of the animal to two metal stakes spaced ~0.6 m apart. Scientific licenses and permits were obtained to relocate the kangaroo carcasses (SL 101901 and SPP WA0006737) and all research was approved by the University of Sydney Animal Ethics Committee (Project number: 2017/1173).

We sampled insects using two pitfall traps at each carcass, such that one pitfall trap was positioned adjacent to the anus and one next to the mouth of the carcass (Figure 2.1e). Pitfall traps were 120 ml in volume (40 mm in diameter) and were filled with 60 ml ethylene glycol solution. To capture the diversity of insects associated with early and later-stage decomposition, pitfall traps were deployed over two time periods that included the first three days of week 1 (early stage) and week 3 (later stage) following the deployment of the carcasses. We removed all adult flies, beetles, ants, and wasps from each trap, and then counted each. We identified flies and beetles to family level but grouped all wasps and all ants, separately, for analyses. We chose to collect and identify these insect groups because they appeared in high abundance in pitfall traps at one or more of our study bioregions and have been associated with vertebrate carrion and the decomposition process in previous studies (Barton et al. 2013, Olea et al. 2019). Identification of beetles and flies to family, rather than species or morphospecies, was used because of the high variability in species across each of the three bioregions, and because family-level data were adequate to answer the ecological questions posed by this study. Identifications were made using appropriate keys (CSIRO 1991, Hangay and Zborowski 2010, Kavazos et al. 2011) and a reference collection was established.

2.3.3 Statistical analyses

To address our main study questions and to determine how carrion-associated insect communities varied by bioregion, season, and habitat, we first analysed the abundance of the four main insect groups (i.e. beetles, flies, ants, and wasps) collected in pitfall traps. Second, we conducted more detailed analyses on the beetle and fly groups (as they are the most common groups), considering measures of family richness, composition, and abundance.

Before conducting statistical analyses, we excluded all data points where pitfall traps were disturbed (i.e. filled with rain or dirt or removed or emptied by vertebrates). Then, to prevent bias towards insect groups that associate with either early or later decomposition stages, we also excluded all data points from carcasses where both pitfall traps were disturbed in either the early stage (week 1) or the later stage (week 3) sampling periods. For example, if two pitfall

traps were disturbed in the early stage sampling period at a given carcass, all pitfall traps at that carcass site (i.e. including the two pitfall traps collected in the later stage sampling period) would be excluded. We then standardised our results, to assign a single value for every insect group or family examined, across each carcass. These values were calculated by determining the total number of individuals within each insect group or family, collected during each sampling period at each carcass. We then divided these numbers by the total number of undisturbed pitfalls collected at that carcass site during that sampling period. Finally, we added these data for each carcass, across both of the sampling periods to obtain one value for each carcass site (n = 117). All analyses and all figures in the results reflect this "standardised carcass site" metric. We conducted all analyses in R version 4.0.2 (R Development Core Team 2020).

2.3.4 Insect group abundance

We compared differences in abundance for the key insect groups, including (i) beetles, (ii) flies, (iii) ants, and (iv) wasps. To explore how bioregion, season and habitat affected the abundance of these different groups at carcasses, we constructed generalised linear models (GLMs) of abundance for each group (total of 4 separate GLMs) using the negative binomial distribution, and bioregion (Alpine, Forest, Desert), season (cool, warm), and habitat (open, closed) as fixed effects (Package: lme4; Bates et al. 2015) (Package: MASS; Ripley et al. 2021). The negative binomial distribution was used because data were overdispersed for each and because quasi-Poisson models did not produce acceptable residual versus fitted plots. We interpreted models fitted with all possible parameters and the bioregion × season and bioregion × habitat interactions. We used Holm-Bonferroni log-rank *post hoc* analyses to investigate differences in insect abundances across the three bioregions, and the interaction terms bioregion × season and bioregion × habitat (Package: emmeans; Russell et al. 2021). We also visually assessed model-predicted values against residual values to confirm that all models met their necessary assumptions.

2.3.5 Fly and beetle family richness, composition, and abundance

We calculated beetle and fly family richness separately, by summing the number of fly and beetle families we sampled at each carcass. To determine how bioregion, season and habitat affected beetle and fly family richness, we constructed two separate GLMs of either fly or beetle family richness with a Poisson distribution and a log-link function, and bioregion (Forest, Alpine and Desert), season (cool, warm) and habitat (open, closed) as fixed effects.

We also included the two interaction terms bioregion × season, and bioregion × habitat. *Post hoc* analyses were used to investigate differences in species richness and abundance across the three bioregions, and the interaction terms, and were calculated using Holm-Bonferroni log-rank tests. We visually assessed model-predicted values against the residual values to confirm that all models met their necessary assumptions.

To determine how bioregion, season, and habitat affected community composition, we conducted multivariate analyses on the beetle and fly families separately. To do this, we first constructed a matrix of site (carcass) × families (fly or beetle families) using the abundance of individuals sampled within each fly or beetle family, recorded at each carcass site. Before conducting these analyses, we excluded any family groups with less than 5% representation at carcasses across all study bioregions. We also removed any pitfall traps where no beetle (n = 1; for the beetle family composition analysis) or fly family (n = 4; for the fly family composition analysis) groups were captured. To decrease the influence of highly abundant families, family group abundances were square-root transformed. We modelled bioregion, season, and habitat against differences in species composition using permutational multivariate analysis of variance (PERMANOVA) via *adonis* (Package: vegan; Oksanen et al. 2012). Differences were calculated using the Bray-Curtis metric because this excludes joint species absences in the calculation of pair-wise similarity. We permuted dissimilarities within seasons 999 times to assess significance. We used Holm-Bonferroni *post hoc* analyses to investigate differences in the composition of beetles and flies across the three bioregions, and the interaction terms bioregion × season and bioregion × habitat. We investigated significant main effects further using non-metric multidimensional scaling (nMDS). We further explored family composition by calculating the percentage occurrence for every fly and beetle family documented visiting carcasses across the different bioregions, seasons, and habitats. Percentage occurrence of fly and beetle families was calculated as the number of carcasses at which a family occurred, divided by the total number of carcasses.

Finally, we compared differences in abundance for key beetle and fly family groups, which we selected based on abundance. Specifically, we selected the top four most abundant family groups that were also present across all three bioregions (i.e. beetle families: Trogidae, Staphylinidae, Histeridae, Dermestidae, and fly families: Calliphoridae, Muscidae, Phoridae, Chloropidae). To explore how bioregion, season and habitat affected the abundance of these families, we constructed GLMs of abundance for each (total of 8 separate GLM models) using the negative binomial distribution and a log-link function, and bioregion (Forest, Alpine,

Desert), season (cool, warm) and habitat (open, closed) as independent variables. The negative binomial distribution was again used because the data were overdispersed. We interpreted models fitted with all possible parameters and the bioregion × season, and bioregion × habitat interactions. Where data were limited across certain seasons within bioregions (i.e. for staphylinids, dermestids and chloropids), we removed interactions until we obtained a model that reached convergence. We used Holm-Bonferroni log-rank *post hoc* analyses to investigate differences in abundance across the three bioregions, and the interaction terms bioregion × season and bioregion × habitat. Model-predicted values were visually assessed against residual values to confirm that each model met the necessary assumptions.

2.4 Results

In total, we identified 7,950 individual beetles, 4,105 flies, 66,756 ants and 1,145 wasps, totalling 79,956 individuals from 480 insect pitfall traps positioned on 120 kangaroo carcasses (see section 2.8 Supplementary Information: Table S1 for standardised insect group/family abundances). We also identified 20 beetle families and 17 fly families. In total, only 15 pitfall traps were disturbed in some way (3.1% of total pitfall traps) and had to be removed from analyses. They were, however, generally well-spaced across the bioregions with 4 traps disturbed in the Alpine, 3 in the Forest and 8 in the Desert bioregion. Kangaroo carcasses weighed on average ($\alpha \pm$ se) 27 ± 1 kg (n = 120; range: 15 – 54 kg), with 71% of carcasses (n = 85) weighing 20 – 30 kg.

2.4.1 Insect group abundance

Fly and beetle abundances were higher in the warm than the cool season, and in the closed compared to the open habitat (Figure 2.2; Table 2.1). Wasp abundance was higher in the cool than the warm season, and in the closed compared to the open habitat, and ant abundance was similar across season and habitat (Figure 2.2; Table 2.1). *Post hoc* Holm-Bonferroni log-rank tests indicated that there were more beetles, flies and wasps in the Alpine compared to the Forest (beetle/fly/wasp: p < 0.001) and the Desert bioregions (beetle: p = 0.002, fly/wasp: p < 0.001), but that fly abundance was higher in the Forest compared to the Desert bioregion (p = 0.024) while beetle and wasp abundances were similar between these bioregions (beetle: p = 0.698; wasp: p = 0.622) (Figure 2.2). Ant abundance, on the other hand, was higher in the Desert compared to the Alpine (p < 0.001) and the Forest bioregions (p < 0.001) and was similar across the Alpine and Forest bioregions (p = 0.632) (Figure 2.2).
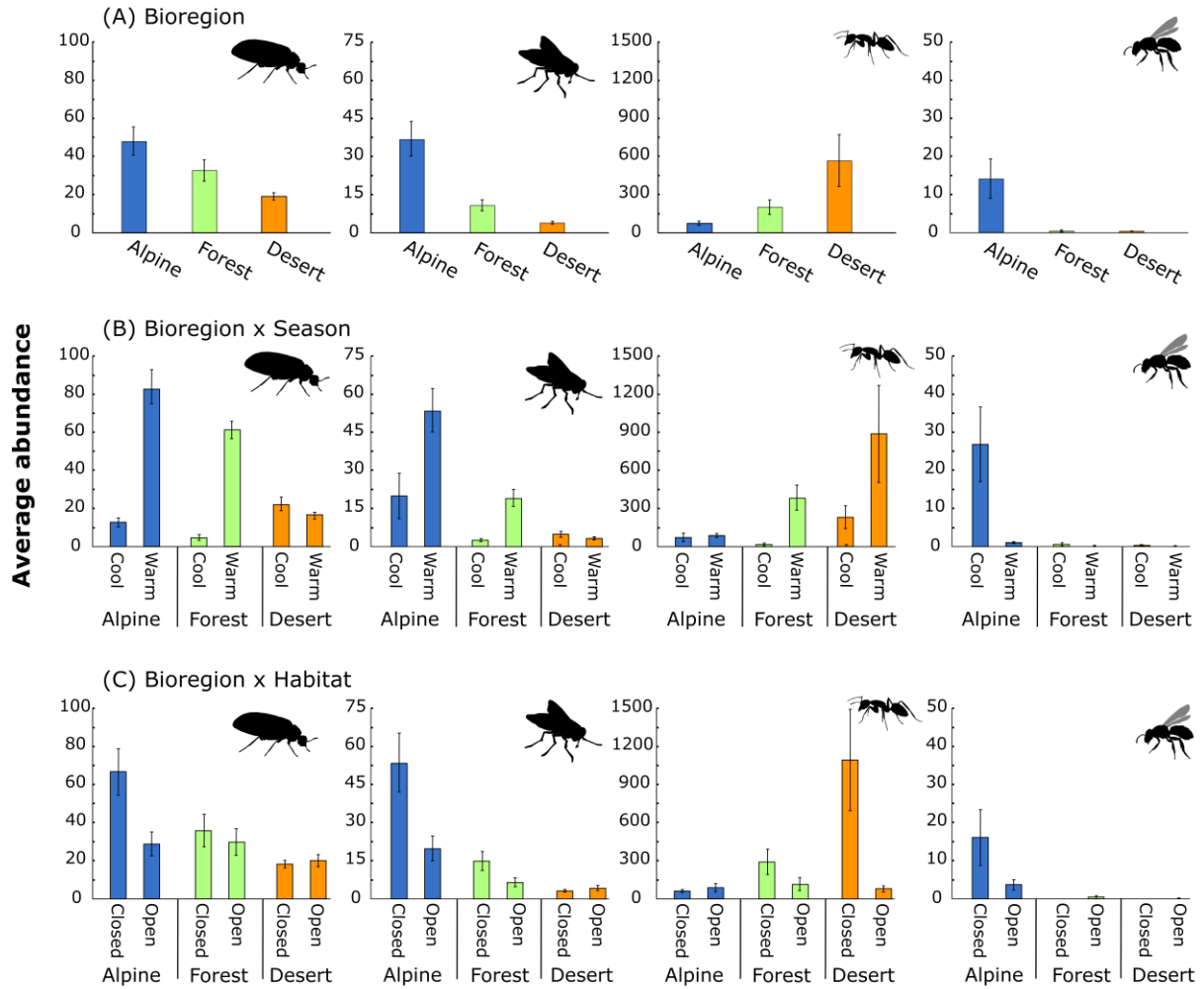
Figure 2.2 Average abundance (± standard error) of taxonomic groupings per standardised carcass site, including beetles (figures on left), flies (figures on middle left), ants (figures on middle right), and wasps (figures on right), across different bioregions (A), different seasons within different bioregions (B) and different habitats within different bioregions (C).

Table 2.1 Results of generalised linear models (GLMs) testing for differences in fly, beetle, ant, and wasp abundance, across different bioregions, seasons, and habitats.

Response variable	Effect	Estimate	Std. error	z-value	p
Beetle abundance	(Intercept)	2.897	0.154	18.82	<0.001*
	Bioregion [Desert]	0.195	0.221	0.88	0.377
	Bioregion [Forest]	-1.184	0.236	-5.03	<0.001*
	Season [Warm]	1.901	0.177	10.73	<0.001*
	Habitat [Open]	-0.905	0.176	-5.13	<0.001*

	Bioregion [Desert] × Season [Warm]	-2.204	0.252	-8.74	<0.001*
	Bioregion [Forest]× Season [Warm]	0.624	0.266	2.35	0.019*
	Bioregion [Desert] × Habitat [Open]	0.936	0.252	3.72	<0.001*
	Bioregion [Alpine] × Habitat [Open]	0.651	0.260	2.50	0.012*
Fly abundance	(Intercept)	3.284	0.192	17.08	<0.001*
	Bioregion [Desert]	-1.835	0.305	-6.02	<0.001*
	Bioregion [Forest]	-1.984	0.303	-6.56	<0.001*
	Season [Warm]	1.403	0.225	6.24	<0.001*
	Habitat [Open]	-1.403	0.225	-6.24	<0.001*
	Bioregion [Desert] × Season [Warm]	-1.707	0.350	-4.88	<0.001*
	Bioregion [Forest]× Season [Warm]	0.576	0.351	1.64	0.101
	Bioregion [Desert] × Habitat [Open]	1.587	0.350	4.53	<0.001*
	Bioregion [Alpine] × Habitat [Open]	0.596	0.345	1.73	0.084
Ant abundance	(Intercept)	3.298	0.238	13.89	<0.001*
	Bioregion [Desert]	2.191	0.341	6.42	<0.001*
	Bioregion [Forest]	-0.940	0.340	-2.77	0.006*
	Season [Warm]	0.165	0.274	0.60	0.548
	Habitat [Open]	0.465	0.274	1.70	0.089
	Bioregion [Desert] × Season [Warm]	0.993	0.389	2.55	0.011*
	Bioregion [Forest]× Season [Warm]	2.763	0.394	7.01	<0.001*
	Bioregion [Desert] × Habitat [Open]	-2.892	0.389	-7.44	<0.001*
	Bioregion [Alpine] × Habitat [Open]	-0.523	0.394	-1.33	0.184
Wasp abundance	(Intercept)	3.017	0.305	9.88	<0.001*
	Bioregion [Desert]	-5.449	0.829	-6.57	<0.001*
	Bioregion [Forest]	-6.744	1.483	-4.55	<0.001*
	Season [Warm]	-3.189	0.413	-7.72	<0.001*

Habitat [Open]	-1.313	0.394	-3.33	0.001*
Bioregion [Desert] × Season [Warm]	2.585	1.033	2.50	0.012*
Bioregion [Forest]× Season [Warm]	-0.003	1.573	-0.002	0.999
Bioregion [Desert] × Habitat [Open]	1.397	1.003	1.39	0.164
Bioregion [Alpine] × Habitat [Open]	4.505	1.569	2.87	0.004*

Post hoc Holm-Bonferroni log-rank tests indicated that there were more beetles and flies in warm compared to cool seasons in the Alpine bioregion (beetle/fly: p < 0.001) and the Forest bioregion (beetle/fly: p < 0.001), but that wasp abundance on carcasses was higher in the cool compared to the warm season in the Alpine bioregion (p < 0.001) and in the Forest bioregion (p = 0.036) (Figure 2.2). On the other hand, fly, beetle, and wasp abundances were similar across seasons in the Desert bioregion (beetle: p = 0.092, fly: 0.257, wasp: p = 0.523) (Figure 2.2). Ant abundance was higher in the warm season in both the Desert (p < 0.001) and the Forest bioregions (p < 0.001) but was similar across seasons in the Alpine bioregion (p = 0.548) (Figure 2.2). There were more beetles, flies, and wasps in closed compared to open habitat in the Alpine bioregion (beetle/fly/wasp: p < 0.001) (Figure 2.2). There were also more flies in closed compared to open habitat in the Forest bioregion (flies: p = 0.002, wasps: p = 0.036), and there were more ants in closed compared to open habitat in the Desert bioregion (p < 0.001) (Figure 2.2). There were more wasps in open compared to closed habitat in the Forest bioregion (wasps: p = 0.036) (Figure 2.2). Beetle and ant abundances were similar across habitats in the Forest bioregion (beetle: p = 0.185, ant: p = 0.838), and beetle, fly, and wasp abundance were similar across habitats in the Desert bioregion (beetle: p = 0.863, fly: p = 0.493, wasp: p = 0.928) (Figure 2.2). Finally, ant abundance was similar across habitats in the Alpine bioregion (p = 0.089) (Figure 2.2).

2.4.1.1 Family richness

Across all sites combined (n = 117), the mean combined fly and beetle family richness was (α ± s.e.) 8.3 ± 0.4 (range 1–18) at each carcass site. Combined beetle family richness was 4.5 ± 0.2 (range 1–10) at each carcass site and combined fly family richness was 3.8 ± 0.21 (range 0–9) at each carcass site. The GLMs testing differences in beetle and fly family richness both showed that warm seasons were associated with higher mean family richness than cool seasons,

and that closed habitat had higher family richness than open habitat (Figure 2.3; Table 2.2). *Post hoc* Holm-Bonferroni log-rank tests indicated that beetle and fly family richness was higher in the Alpine compared to the Desert bioregion (beetle/fly: $p < 0.001$) (Figure 2.3). Fly family richness was also higher in the Forest than the Desert bioregion ($p < 0.001$), while beetle family richness was similar between these bioregions ($p = 0.188$) (Figure 2.3). Both beetle and fly family richness were similar between the Forest and Alpine bioregions (beetle: $p = 0.058$, fly: $p = 0.355$) (Figure 2.3). Beetle and fly family richness in the Forest and the Alpine bioregions were higher in the warm compared to the cool seasons (Beetles-Forest: $p < 0.001$, Flies-Forest: $p < 0.001$ and Beetles-Alpine: $p < 0.001$, Flies, Alpine: $p < 0.001$), but there were no differences between cool and warm seasons for the Desert bioregion (Beetles: $p = 0.484$, Flies: $p = 0.651$) (Figure 2.3). There were no differences in beetle family richness between closed and open habitats in any of the bioregions (Alpine: $p = 0.228$, Forest: $p = 0.905$, Desert: $p = 0.384$) (Figure 2.3). Similarly, there were no differences in fly family richness between closed and open habitats in the Forest ($p = 0.275$) and Desert bioregions ($p = 0.366$) but fly family richness was greater in closed than in open habitats in the Alpine bioregion ($p = 0.012$) (Figure 2.3).

2.4.1.2 Composition

For both fly and beetle composition, the greatest dissimilarity occurred across study bioregion (flies; $R^2 = 0.273$ and beetles; $R^2 = 0.419$), habitat explained the least dissimilarity (flies; $R^2 = 0.061$ and beetles; $R^2 = 0.028$). The beetle and fly assemblages differed significantly among bioregions (PERMANOVA: $F_{(2, 104)} = 31.67$, $p = 0.001$ and $F_{(2, 107)} = 75.82$, $p = 0.001$, respectively), with pairwise tests indicating significant differences between all study areas for both fly family composition and beetle family composition (all p-values; $p = 0.003$). Season influenced both beetle (PERMANOVA: $F_{(1, 104)} = 11.94$, $p = 0.001$) and fly assemblages (PERMANOVA: $F_{(1, 107)} = 37.47$, $p = 0.001$). There were also significant interactions between bioregion and season for flies (PERMANOVA: $F_{(1, 104)} = 16.76$, $p = 0.001$) and beetles (PERMANOVA: $F_{(1, 107)} = 22.34$, $p = 0.001$), although pairwise tests showed differences across seasons in all bioregions (all p-values; $p = 0.003$). Finally, interactions occurred between bioregion and habitat for flies (PERMANOVA: $F_{(2, 104)} = 2.44$, $p = 0.013$) and beetles (PERMANOVA: $F_{(2, 107)} = 5.29$, $p = 0.001$), although pairwise tests showed differences in fly and beetle family composition across open and closed habitats in the Alpine bioregion (all p-values; $p = 0.003$), but only in fly family composition across habitat in the Desert bioregion

(flies; p = 0.004 and beetles; p = 0.457); neither fly nor beetle family composition varied in the Forest bioregion (flies; p = 0.123 and beetles; p = 0.058).
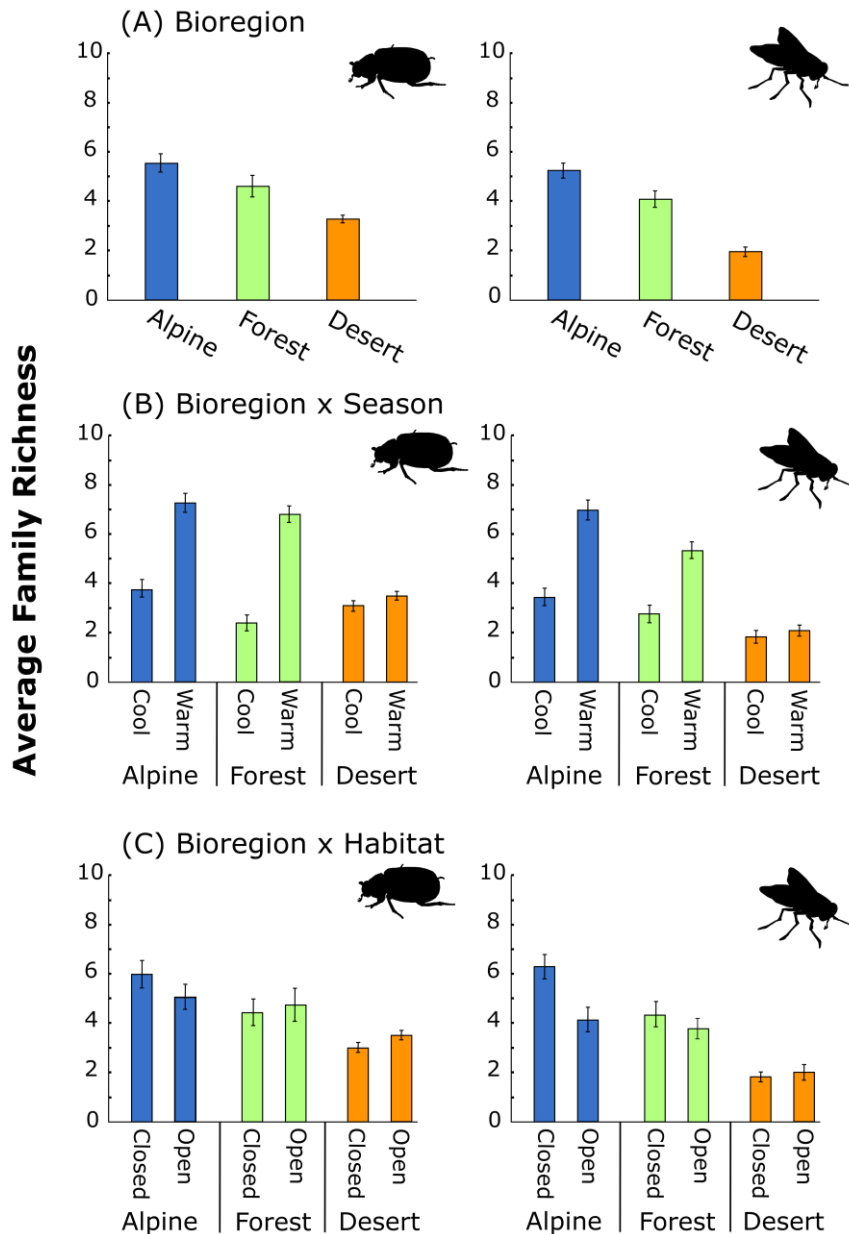
Figure 2.3 Average family richness (± standard error) of beetles (figures on left) and flies (figures on right) per standardised carcass site, across different bioregions (A), different seasons within different bioregions (B) and different habitats within different bioregions (C).

Table 2.2 Results of generalised linear models (GLMs) testing for differences in beetle and fly family richness, across different bioregions, seasons, and habitats.

Response variable	Effect	Estimate	Std. error	z-value	p
Beetle family richness	(Intercept)	1.413	0.130	10.84	<0.001*
	Bioregion [Desert]	-0.364	0.210	-1.74	0.083*
	Bioregion [Forest]	-0.537	0.210	-2.56	0.010*
	Season [Warm]	0.653	0.141	4.62	<0.001*
	Habitat [Open]	-0.163	0.135	-1.21	0.228
	Bioregion [Desert] × Season [Warm]	-0.529	0.226	-2.34	0.019*
	Bioregion [Forest]× Season [Warm]	0.385	0.223	1.73	0.084
	Bioregion [Desert] × Habitat [Open]	0.317	0.223	1.42	0.155
	Bioregion [Alpine] × Habitat [Open]	0.181	0.202	0.89	0.372
Fly family richness	(Intercept)	1.407	0.135	10.45	<0.001*
	Bioregion [Desert]	-0.719	0.244	-2.94	0.003*
	Bioregion [Forest]	-0.301	0.204	-1.47	0.140
	Season [Warm]	0.570	0.151	3.78	<0.001*
	Habitat [Open]	-0.371	0.147	-2.52	0.012*
	Bioregion [Desert] × Season [Warm]	-0.464	0.278	-1.67	0.095
	Bioregion [Forest]× Season [Warm]	0.094	0.227	0.41	0.679
	Bioregion [Desert] × Habitat [Open]	0.160	0.276	0.58	0.563
	Bioregion [Alpine] × Habitat [Open]	0.195	0.218	0.89	0.372

Fly family nMDS plots showed clear separation between the Desert and Alpine bioregions, with overlap between the Forest and Alpine bioregions and some overlap between the Forest and Desert bioregions (Figure 2.4). Similarly, beetle family plots showed clear separation between the Desert and Alpine bioregions and overlap between the Forest and Alpine bioregions. For the beetle family plots, separation between bioregions was more defined in contrast to fly composition, particularly between the Alpine and Forest bioregions and the Desert bioregion (Figure 2.5). Seasonal separation within bioregions was far clearer than habitat separation in the nMDS plots for both flies and beetles, with seasonal separation in the nMDS plots also most distinct for the beetles compared with the flies (see section 2.8 Supplementary Information: Figure S1). The percentage occurrence of species results indicated

(A) Fly families - Bioregion x season

(B) Fly families - Bioregion
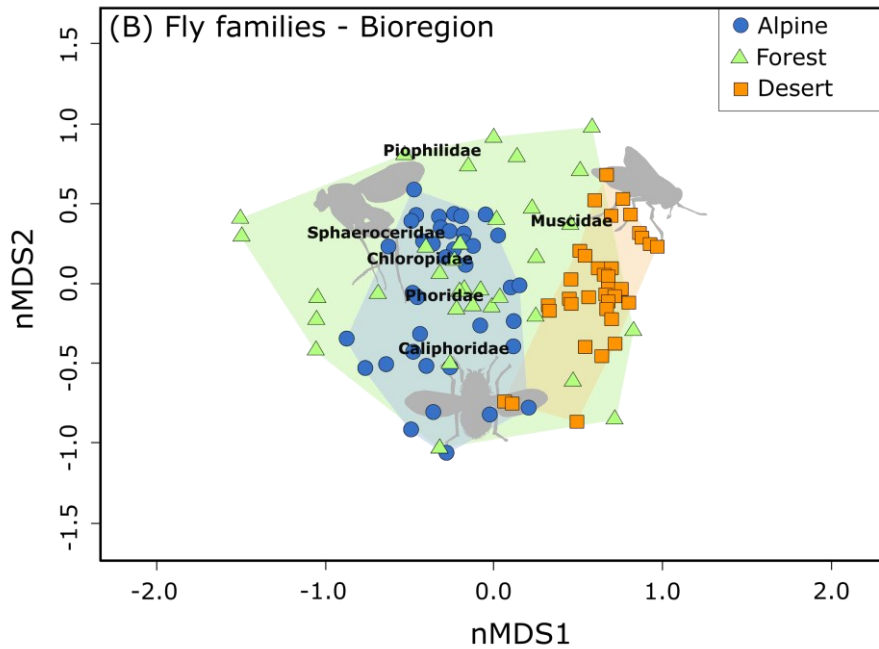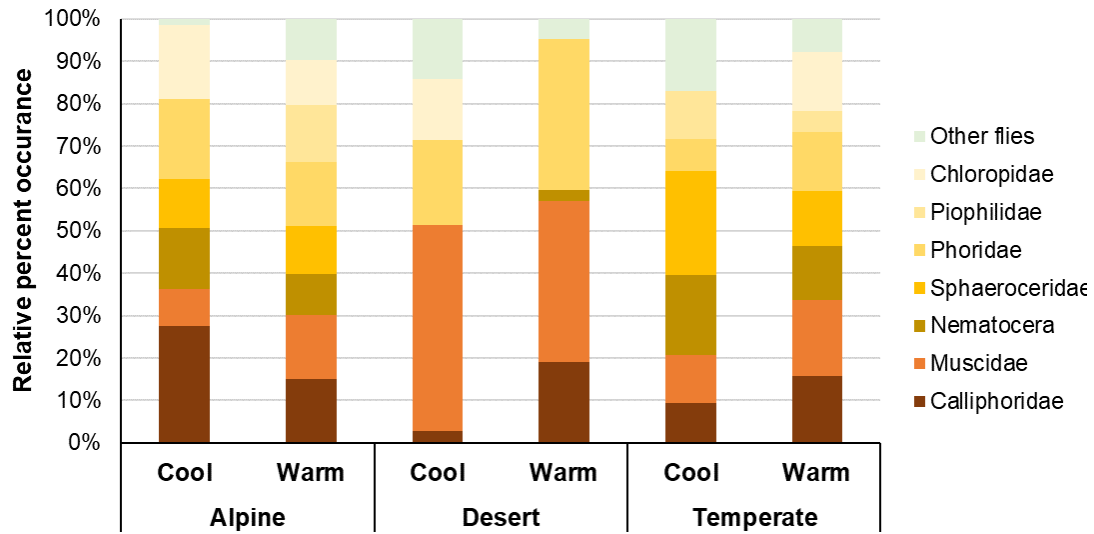
Figure 2.4 Composition of insect communities at kangaroo carcasses across different seasons (cool, warm) and bioregions (Alpine, Forest, and Desert) for fly families. Bar plot shows occurrence (as percentage relative to the sum of all the occurrence frequencies at each season and bioregion; A). nMDS plot shows the similarity of the carrion-associated insect communities considering the families groups with more than 5% representation at carcasses across all study bioregions. (B).

(A) Beetle families - Bioregion x season
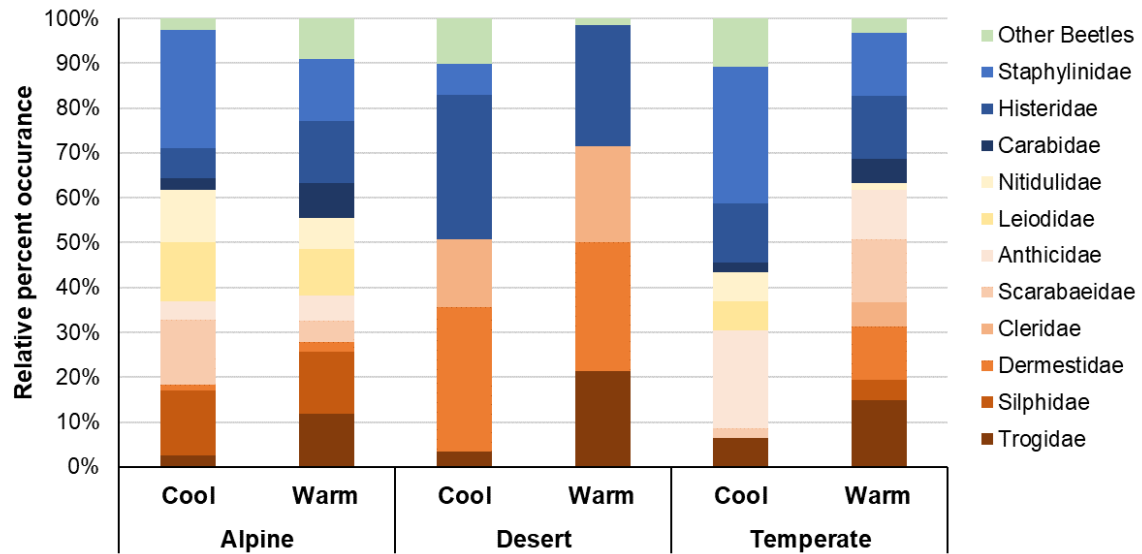
Figure 2.5 Composition of insect communities at kangaroo carcasses across different seasons (cool, warm) and bioregions (Alpine, Forest, and Desert) for beetle families. Bar plot shows occurrence (as percentage relative to the sum of all the occurrence frequencies at each season and bioregion; A). nMDS plot shows the similarity of the carrion-associated insect communities considering the families groups with more than 5% representation at carcasses across all study bioregions (B).

that in the warmer season, in the Forest bioregion, Calliphoridae (13.7%), Muscidae (15.4%), as well as Trogidae (16.2%), Staphlinidae, Scarabaeidae and Histeridae (all 15.4%) occurred on carcasses frequently, while in cooler seasons only Staphlinidae (12.0%) and Sphaeroceridae (11.1%) were frequent carcass visitors. In the Alpine bioregion, in both seasons, Calliphoridae (warm: 16.2%, cool: 17.1%), and Staphlinidae (warm and cool: 17.1%) occurred on carcasses frequently, while Muscidae, Phoridae, Histeridae and Silphidae (all 17.1%) frequented carcasses in the warm season only. In both the warm and cool season in the Desert bioregion, Muscidae (warm: 13.7%, cool: 14.5%), Histeridae (warm and cool: 16.2%), and Dermestidae (warm: 16.2%, cool: 17.1%) occurred on carcasses most frequently.

2.4.1.3 Family abundance

Among the beetles, Staphylinidae and Histeridae abundance was highest in the warm seasons and in closed habitat, although Trogidae and Dermestidae abundance was highest in the warm seasons, but similar across habitat types (Table 2.3, see section 2.8 Supplementary Information: Table S1). Trogids and dermestids were more abundant in the Desert compared to the Forest

bioregion (Trogids: p = 0.008; p < 0.001), and dermestids were also more abundant in the Desert compared to the Alpine bioregion (p < 0.001) and in the Forest compared to the Alpine bioregion (p = 0.002). There were more staphylinids and histerids in the Alpine compared to the Forest bioregion (staphylinids: p < 0.001; histerids: p = 0.024) and more staphylinids also in the Alpine compared to the Desert bioregion (p < 0.001). Trogids were more abundant in the warm compared to the cold season, in all bioregions (Alpine/Forest: p < 0.001; Desert: p = 0.003), as were staphylinids (Alpine/Forest: p < 0.001) although there were few staphylinids in the Desert bioregion, and they appeared only in the cool season. Histerids were more abundant in the warm than the cold season in both the Alpine and Forest bioregions (both: p < 0.001), but they were more abundant in the cool in the Desert bioregion (p < 0.001). Dermestids were present only in the warm season in the Forest bioregion but were similarly abundant across seasons in both the Alpine (p = 0.381) and Desert bioregions (p = 0.139). Staphylinids were more abundant in closed compared to open habitat in both the Alpine and Forest bioregions (both: p < 0.001), while histerids were more abundant in closed compared to open sites in the Alpine bioregion (p = 0.034); trogid and dermestid abundances were similar across habitats in all bioregions.

Among the flies, chloropids were more abundant in the warm season and in closed habitat (Table 2.3, see section 2.8 Supplementary Information: Table S1). Muscids were more abundant in warm than cool seasons and phorids were more abundant in closed compared to open habitat, while there were no differences in abundances of calliphorids across seasons or habitats (Table 2.3, see section 2.8 Supplementary Information: Table S1). There were also no differences in the abundance of calliphorids across the bioregions (Alpine – Forest/ Alpine – Desert: p < 0.001; Desert – Forest: p = 0.037). Muscid abundance was similar across all bioregions while phorids were more abundant only in the Alpine compared to the Desert and the Forest bioregions (both: p < 0.001) and chloropids were more abundant only in the Alpine compared to the Desert (p < 0.001) and the Forest compared to the Desert (p = 0.016). Calliphorids were more abundant in the warm season in the Forest bioregion (p < 0.001), while muscids were more abundant in the warm season in both the Forest and Alpine bioregions (both: p < 0.001) but more abundant in the cool season in the Desert (p = 0.018). Phorids were more abundant in the warm season in both the Desert (p = 0.041) and the Forest bioregions (p < 0.001) and chloropids more abundant in the warm in the Alpine bioregion (p < 0.001) but were absent in the cool season in the Forest and in the warm season in the Desert bioregions. Calliphorid abundance was similar across habitats in all bioregions, while muscids were more

abundant in the closed habitat in the Desert bioregion (p = 0.024). Phorids were more abundant in the closed habitat in the Alpine and Forest bioregions (phorids Alpine/Forest: p < 0.001; chloropids Alpine: p < 0.001, Forest: p = 0.029) and phorids were also more abundant in closed habitat in the Desert bioregion (p = 0.005).

Table 2.3 Results of generalised linear models (GLMs) testing for differences in fly and beetle family abundance, across different bioregions, seasons, and habitats.

Response variable	Effect	Estimate	Std. error	z-value	p
Beetle families					
Trogidae abundance	(Intercept)	-3.023	1.013	-2.98	0.003*
	Bioregion [Desert]	0.075	1.445	0.05	0.958
	Bioregion [Forest]	0.897	1.240	0.72	0.469
	Season [Warm]	4.290	1.013	4.24	<0.001*
	Habitat [Open]	0.054	0.278	0.19	0.847
	Bioregion [Desert] × Season [Warm]	-1.251	1.444	-0.87	0.386
	Bioregion [Forest]× Season [Warm]	1.158	1.241	0.93	0.351
	Bioregion [Desert] × Habitat [Open]	-0.048	0.523	-0.09	0.927
	Bioregion [Alpine] × Habitat [Open]	-0.337	0.333	-1.01	0.312
Staphylinidae abundance	(Intercept)	2.781	0.184	15.12	<0.001*
	Bioregion [Desert]	-7.289	1.427	-5.11	<0.001*
	Bioregion [Forest]	-1.446	0.237	-6.10	<0.001*
	Season [Warm]	1.304	0.187	6.99	<0.001*
	Habitat [Open]	-1.837	0.241	-7.64	<0.001*
	Bioregion [Desert] × Habitat [Open]	3.231	1.606	2.01	0.044*
	Bioregion [Alpine] × Habitat [Open]	-0.012	0.394	-0.03	0.976
Histeridae abundance	(Intercept)	-0.867	0.479	-1.81	0.071
	Bioregion [Desert]	3.187	0.559	5.71	<0.001*
	Bioregion [Forest]	1.432	0.574	2.49	0.013*
	Season [Warm]	3.790	0.511	7.42	<0.001*
	Habitat [Open]	-0.830	0.391	-2.12	0.034*
	Bioregion [Desert] × Season	-6.030	0.625	-9.64	<0.001*

	[Warm]				
	Bioregion [Forest]× Season [Warm]	-1.886	0.621	-3.04	0.002*
	Bioregion [Desert] × Habitat [Open]	1.057	0.524	2.02	0.044*
	Bioregion [Alpine] × Habitat [Open]	0.650	0.521	1.25	0.213
Dermestidae abundance	(Intercept)	-2.775	0.740	-3.75	<0.001*
	Bioregion [Desert]	4.824	0.746	6.46	<0.001*
	Bioregion [Forest]	2.019	0.791	2.55	0.011*
	Season [Warm]	0.789	0.208	3.80	<0.001*
	Habitat [Open]	-1.387	1.600	-0.87	0.386
	Bioregion [Desert] × Habitat [Open]	1.399	1.617	0.87	0.387
	Bioregion [Alpine] × Habitat [Open]	1.632	1.655	0.99	0.324

Fly families					
Calliphoridae abundance	(Intercept)	0.917	0.257	3.56	<0.001*
	Bioregion [Desert]	-5.189	1.505	-3.45	0.001*
	Bioregion [Forest]	-2.983	0.619	-4.82	<0.001*
	Season [Warm]	0.442	0.295	1.50	0.134
	Habitat [Open]	-0.143	0.294	-0.48	0.628
	Bioregion [Desert] × Season [Warm]	2.141	1.516	1.41	0.158
	Bioregion [Forest]× Season [Warm]	1.989	0.660	3.01	0.003*
	Bioregion [Desert] × Habitat [Open]	0.031	0.861	0.04	0.971
	Bioregion [Alpine] × Habitat [Open]	-0.297	0.535	-0.56	0.579
Muscidae abundance	(Intercept)	-1.806	0.486	-3.71	<0.001*
	Bioregion [Desert]	1.916	0.581	3.30	0.001*
	Bioregion [Forest]	-0.431	0.751	-0.57	0.566
	Season [Warm]	4.030	0.500	8.07	<0.001*
	Habitat [Open]	-0.224	0.372	-0.60	0.546
	Bioregion [Desert] × Season [Warm]	-4.885	0.616	-7.93	<0.001*
	Bioregion [Forest]× Season [Warm]	-0.789	0.769	-1.03	0.305
	Bioregion [Desert] × Habitat [Open]	1.044	0.520	2.01	0.044*
	Bioregion [Alpine] × Habitat [Open]	0.193	0.557	0.35	0.728
Phoridae abundance	(Intercept)	3.018	0.286	10.56	<0.001*
	Bioregion [Desert]	-3.499	0.563	-6.21	<0.001*

	Bioregion [Forest]	-4.395	0.744	-5.91	<0.001*
	Season [Warm]	0.263	0.366	0.72	0.472
	Habitat [Open]	-3.419	0.399	-8.57	<0.001*
	Bioregion [Desert] × Season [Warm]	0.895	0.674	1.33	0.184
	Bioregion [Forest]× Season [Warm]	3.529	0.842	4.19	<0.001*
	Bioregion [Desert] × Habitat [Open]	1.748	0.719	2.43	0.015*
	Bioregion [Alpine] × Habitat [Open]	-0.028	0.792	-0.04	0.972
Chloropidae abundance	(Intercept)	0.596	0.366	1.63	0.104
	Bioregion [Desert]	-3.214	0.610	-5.27	<0.001*
	Bioregion [Forest]	-1.534	0.468	-3.28	0.001*
	Season [Warm]	1.990	0.388	5.13	<0.001*
	Habitat [Open]	-2.648	0.537	-4.93	<0.001*
	Bioregion [Desert] × Habitat [Open]	0.201	1.606	0.13	0.900
	Bioregion [Alpine] × Habitat [Open]	1.343	0.797	1.68	0.092

2.5 Discussion

In this study we examined the composition of insect communities across different seasons and habitats in three contrasting bioregions. We identified key insect groups that characterised each bioregion, with ants dominating carcasses in the Desert bioregion, and beetles and flies most abundant in the Alpine and Forest bioregions. We also found variation in beetle and fly families across the bioregions and in the insect communities we examined over different seasons and habitats although, as predicted, there were some overarching trends in insect diversity and abundance across seasons and habitats within the bioregions. For example, warmer seasons generally supported more diverse and abundant insect communities, however beetle and fly activity was similar across winter and spring in the Desert bioregion and wasps were generally most abundant in cooler seasons. Similarly, closed habitats were more likely to host higher family richness and abundances compared with open habitats. Overall, our study has provided new insights into the drivers of insect diversity and heterogeneity around carrion in ecosystems. We expand on these insights below and discuss the potential implications of our findings on important ecological functions and services related to carrion.

2.5.1 How do carrion insect communities differ across contrasting bioregions?

There is a strong literature base suggesting that insect communities vary in structure and composition across different geographies (Moran and Southwood 1982, Kocher and Williams 2000, e.g. Guénard et al. 2012). To our knowledge, however, we present herein the first large-scale standardised study that compares carrion insect communities across different bioregions. Our results revealed clear differences in the structure and composition of the carrion insect communities that characterised each of the three study bioregions. This was despite the insect communities all sharing a relatively comparable focal food resource (i.e. ~30 kg kangaroo carcasses). As we anticipated, insect communities were most similar between the Forest and Alpine bioregions. There was clear overlap observed in terms of the composition of fly and beetle families for these bioregions, with all the major carrion families (i.e. family groups with more than 5% representation at carcasses across all study bioregions) present in the Forest bioregion, also being present in the Alpine bioregion. In contrast, Desert family compositions were relatively distinct from those in the two other bioregions, especially for beetle families and for fly families in the warm season. The Desert bioregion also had lower fly and beetle diversities compared to the Forest and Alpine bioregions, with one of the major fly families (Piophilidae) and six of the major beetle families (Scarabaeidae, Staphylinidae, Anthicidae, Carabidae, Nitidulidae, and Leiodidae) absent only in the Desert bioregion.

There were also strong associations between the Forest and Alpine bioregions in terms of the overall abundance of different fly, beetle, and ant insect groups. Indeed, the Forest and Alpine bioregions were characterised by higher abundances of beetles and flies compared to the Desert bioregion, while ants were far more abundant in the Desert bioregion compared to the Forest and Alpine bioregions. Insect diversity and abundance, including that of beetles and flies, is generally higher in more productive environments (Samways 1994), although these trends also hold true for ants (Kaspari et al. 2000). It is possible that ant colonies were present in lower densities in the Forest and Alpine bioregion, which decreased the chance that they discovered carrion resources in these locations. For example, ant abundances in the Alpine bioregion may have been suppressed due to the higher altitudes. Our sites in the Alpine bioregion were approximately 625 – 1475 m higher than those in the Forest and Desert bioregions. While we didn't specifically compare altitude within or across our study bioregions, it has been noted as an important variable impacting carrion insect communities and carcass decomposition (De Jong and Chadwick 1999, Baz et al. 2007). Further, sharp declines in ant species richness from mid to high elevations have been shown globally, with the stronger seasonal changes at higher

elevations making it more difficult for ant colonies to persist through the year (Samson et al. 1997, McCain and Grytnes 2010).

The differences in carrion-associated ant abundance were, however, probably also linked to variation in the foraging and dispersal strategies of these insects across each of the bioregions. In the Desert bioregion, carcasses represent a protein-rich source of food in an environment where alternative resources can be sparse, and protein limited. While ants in more productive forested regions may be able to successfully forage for resources in close proximity to their nest, in more sparse desert regions ants might disperse longer distances to find protein sources (McIver 1991, Schultheiss and Cheng 2013). So, while ants may not have been present at higher densities in the Desert bioregion compared to the Forest and Alpine bioregions, they may be more likely to encounter carrion resources due to increased dispersal capabilities. This might, in turn, influence their competitive and predatory interactions with carrion-associated flies and beetles (Barton et al. 2013), possibly explaining why fewer beetles and flies were found on the desert carcasses compared to the temperate and sub-alpine carcasses. Desert ants may also have other specific qualities that provide them with competitive advantages over fly and beetle species. For example, many Australian desert ant species are thermophilic and have specific adaptations that allow them to deal with extreme heat, or otherwise they can retreat into their thermally insulated nests when the temperatures get too extreme (e.g. Christian and Morton 1992, Muser et al. 2005). Additionally, the dry conditions of the Desert bioregion might also have reduced beetle and fly recruitment to the carcass by desiccating the resource and suppressing larval activity (Barton and Bump 2019). On the other hand, ant recruitment is not dependent on reproduction on or within the carcass itself, as ants will reproduce and raise their young within underground nests.

The presence and absence of specific beetle and fly families in the Desert bioregion probably also reflected how capable or not these insects were at dealing with the hot and dry arid conditions. For example, smaller flies and beetles, such as staphylinids, anthicids, sphaerocerids, chloropids and piophilids were either absent or recorded at much reduced numbers in the Desert compared to Alpine and Forest bioregions, probably because they were less resistant to desiccating conditions due to their smaller body mass affecting water retention (Addo-Bediako et al. 2001). Some of these groups, such as staphylinids and anthicids, are also commonly associated with environments high in leaf litter, depending on moist soils to complete life cycles (Scientific and Entomology 1991) and feeding on detritus that is more common in forested temperate areas. On the other hand, beetles from families including

Dermestidae and Trogidae were likely more abundant in the Desert bioregion because of their larger and more robust bodies. Dermestids and trogids might also benefit from other morphological and behavioural adaptations that allow them to manage high temperatures and limit water loss. Similar to some Australian carabid and tenebrionid beetle species, they may not exhibit discontinuous gas exchange cycles (a mechanism that reduces water loss via respiration) or may be nocturnally active (Duncan and Dickman 2001). Alternatively, the higher abundance of Dermestidae and Trogidae beetles in the Desert bioregion could also reflect their foraging preferences, as species within these families will readily target desiccated remains that are commonly associated with dry, arid environments (Munkres 2009).

The high numbers of wasps observed on carcasses in the Alpine bioregion, but not the Forest and Desert bioregion, are also of note. While wasps associate with carrion for varied reasons, such as to depredate or parasitise other insects or their larvae (Voss et al. 2009), or to draw nutrients from it as a food source for their larvae, they typically do not appear at carcasses in high numbers (e.g. Moretti et al. 2008; Silveira et al. 2005). Certain social wasps, such as *Vespula* spp. may, however, swarm nutrient-rich resources (e.g. Honeydew; Beggs 2001). This was indeed the case in the Alpine bioregion, where 93.1% of the wasps collected on carcasses in this area were identified as invasive European wasps (*Vespula germanica*) (see Chapter 6 for more details on the association of European wasps with carrion in the Alpine bioregion).

While there was much variation across the different bioregions surveyed, we did observe some similarities too. For example, muscids and calliphorids were relatively active across all bioregions. This was unsurprising, as these families comprise some of the most prolific and diverse scavenging flies that colonise carcasses across a range of geographies worldwide (Benbow et al. 2016, Olea et al. 2019). Histerids were also very abundant across all bioregions; they commonly associate with carcasses as predators of calliphorid eggs and larvae (Nuorteva 1970), perhaps explaining why they were as widespread across bioregions as the calliphorids in our study.

2.5.2 Do the effects of season and habitat on carrion insect communities vary across bioregions?

Our study indicates that season and habitat are both responsible for structuring carrion insect communities. The crucial role that these factors play in driving these communities is already well established (e.g. Bajerlein et al. 2011, Barton and Evans 2017, Barton et al. 2017), however, our study extends upon this previous research. Namely, it demonstrates for the first

time with empirical data that the effects of season and habitat on different carrion insect taxa are intrinsically linked to bioregional context.

Compared to habitat, season had the strongest influence on carrion insects and insect abundance and diversity were generally higher in the warm compared to the cool seasons as predicted. However, while we observed lower beetle and fly family richness and abundance in the cool compared to warm season in both the Alpine and Forest bioregions, their richness and abundance were similar across seasons in the Desert bioregion. Insects are greatly influenced by the temperature of the surrounding environment (Mellanby and Gardiner 1939). Lower temperatures generally inhibit insect activity, but high temperatures may also limit their activity, particularly if the species in question do not have an effective means of retaining body water (May 1979). As the warmer Desert study season recorded temperatures that surpassed 45°C, activity by certain beetle and fly species may have been suppressed due to the heat. However, it is also probable that the cool season temperatures in this bioregion were not low enough to substantially suppress beetle and fly activity, especially compared to the temperatures recorded at the Alpine and Forest bioregions (Figure 2.6). The higher abundance of ants during the warm compared to cool season in the Desert bioregion again might suggest that the dominant scavenging ants acquire competitive advantages against beetles and flies during extreme heat. Many Australian desert ants are able to remain active in the hottest parts of the day, even when air temperatures exceed 50°C (Muser et al. 2005).

It is also likely that temperature was not the only variable shaping carrion-insect trends across seasons. Indeed, in arid environments, including the Desert bioregion, rainfall is a key driving force behind productivity and abundance of insects such as the bushfly (*Musca vetustissima*) (Hughes et al. 1972), which was the dominant muscid collected in the Desert bioregion. Moisture is also an important factor driving the activity of carrion insects, and particularly the activity of larval forms (Archer 2004). Further, hibernation or diapause over winter periods may influence when insects are present or most active in the environment. Winter hibernation can, for example, mean that summer seasons do not record peak activities of certain species, as they have not yet grown in numbers. For example, in Australia, European wasps reach a peak of activity during autumn after building their numbers over the summer following a period of hibernation in winter (Ward et al. 2002). This explains why, in the Alpine bioregion, wasps were most abundant on carcasses during the cool rather than the warm season. Finally, differences in vertebrate use of carcasses may also vary across seasons, which could alter carrion insect communities by influencing their ability to colonise the resource (Munoz-Lozano

Alpine
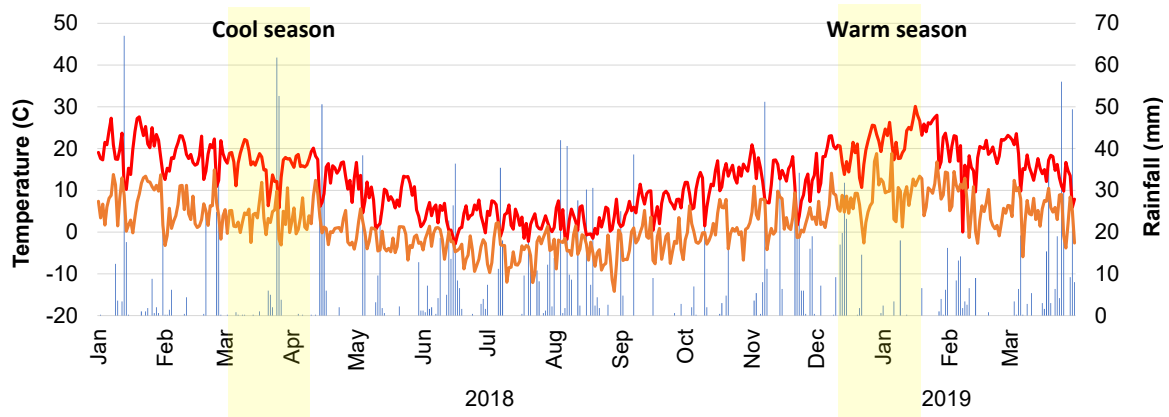
Forest
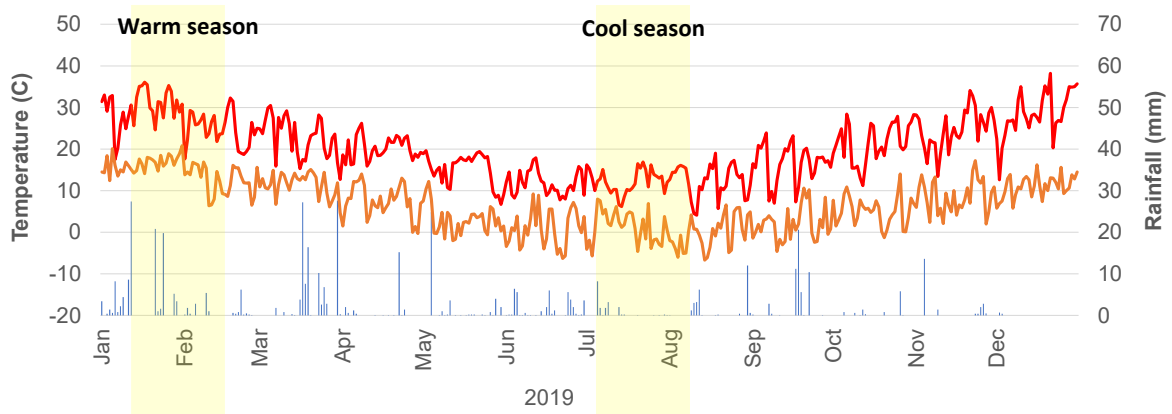
Desert
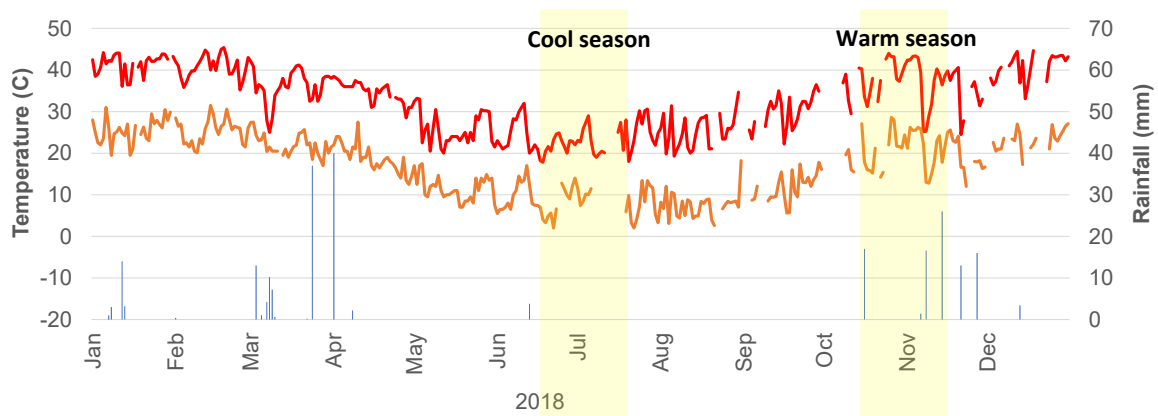
Figure 2.6 Minimum (orange line) and maximum (red line) daily temperatures (°C) across the three bioregions during the time of the study. The study seasons in each bioregion are shaded in yellow. Climate data for the bioregions were taken from the nearest weather stations (Alpine: nearest station 20 km away at Perisher Valley, Forest: nearest station 30 km away at Lithgow, Desert: nearest station 100 km away at Bedourie; Bureau of Meteorology 2020).

et al. 2019). For example, some carcasses in the Forest bioregion, during the cooler season, were removed entirely in the first few days by large vertebrate scavengers such as dingoes (see Thesis Chapter 4). These carcasses received very few insect visitors during the later sampling period, presumably because there was no resource left to scavenge.

Our results revealed that habitat was also an important predictor of carrion-associated insect community structure, although it had less of an effect on insects compared with season. This was unsurprising, as while season may restrict the overall abundance and activity of insect taxa in the environment, most insects were probably capable of moving between the two habitat types (especially as at some carcasses habitats were separated by only 50 m). We found that the more vegetatively complex 'closed' habitat type was generally more favoured by insect groups and families. Habitat complexity is often positively associated with insect richness (Uetz 1979, Humphrey et al. 1999, Hansen 2000, Lassau et al. 2005), although ant community richness and abundance may be lower in structurally complex habitats (Lassau and Hochuli 2004). We didn't, however, find any evidence to suggest that ant abundance was higher in the less complex open habitat type, and instead observed greater ant numbers in the closed compared to the open habitat in the Desert bioregion. This result could be explained by differences in plant productivity in the Desert's closed 'swale' habitats compared to the open 'dune crest' habitats. Prior studies have shown that vegetation cover is often higher in dune swales than on crests and that ant communities here often mirror plant productivity, with several species (of those studied) being more abundant in swales and with only one species more abundant on crests (Gibb et al. 2019).

Our results further suggested that if insects were affected by habitat, they were generally affected similarly across multiple bioregions. Indeed, beetles in the family Staphylinidae and flies in the family Chloropidae were more abundant in the closed habitat in both the Alpine and Forest bioregions, while flies in the family Phoridae were more abundant in closed habitat across all three bioregions. Previous studies have also shown that generalist beetles, such as some Staphylinidae, may be strongly associated with the habitat context of the carrion (Barton and Evans 2017). Some Staphylinidae also require distinct soil and forest features for their occurrence on vertebrate carrion (Pohl et al. 2008, Caballero et al. 2009). The effects of habitat on Chloropidae and Phoridae, on the other hand, might be explained by their small body sizes, which make them less capable of dispersing long distances between habitats (Evans et al. 2020). This result provides partial support for our final prediction that habitat would have a stronger effect on less mobile insects, although the variability in our findings across different

taxa and across bioregions also cautions against generalisation. While the habitat affinities of different insect taxa clearly play an important role in structuring carrion insect communities, this role is also highly dependent on bioregional context.

2.5.3 Conclusions and study implications

In this study, we showed that large scale bioregional differences provide important context to the effects of local drivers, including season and habitat, on carrion-associated insect groups. This has important implications for understanding carrion insect community diversity and heterogeneity across different scales and opens new areas of inquiry regarding central ecological functions and services related to carrion. One important point of inquiry, for example, is to determine whether context-dependent variation in the diversity and abundance of key scavenger groups such as beetles and flies also affects the relative roles these groups play in carrion removal. Similarly, our research further supports investigation of the roles that the lesser studied insect groups play in carrion removal across different environmental scales. For example, while ants have been overlooked as unimportant, opportunistic scavengers (Eubanks et al. 2018), our research has shown that they visit carcasses in particular locations at very high abundances. We also found that wasps may play important roles as decomposers and/or predators within certain carrion food webs. Indeed, large swarms of invasive European wasps were observed scavenging carrion resources and depredating adult blowflies and their larvae in the Alpine bioregion (See Thesis Chapter 6). These species are known to have cascading impacts on ecosystems including via monopolisation of key resources (Beggs 2001), which makes them a particularly important subject for future research. Functional redundancy of different insect groups can be examined via the removal or addition of key species in controlled experimental environments (e.g. Heo et al. 2019), or by excluding insects from carcasses using barriers such as mesh wire (e.g. Barton and Evans 2017). While these exclusion experiments have been carried out before, none has attempted to examine the effects of exclusion according to different environmental drivers, or across multiple bioregions.

Empirical large-scale studies such as ours are essential if we wish to develop a more comprehensive understanding of the drivers that shape carrion insect community diversity and heterogeneity from local to global scales, although further research is required to continue what we have begun here. We suggest that future studies focus on the application of standardised surveys like ours, which examine carrion insect communities across multiple spatial and temporal scales. Emphasis should be placed on examining additional regions or biomes,

especially in lesser studied areas such as the tropics (Barton et al. 2013), and on making comparisons across different environmental gradients including aridity, temperature, and elevation. To better assess the effects of temporal scale, carrion ecologists should also consider developing standardised, long-term surveys that are conducted over multiple seasons and years. While the importance of long-term studies in ecology has been long appreciated (Franklin 1989), we are yet to see their application in studies of carrion ecology. Data generated from this kind of work would not only provide more comprehensive insights into the drivers that influence carrion insect community variation across different scales, but also help ecologists to assess long-term variation in insect community dynamics. Such assessments are integral for understanding the effects of complex global processes, such as those related to anthropogenic climate change.

2.6 Acknowledgements

2.7 References

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2.8 Supplementary Information

Table S1 Standardised abundance of beetles, flies, ants, and wasp groups, including beetle and fly family groups, observed visiting kangaroo carcasses across bioregions (Alpine, Forest, Desert) and seasons (warm, cool) based on carcass trials completed between March 2018 and August 2019, in Australia.

Insect taxa	Alpine		Forest		Desert		Overall abundance (n = 117)
	Cool (n = 20)	Warm (n = 20)	Cool (n = 19)	Warm (n = 19)	Cool (n = 19)	Warm (n = 20)	
Flies	401.5	1072	50.5	364	90.5	68.5	2047
Calliphoridae	95.5	142	4	44.5	0.5	7	293.5
Muscidae	6	327.5	4	102	72	30.5	542
Sarcophagidae	0.5	0	0	0	5	0	5.5
Nematocera	9	21.5	7.5	17	0	0.5	55.5
Sphaeroceridae	5.5	41	17.5	31.5	0	0	95.5
Phoridae	269.5	199	2.5	108.5	7	22.5	609
Drosophilidae	0	0	0	7.5	0	0	7.5
Sciaridae	0	1	6.5	0	0	0	7.5
Anisopodidae	0	0	0.5	0	0	0	0.5
Piophilidae	0	98	8	4.5	0	0	110.5
Sepsidae	0	1.5	0	0.5	0.5	0	2.5
Chloropidae	15.5	170	0	48	4.5	0	238
Therevidae	0	1	0	0	0	1.5	2.5
Heleomyzidae	0	3.5	0	0	0	0	3.5
Platystomatidae	0	12	0	0	0	0	12
Hybotidae	0	2.5	0	0	0	0	2.5
Ephydridae	0	4	0	0	0.5	0	4.5
Unknown	0	47.5	0	0	0.5	6.5	54.5
Beetles	260	1665.5	94	1162	426.5	329.5	3937.5
Trogidae	1	73	2	459	1	22	558
Anthicidae	2	12	11	65.5	0	0	90.5
Elateridae	0	1	0	4	0	0.5	5.5

Staphylinidae	188	690	36.5	164.5	2.5	0	1081.5
Carabidae	1.5	8	0.5	5.5	0	0	15.5
Scarabaeidae	18	5.5	0.5	202.5	0	0	226.5
Histeridae	5.5	291	29.5	214	223.5	24	787.5
Silphidae	8.5	491.5	0	5	0	0	505
Dermestidae	0.5	2	0	35	187	268.5	493
Cleridae	0	0	0	3.5	7.5	14.5	25.5
Leiodidae	12	52	6	0	0	0	70
Nitidulidae	22	25.5	2.5	1	0	0	51
Cryptophagidae	0	4.5	0.5	0	0	0	5
Latridiidae	0	0	4	0	0	0	4
Anthribidae	0	0	0	1	0	0	1
Coccinellidae	0	0	0	0.5	0	0	0.5
Curculionidae	0.5	1	0	0.5	4.5	0	6.5
Endomychidae	0.5	0	0	0	0	0	0.5
Chrysomelidae	0	8	0.5	0.5	0.5	0	9.5
Tenebrionidae	0	0.5	0	0	0	0	0.5
Unknown	0	0	0.5	0	0	0	0.5
Ants	1492.5	1546.5	385	7383	4466.5	17771	33044.5
Wasps	539.5	20.5	11	0.5	3.5	2	577
European Wasp *Vespula germanica*	537	0	0	0	0	0	537
Other wasps	2.5	20.5	11	0.5	3.5	2	40

Figure S1 nMDS plots showing the similarity of the carrion-associated insect communities at kangaroo carcasses across different seasons (cool, warm) and bioregions (Alpine, Forest, and Desert) for fly families across different seasons (A) and habitats (B) and for beetle families across different seasons (C) and habitats (D). Families included in each of the plots reflect those in the bar plots (Figure 2.4; Figure 2.5).

(C) Beetle families - Season

Legend:
- Alpine (cool)
- Forest (cool)
- Desert (cool)
- Alpine (warm)
- Forest (warm)
- Desert (warm)

Family labels: Anthicidae, Scarabaeidae, Trogidae, Histeridae, Staphylindae, Nitidulidae, Silphidae, Cleridae, Dermestidae

(D) Beetle families - Habitat

Legend:
- Alpine (closed)
- Forest (closed)
- Desert (closed)
- Alpine (open)
- Forest (open)
- Desert (open)

Family labels: Anthicidae, Scarabaeidae, Trogidae, Histeridae, Staphylindae, Nitidulidae, Silphidae, Cleridae, Dermestidae

CHAPTER 3

BIOREGIONAL DIFFERENCES IN THE EFFECTS OF SEASON AND HABITAT ON VERTEBRATE SCAVENGING DYNAMICS

A variety of scavengers feeding on kangaroo (*Osphranter* and *Macropus* spp.) remains across the three study bioregions. Photographs by Emma Spencer.

3.1 Abstract

Carcass scavenging by vertebrates is a critical ecosystem service, as it can reduce disease spillover and accelerate nutrient cycling. However, there is a deficit in understanding of the drivers that shape scavenger communities and their use of carrion, especially across large regional scales where seasons and habitats vary. In this study, we used wildlife cameras to monitor scavengers at experimentally positioned kangaroo carcasses across different seasons and habitats in three disparate desert, sub-alpine and temperate bioregions in Australia. We identified twenty-seven vertebrate species that scavenged on the carcasses, including nineteen birds, five mammals, and three reptiles. We also identified four invasive species including red foxes (*Vulpes vulpes*), feral pigs (Sus scrofa), and Indian mynas (*Acridotheres tristis*). Across regional scales there was clear variation in carrion-associated vertebrate communities, with corvids (*Corvus* spp.), wedge-tailed eagles (*Aquila audax*), and red foxes using carcasses more frequently in the Desert bioregion, while dingoes (*Canis dingo*) used carcasses more frequently in the Alpine and Forest bioregions. Within bioregions, we also observed variation in vertebrate scavenging. For example, most mammals and birds scavenged carcasses more in cool seasons across the three bioregions, but in the Alpine bioregion dingoes and corvids were more active in the warm season. Similarly, while birds of prey used carcasses more in open habitats in the Forest and Alpine bioregions, and corvids and foxes in the Forest and Desert bioregions, respectively, their use of carcasses was not affected by habitat in any of the other study bioregions. Our results illuminate the highly variable and context-dependent nature of vertebrate scavenger assemblages and have implications for key scavenging-related ecosystem processes including nutrient cycling and disease transfer. They further support the need to conduct standardised carcass monitoring surveys across a range of bioregions to build understanding of the factors that influence vertebrate scavenger dynamics.

3.2 Introduction

Scavengers represent an important functional group in terrestrial ecosystems (Wilson and Wolkovich 2011, Barton and Evans 2017). By removing decaying necromass, scavengers reduce potential disease spillover from pathogenic organisms that are often associated with decomposition (Vicente and VerCauteren 2019), and they contribute to the dispersion of energy and nutrients throughout the environment and accelerate nutrient cycling (Pereira et al. 2014). Scavengers also can contribute to the stabilisation of food webs, to a level above even that of predators. Indeed, it has been suggested that 124-fold more energy is transferred per scavenging

link than per predation link (Wilson and Wolkovich 2011). Despite the apparent importance of vertebrate scavengers, however, there remains a deficit in understanding of the drivers that shape scavenger communities and their use of carrion.

Most carnivorous vertebrates engage in scavenging behaviour, but the propensity to scavenge varies by species (DeVault et al. 2003). Obligate scavengers such as old and new world vultures (Families: Accipitridae and Cathartidae) have adaptations that allow them specifically to find and consume carrion (Kane et al. 2015, Di Vittorio et al. 2018, Hill et al. 2018). Most other vertebrates that scavenge (i.e. facultative scavengers) supplement their diet with carrion but often also rely on predation to meet their energy requirements (DeVault et al. 2003). Finally, there are other species that associate with carrion but do not feed directly off the meat biomass. This group includes, for example, some passerine bird species that feed on detritivores such as fly larvae or beetles or use the remains of fur on carcasses to build their nests (Moreno-Opo and Margalida 2013).

The structure of vertebrate scavenger communities and the degree to which different species engage in scavenging are further influenced by a variety of extrinsic and intrinsic factors. Access to alternative resources (Needham et al. 2014), anthropogenic disturbance (Sebastián-González et al. 2019) and habitat fragmentation (Olson et al. 2016), as well as abiotic variables such as temperature (DeVault et al. 2004) and carcass characteristics such as carcass size, type and condition (Moleón et al. 2015, Turner et al. 2017), have all been reported as important factors shaping dynamics in scavenger communities. Scavenger community structure can also differ between seasons (Selva and Fortuna 2007). The effect of seasonality on vertebrate scavengers is largely linked to the modulation of insect and microbial activities at different temperatures. Warmer temperatures facilitate insect and microbial activity, increasing carcass decomposition, which then enhances competitive interactions with vertebrates (DeVault et al. 2004, Ray et al. 2014). On the other hand, microbial growth in warm periods may also facilitate the discovery of carcasses by vertebrates that use scent to find their food, as microbes release strong chemical odours through the decomposition process (Metcalf et al. 2016). Animal activities may also vary across seasons, influencing the community of scavengers present in the environment at the time. For example, reptiles are typically less active when temperatures are cool, which may result in decreased scavenging behaviours by these animals (Rahman et al. 2015). In addition, during dry seasons or periods of high snowfall, carrion may be more abundant in the landscape (e.g. due to animal death via starvation) while alternative resources

are sparse, and vertebrates then may increase their reliance on carrion (Roth 2003, Kendall et al. 2014).

Vertebrate scavenging may also be strongly influenced by the vegetation surrounding carcasses. Different habitat characteristics such as vegetation cover influence scavenger communities at carcasses by favouring the detection of carcasses by species that rely on sight to locate food resources (Fernández-Juricic et al. 2004). Predation risk can further influence habitat use and therefore scavenging activity, as some species may avoid feeding at food resources that are positioned in "risky" habitats such as open fields (Wikenros et al. 2014). Similarly, scavenger density in certain areas may depend on their habitat needs, such as for foraging or breeding, which could then influence their chance of encountering carcasses in certain habitats (Hager et al. 2012).

The effects of factors such as season and habitat on scavenger assemblages and carcass use are likely to vary also with spatial scale. Across large, regional scales this variation may be pronounced. Habitat types and climatic conditions often vary widely between regions, and will, alongside other factors, influence the potential pool of species that scavenge (Mittelbach and McGill 2019). Some regions experience great climatic variability and periods of high and low resource availability (e.g. deserts and tundra), so that animals may place greater reliance on carcasses in certain locations, particularly during dry or cool seasons (Roth 2003, Kendall et al. 2014). Similarly, different temperature extremes may also influence the activity of scavengers, with very low or high temperatures reducing their activity (Cook 2012). There is also some evidence that vertebrate scavenger diversity is lower in regions that have greater temperature extremes (Mateo-Tomás et al. 2015). The effects of habitat on scavenging patterns are likely also to vary across different spatial scales, with vegetation characteristics, including vegetation complexity, influencing scavenger species richness differently at local and landscape levels (Pardo-Barquín et al. 2019).

While growing numbers of studies investigate scavenger communities in terrestrial systems, those exploring the effects of abiotic factors on scavenging patterns are usually restricted to single study regions (e.g. DeVault et al. 2004, Selva et al. 2005). Each study has different experimental designs, making it difficult to compare results among different locations (but see: Mateo-Tomás et al. 2015, Sebastián-González et al. 2019). It is important therefore to undertake studies using standardised methods to explore the impact of abiotic factors on scavenging in different regions, not only because of the potential for wide variability in the

conditions experienced and animal assemblages present at these locations, but also because of the impact that using different survey methods might have on the results (e.g. different carcass types; Moleón et al. 2015). Finally, as most scavenger studies are biased towards temperate environments (Barton et al. 2013), it is also critical that more research is conducted in environments with greater climatic extremes, such as deserts or alpine systems. These systems are often resource-limited and may also experience changes in carcass availability, for example, due to drought or following snowfall. Research into the factors underlying complex region–community scavenger relationships will increase our understanding of the key ecosystem functions and services that scavengers fulfil. This is particularly crucial when we consider that carcasses may provide essential resources to regionally restricted, rare or endangered animals (e.g. vultures; Di Vittorio et al. 2018) or alternatively, sustain invasive species (Schlacher et al. 2015, Abernethy et al. 2016) that may threaten native plants and animals in the surrounding environment (Spencer et al. 2021).

In this study we used a standardised methodology to investigate how patterns in vertebrate scavenging vary across different biogeographic regions, while also assessing the effects of season and habitat factors on scavenging at local scales and among bioregions. To do so, we monitored experimentally positioned kangaroo carcasses in two different seasons, representing cooler and warmer temperature averages, and two different habitats, comprising open or closed (treed) vegetation communities, across three distinct bioregions in Australia. Each study bioregion contrasted sharply in climate and vegetation, representing either a desert, a sub-alpine or a temperate environment. We addressed the specific question: does the community structure of carrion-associated vertebrates and their use of carcasses, vary by bioregion, season and/or habitat? We expected that variation in vertebrate scavenger community structure would be most pronounced across different bioregions, compared with seasonal and habitat variation (*Prediction 1*). We also predicted that vertebrate carcass use would differ seasonally, with most scavenging occurring in cooler seasons when insect and microbial activity and thus resource competition was reduced (*Prediction 2*). Finally, we expected that there would be habitat variation in the use of carcasses by vertebrates and predicted that the effects of habitat on carcass use would vary across different animal groups and species (*Prediction 3*). We use our results to identify bioregional differences in scavenger guilds and carcass use and to discuss the implications of highly variable and context-dependent scavenger assemblages for important ecosystem processes such as nutrient cycling and predator-prey dynamics.

3.3 Materials and Methods

Fieldwork was conducted across three district bioregions in Australia: the Wolgan Valley, Newnes, eastern New South Wales (hereafter, Forest bioregion; 33°14'S, 150°10'E; 50 km^2; 540–680 m a.s.l), which is a temperate site, the Snowy and Botherum Plains in Kosciuszko National Park, southern New South Wales (hereafter, Alpine bioregion; 36°14'S, 148°32'E; 70 km^2; 1305–1540 m a.s.l), which is a sub-alpine area, and Ethabuka Reserve in the Simpson Desert, western Queensland (hereafter, Desert bioregion; 23°51'S, 138°28'E; 80 km^2; 65–120 m a.s.l), which is a hot-dry desert (Figure 3.1). For further details on the study bioregions see Section 2.3.1.

All three bioregions have a history of agricultural operations, with extensive livestock grazing occurring in the Forest and Desert bioregions until the early 2000s, and in the Alpine bioregion up until the 1980s. Each bioregion is now managed either as a conservation reserve (Forest and Desert bioregion) or is protected as National Park (Alpine bioregion). Ongoing human disturbance is generally low in each bioregion, with roads around the study areas experiencing low use or restricted use (e.g. parks vehicles only). Extensive grazing by kangaroos in the Forest bioregion, feral pigs (S*us scrofa*), feral horses (*Equus caballus*), and deer (*Cervus elaphus, Rusa unicolor, Dama dama*) in the Alpine bioregion and feral camels (*Camelus dromedarius*) in the Desert bioregion occurs and regular lethal control of animals such as pigs, deer, red foxes (*Vulpes vulpes*), camels and dingoes (*Canis dingo*) is carried out across the bioregions (although dingoes are not targeted in the Desert bioregion). Kangaroos are controlled in agricultural areas adjacent to each study site and the carcasses are often left to rot *in situ*. There is no obligate scavenger presence in these bioregional areas, or in Australia generally, but there is a diverse array of facultative scavengers that occurs across all sites, including birds such as corvids (*Corvus coronoides, C. mellori* and *C. bennetti*) and wedge-tailed eagles (*Aquila audax*), mammals such as red foxes, feral cats (*Felis catus*) and dingoes and reptiles, including lace monitors (*Varanus varius*) and sand goannas (*V. gouldii*).

3.3.1 Field methods

Fieldwork took place across two seasons in each of the study bioregions, such that a cooler and a warmer period were surveyed (see Figure 2.6 for details on temperature and rainfall variation across the three bioregions at the times of the study). The Forest bioregion was surveyed in January/February (summer; warmer period) and July/August (winter; cooler) of 2019. The Alpine bioregion was surveyed in March/April (Autumn; cooler) and December/January

(summer; warmer period) 2018. The Desert bioregion was surveyed in June/July (Winter; cooler) and October/November (spring; warmer period) 2018.
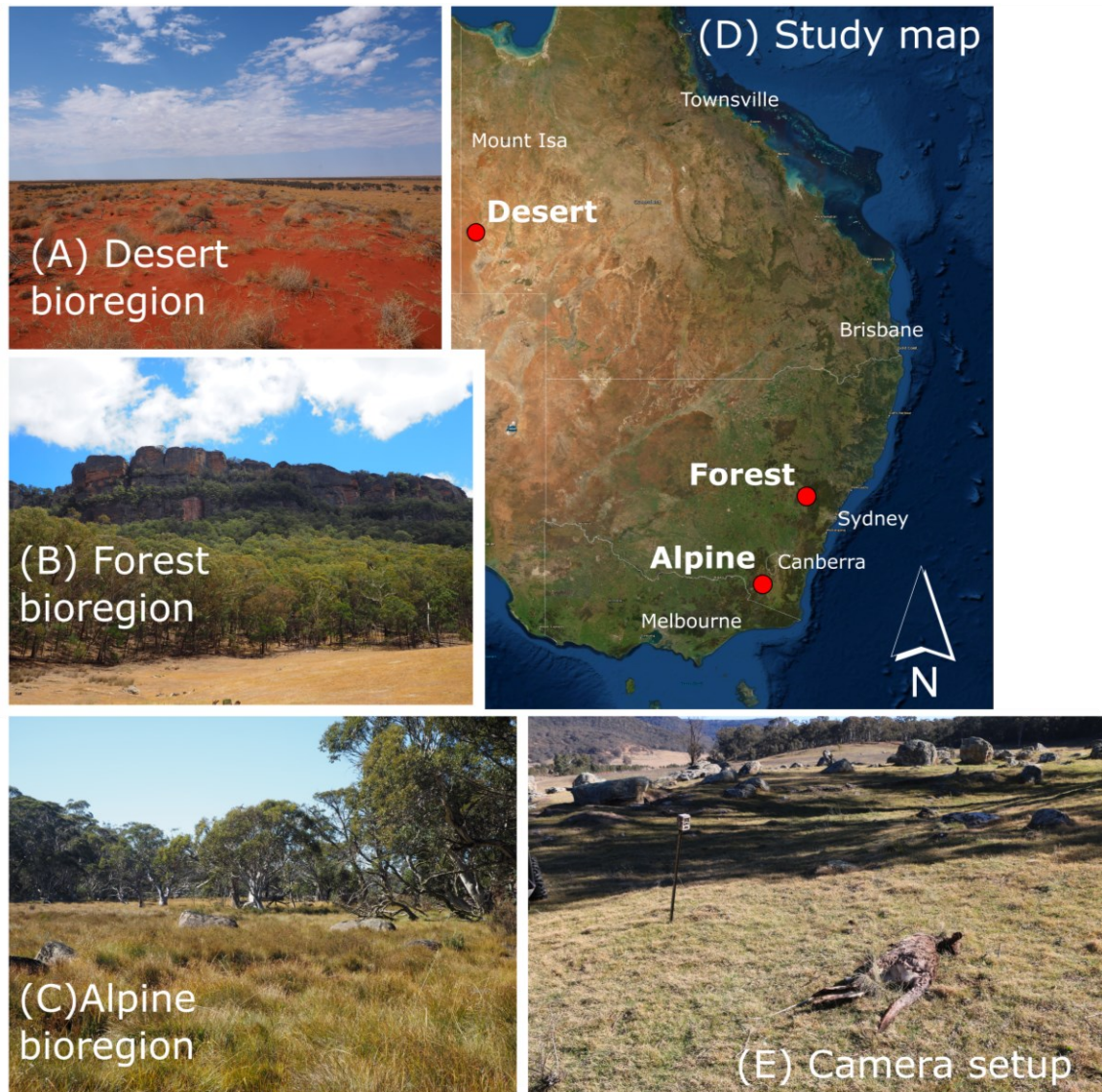
Figure 3.1 Study area map and carcass site set-up; images displaying the typical habitat in which carcasses were distributed across the three study bioregions, including the Desert (A), Forest (B) and Alpine (C) bioregions in Australia. The location of the three study sites in Australia are shown in (D). (E) provides an example carcass site set-up with the remote monitoring camera positioned ~4 m from the staked kangaroo carcass.

Across each season in each study bioregion, we distributed 20 animal carcasses (total of 40 carcasses per bioregion, and 120 carcasses in total). Carcass sites were selected to represent two distinct habitat types in each bioregion, with half placed in 'open' and half placed in

'closed' canopy habitats. In the Forest and Alpine bioregions, carcass sites included an even mix of grassland (open) and woodland (closed) habitats. In the Desert bioregion, sites comprised an even mix of dune crest (open) and dune valley (closed) habitats. Open canopy habitats lacked canopy cover and were at least 50 m from any densely forested or vegetated land. Closed canopy habitats had more than 20% canopy cover. We tried to ensure that these closed canopy sites were at least 50 m from any open space; however, this was not possible in the Desert bioregion due to the general sparsity of trees in the desert.

We sourced dead, adult eastern grey kangaroos (*Macropus giganteus*; Forest and Alpine bioregions) or dead adult red kangaroos (*Osphranter rufus;* Desert bioregion) from nearby management culls. All kangaroo carcasses were intact, generally only with a single bullet wound to the head. Carcasses displaying evidence of disease (e.g. heavy parasite loads) were not used. Each carcass was weighed (precision: ± 50 g) and placed into the field without freezing within 24 hours (warm period) or 36 hours (cool period) of collection. Within each study bioregion and season, carcasses were separated by a minimum distance of 1 km to minimise scent travel between carcasses. Carcass sites between seasons were separated by at least 200 m; carcass placements at this distance were considered unlikely to have had any marked effect on each other, because the time between study seasons was more than 4 months and only bones remained at old carcass sites. Scientific licenses and permits were obtained to relocate the kangaroo carcasses (SL 101901 and SPP WA0006737) and research was approved by the University of Sydney Animal Ethics Committee (Project number: 2017/1173).

We monitored each carcass with a Reconyx PC800 Hyperfire™ camera trap (Professional Reconyx Inc., Holmen, WI, USA). We attached the cameras to a free-standing star picket, 3–4 m away from each carcass (Figure 3.1e). Cameras were programmed to take continuous photographs when triggered by thermal movement around the carcass (10 shots, rapidfire, no wait period). To prevent complete removal of the carcasses from the remote camera monitoring frame, each carcass was secured to the ground by a wire attaching the neck and Achilles tendon of the animal to two metal stakes spaced ~0.6 m apart. Cameras were used to monitor carcasses for 1 month to capture the time of greatest scavenging activity and to ensure that sampling was even across all sites.

3.3.2 Data collection

We used the photo management program Digikam (ver. 6.2.0) to sort all photographs collected over the study. Photographs were tagged according to the species and the number of each

species present, and whether each species engaged in scavenging behaviour or not. Because some species appeared in high numbers and moved in and out of photographs frequently, to maintain efficiency in tagging protocols we tagged species and species numbers according to visitation events. A visitation event included all photos from when a species first entered the frame to when it exited the frame and did not return for at least 10 minutes. This time gap was determined by observation of species' movements around carcasses. Tags were then written into the exif photo data and extracted, along with date and time information, for analysis using exiftool (ver. 12.3.0.0) (Harvey 2021). In addition to extracting scavenger information, we also determined the number of days until carcass removal using a combination of in-person visual inspection of the carcasses and examination of camera images. A carcass was defined as "removed" when less than 5% of meat biomass, and the skin, hair and/or bone remained.

3.3.3 Statistical methods

We analysed differences in vertebrate scavenger community richness and composition, and in scavenging activity across different bioregions, habitats, and seasons. Vertebrates belonging to the scavenger guild were defined as species that fed on at least one carcass at any one of the three study bioregions. We included only those species that clearly consumed the carcass meat, or in the case of passerines and smaller reptiles, that may have fed upon insects associated with carcasses. We did not consider any species that were detected by cameras but did not feed from any carcasses (i.e. generally herbivores). Carcasses that were not monitored for the complete 30-day period (n = 1) were removed from all analyses. We conducted all analyses in R version 4.0.2 (R Development Core Team 2020).

3.3.3.1 Scavenger community structure

To quantify differences in vertebrate scavenger community structure, we considered measures of species richness, abundance, and community composition.

To identify species richness of scavenger guilds per carcass site, we calculated the total number of vertebrate species that visited each carcass. To determine the total abundance of scavengers at each carcass site, we calculated the maximum number of unequivocally different individuals within each species group detected at a single carcass and then summed these numbers to give the total abundance at that carcass. The maximum number of unequivocally different individuals was calculated by identifying the highest number of individuals of a scavenger species simultaneously observed or appearing in a picture (Moleón et al. 2015). For some

species (e.g. dingoes; goannas; wedge-tailed eagles, red foxes, and feral cats), different individuals visiting the same carcass were counted using identifying features like skin patterns, injuries, and sexual dimorphism. Species richness and abundance measures included species belonging to the scavenger guild that visited but did not necessarily feed on the carcass.

To determine how bioregion, season and habitat affected scavenger guild abundance and species richness, we constructed separate generalised linear models (GLMs) of richness with Poisson distribution and a log-link function, or abundance with negative binomial distribution and a log-link function, and bioregion (*Alpine, Forest, Desert*), season (*cool, warm*) and habitat (*open, closed*) as independent variables (Package: lme4; Bates et al. 2015) (Package Mass; Ripley et al. 2021). We also included the two interaction terms bioregion × season and bioregion × habitat. The negative binomial distribution was used for abundance data because data were overdispersed (Global model: $\varphi = 1.41$; $p = 0.006$) and because quasi-Poisson models did not produce acceptable residuals versus fitted plots. *Post hoc* analyses were used to investigate differences in species richness and abundance across the three bioregions, and the interaction terms, and were calculated using Holm-Bonferroni log-rank tests for *post hoc* analysis (Package emmeans; Russell et al. 2021). We also visually assessed model-predicted values against the residual values to confirm that all models met their necessary assumptions.

To determine how bioregion, season and habitat affected scavenger community composition, we determined the percentage occurrence for each vertebrate scavenger species documented visiting carcass sites and conducted a multivariate analysis examining the abundance of scavenger groups across the different bioregions, seasons, and habitats. Percentage occurrence of vertebrate scavenger species was calculated as the number of carcasses at which a species occurred divided by the total number of carcasses. To conduct our multivariate analysis, we first constructed a matrix of site (carcass) × species (scavenger groups) using the abundance of different scavenger groups recorded at each carcass. To reduce the numbers of zeros in matrices and produce more interpretable results, we combined species abundances according to the groups: "Reptiles", "Suids", "Dingoes", "Feral cats", "Red foxes", "Corvids", "Brushtail possums", "Birds of prey", "Artamids" and "Other birds" (see section 3.7 Supplementary Information: Table S2 for further details on grouping). To decrease the influence of highly abundant species, species group abundances were square-root transformed. We modelled bioregion, season, and habitat against differences in species composition using permutational multivariate analysis of variance (PERMANOVA) via *adonis* (Package: vegan; Oksanen et al. 2012). Differences were calculated using the Bray-Curtis metric because this excludes joint

species absences in the calculation of pair-wise similarity. We permuted dissimilarities within seasons 999 times to assess significance. Because *adonis* models do not accommodate *post hoc* analyses, we investigated significant main effects further using non-metric multidimensional scaling (nMDS).

3.3.3.2 Carcass use

To determine how bioregion, season, and habitat affected vertebrate use of carcasses, we constructed GLMs of total scavenging events at each carcass using the negative binomial distribution and a log-link function, and bioregion (*Alpine, Forest, Desert*), season (*cool, warm*) and habitat (*open, closed*) as independent variables. We tested the total time spent scavenging by (i) all mammals, (ii) all birds and (iii) all reptiles on each carcass. We also considered the total time spent scavenging by the 4 most active scavenging species or species groups defined in our multivariate analyses, including (iv) dingoes, (v) red foxes, (vi) birds of prey and (vii) corvids (see section 3.7 Supplementary Information: Table S2 for further details on grouping). The negative binomial distribution was used because data were overdispersed (Global model: φ =19.01; P < 0.001) and because quasipoisson models did not produce acceptable residual versus fitted plots. We interpreted a model fitted with all possible parameters and the bioregion × season and bioregion × habitat interactions where possible. We used Holm-Bonferroni log-rank *post hoc* analyses to investigate differences in the total feeding times across the three bioregions, and the interaction terms bioregion × season and bioregion × habitat. For models where data were deficient (i.e. the models for reptiles, dingoes, and foxes), we dropped the interactions until convergent models were obtained, and conducted further GLMs on subsets of the data to capture differences between seasons and habitats within the different bioregions. We visually assessed model-predicted values against residual values to confirm that all models met their necessary assumptions.

3.4 Results

We conducted successful camera monitoring at 119 kangaroo carcasses over a total of 3,570 camera trap days, resulting in the collection of 1,483,601 images between March 2018 and August 2019. Twenty-seven vertebrate scavenger species were identified (see section 3.7 Supplementary Information: Table S1), including 19 avian, 5 mammalian and 3 reptilian species. This total included species that were suspected to be feeding on insects associated with carcasses (e.g. fly and beetle larvae), but not off the meat biomass itself: willie wagtails, white-winged choughs, kookaburras, Indian mynas, magpie larks, and military dragons. No nationally

or regionally endangered species were identified; however, the total did include four introduced species: the red fox, feral pig, feral cat, and Indian myna (*Acridotheres tristis*).

3.4.1 Scavenger community structure

Across all sites combined, the mean species richness ($\alpha \pm$ s.e.) was 4.28 ± 0.15 (n = 119; range 1–9) on each carcass. Season had a significant effect on species richness (Table 3.1a), with cool seasons harbouring higher richness (5.17 ± 0.21 species) than warm seasons (3.40 ± 0.13). *Post hoc* Holm-Bonferroni log-rank tests indicated that species richness was higher in the Forest than the Alpine bioregion (p = 0.033), but that there were no differences between the Desert and the Forest (p = 0.283) or Alpine bioregion (p = 0.586). Further, species richness in the Forest and Desert bioregions was higher in the cool compared to the warm seasons (Forest: p < 0.001 and Desert: p < 0.001), but there were no differences between seasons for the Alpine bioregion (p = 0.467). There were no differences in species richness between closed and open habitats in any of the study bioregions (Forest: p = 0.201, Desert: p = 0.168 and Alpine: p = 0.943).

Average scavenger abundance on each carcass was 12.24 ± 0.60 (n = 119; range: 2–31). Cool seasons had higher scavenger abundance (15.36 ± 0.95 individuals) than warm seasons (9.18 ± 0.49 individuals) and average abundance was higher in open (14.00 ± 0.91 individuals) than in closed habitat (10.52 ± 0.73 individuals; Table 3.1b). Additionally, *post hoc* Holm-Bonferroni log-rank tests showed that abundance was higher in the Forest and Desert bioregions than the Alpine bioregion (Forest; 13.05 ± 0.92 individuals– Alpine; 8.44 ± 0.62 individuals; p < 0.001, Desert; 15.15 ± 1.20 individuals– Alpine; p < 0.001), but there were no differences between Forest and Desert bioregions (p = 0.576). *Post hoc* Holm-Bonferroni log-rank tests also indicated that abundance was higher in the cool compared to the warm seasons and the open compared to the closed habitats in Forest and Desert bioregions (both Forest and Desert; season: p < 0.001, habitat: p = 0.003) but was similar across seasons and habitats in the Alpine bioregion (season: p = 0.054, habitat: p = 0.148).

Table 3.1. Results of the generalised linear models (GLMs), testing for differences in scavenger species richness (A) and abundance (B), across different bioregions, season, and habitats. Asterisk indicates significant (p ≤ 0.05) results.

Variables	Estimate	Std. error	z-value	p
(A) Species richness				
(Intercept)	1.226	0.139	8.81	<0.001*
Region [Desert]	-0.223	0.208	-1.08	0.282
Region [Alpine]	-0.009	0.203	-0.04	0.966
Season [Cool]	0.495	0.147	3.38	0.001*
Habitat [Open]	0.182	0.143	1.28	0.201
Region [Desert] × Season [Cool]	0.086	0.217	0.40	0.692
Region [Alpine]× Season [Cool]	-0.372	0.223	-1.67	0.096
Region [Desert] × Habitat [Open]	0.030	0.210	0.14	0.886
Region [Alpine] × Habitat [Open]	-0.170	0.221	-0.77	0.440
(B) Total abundance				
(Intercept)	2.226	0.099	22.43	<0.001*
Region [Desert]	-0.184	0.143	-1.29	0.198
Region [Alpine]	-0.312	0.151	-2.06	0.039*
Season [Cool]	0.313	0.107	2.94	0.003*
Habitat [Open]	0.321	0.107	3.01	0.003*
Region [Desert] × Season [Cool]	0.535	0.151	3.55	<0.001*
Region [Alpine] × Season [Cool]	-0.071	0.165	-0.43	0.668
Region [Desert] × Season [Cool]	-0.015	0.148	-0.10	0.919
Region [Alpine] × Season [Cool]	-0.139	0.165	-0.84	0.399

Local scavenger guild centroids (*adonis*) differed across the categories of bioregion ($F_{(2, 110)} = 44.33$, $p = 0.001$), season ($F_{(1, 110)} = 19.27$, $p = 0.001$) and habitat ($F_{(1, 110)} = 8.97$, $p = 0.001$) with significant interactions between bioregion and season ($F_{(2, 110)} = 12.06$, $p = 0.001$) and bioregion and habitat ($F_{(2, 110)} = 2.87$, $p = 0.002$). Less than half of the variation in scavenger guild structure was explained (residual $R^2 = 0.428$), and bioregion ($R^2 = 0.345$) explained > 4.6 times more variation in scavenger guild dissimilarity than season ($R^2 = 0.075$) and > 9.8 times more variation than habitat ($R^2 = 0.035$). Visualizing carcass type centroids (nMDS), we

identified separation between all three bioregions in multivariate space (Figure 3.2). Separation was also clear between different seasons in each bioregion, although it was less clear between seasons at the Alpine bioregion and between habitats across all bioregions (see section 3.7 Supplementary Information: Figure S2). The percentage occurrence of species calculations indicated that the most frequent vertebrate scavenging animals at carcasses were ravens (73.9% of carcasses), red foxes (65.5%), dingoes (61.3%), wedge-tailed eagles (47.9%), and little crows (32.8%). The most frequent carcass visitors in the Forest bioregion were dingoes (97.5%), and then ravens (77.5%) and red foxes (70.0%). In the Alpine bioregion, the most frequent visitors were ravens (89.7%) and then dingoes and feral pigs (both 56.4%), and red foxes (51.3%). In the Desert bioregion, little crows visited almost all carcasses (97.5%) with red foxes (75.0%), wedge-tailed eagles (65.0%) and ravens (55.0%) the next most frequent visitors.

3.4.2 Carcass use

Every monitored kangaroo carcass (n = 119) was detected by at least one vertebrate species. Overall, avian species were the first to detect 73.1% of carcasses ($\alpha \pm$ s.e.: 77.89 ± 11.56 hours to detection; n = 112), while mammals detected 19.3% ($\alpha \pm$ s.e.: 127.4 ± 11.87 hours to detection; n = 116) of carcasses first and reptiles 7.6% ($\alpha \pm$ s.e.: 105.8 ± 27.5 hours to detection; n = 23) of carcasses first. The most common species to first detect carcasses were Australian ravens and little crows (57.1% collectively), with red foxes the most common mammal species to first detect carcasses (8.4%) and lace goannas the only reptile to detect any carcasses first (7.6%). Of all 119 kangaroo carcasses that were monitored for the full 30-day period, 99.2% (n = 118) were fed upon by vertebrates. Birds fed on 87.4% of carcasses (n = 104), while mammals fed on 83.2% (n = 99) of carcasses and reptiles on 17.6% (n = 21) of carcasses.

Mammals and birds spent more time scavenging carcasses in cool compared to warm seasons, but mammals didn't differ in terms of their scavenging activity across habitat types and birds spent more time scavenging carcasses in open compared to closed habitats (Figure 3.3; Table 3.2). *Post hoc* Holm-Bonferroni log-rank tests showed that mammals scavenged for longer in the Forest compared to the Desert bioregion (p = 0.008) and in the Alpine compared to Desert bioregion (p = 0.031), while birds scavenged for longer in the Desert compared to the Forest (p < 0.001) and the Alpine bioregion (p = 0.037) (Figure 3.3). Scavenging time was similar for both mammals and birds across Forest and Alpine bioregions (mammals: p = 0.888; birds: p = 0.330) (Figure 3.3). Mammals and birds spent longer times feeding on carcasses in cool
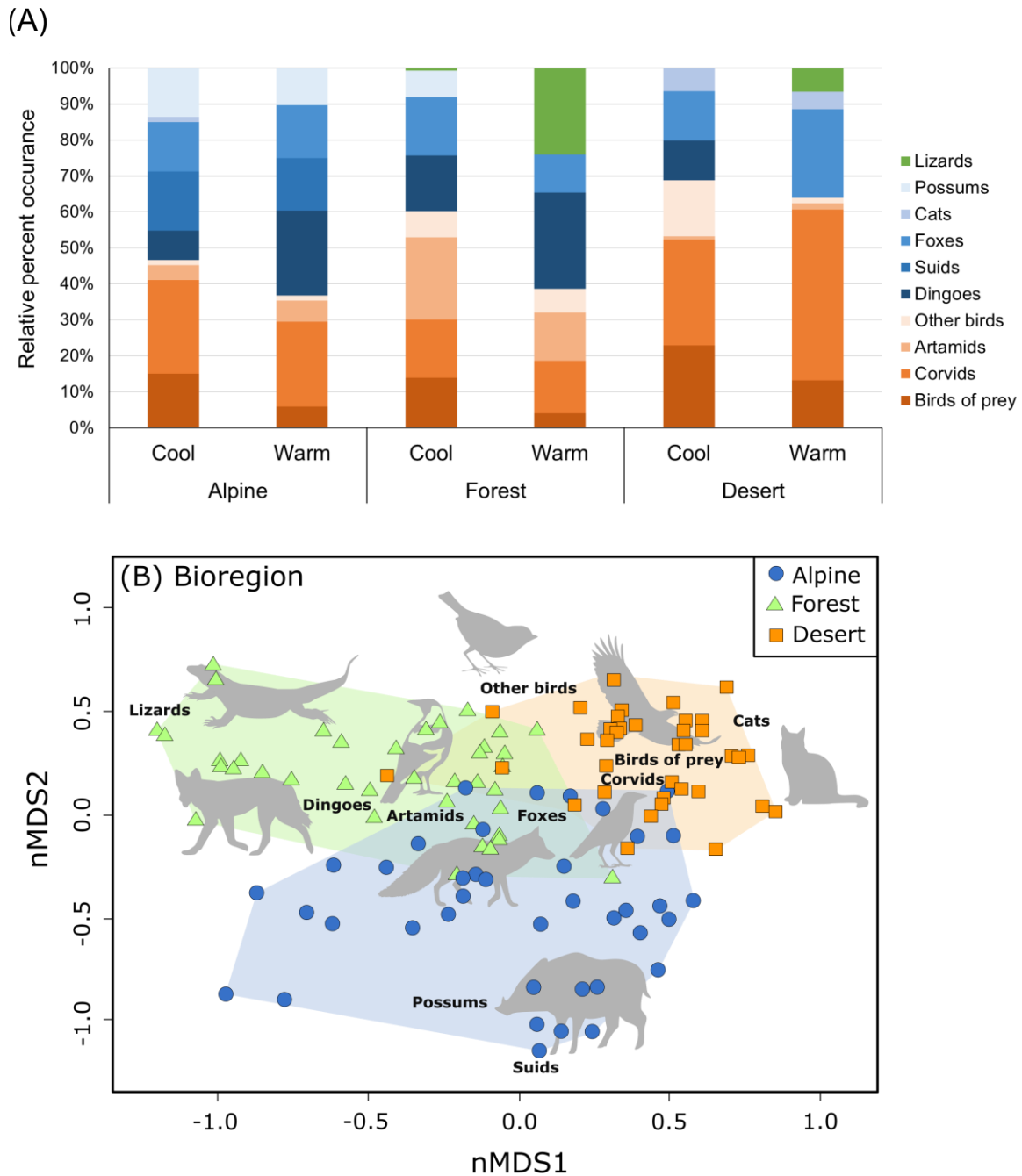
Figure 3.2. Structure and composition of scavenger communities at kangaroo carcasses across different seasons (cool, warm) and bioregions (Alpine, Forest and Desert). (A) Bar plot showing occurrence (as percentage relative to the sum of all the occurrence frequencies at each season and bioregion; top). (B) nMDS plot showing the similarity of the scavenger communities considering the groups in the bar plots (bottom). See 3.7 Supplementary Information: Table S2 for further details on the groups.
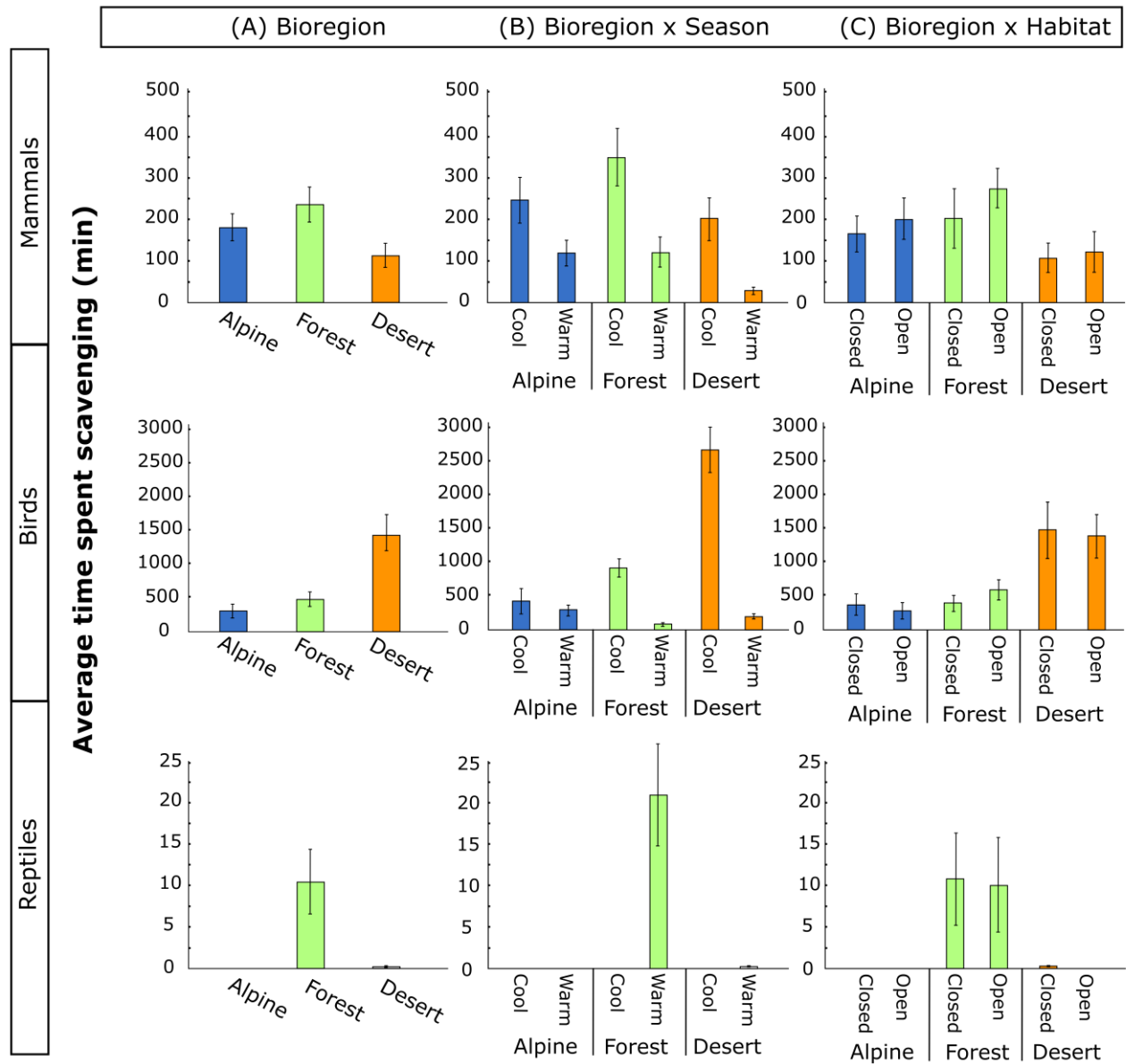
Figure 3.3 Average time (± standard error) spent scavenging by all mammals, all birds, and all reptiles, across different bioregions (A), different seasons within different bioregions (B) and different habitats within different bioregions (C).

Table 3.2. Results of the generalised linear models (GLMs), testing for differences in carcass use (i.e. total scavenging time) at carcass by mammals only (A) and birds only (B), across different bioregions, seasons, and habitats. Asterisk indicates significant ($p \leq 0.05$) results.

Variables	Estimate	Std. error	z-value	p
(A) Scavenging mammals				
(Intercept)	5.385	0.414	13.01	<0.001*
Region [Desert]	-0.202	0.584	-0.35	0.730
Region [Alpine]	0.226	0.584	0.39	0.698
Season [Cool]	0.270	0.482	0.56	0.576
Habitat [Open]	-0.760	0.482	-1.58	0.115
Region [Desert] × Season [Cool]	-0.024	0.679	-0.04	0.972
Region [Alpine] × Season [Cool]	0.281	0.678	0.42	0.678
Region [Desert] × Habitat [Open]	-1.284	0.679	-1.89	0.059
Region [Alpine] × Habitat [Open]	-0.419	0.678	-0.62	0.536
(B) Scavenging birds				
(Intercept)	6.115	0.393	15.57	<0.001*
Region [Desert]	1.644	0.554	2.97	0.003*
Region [Alpine]	0.126	0.555	0.23	0.820
Season [Cool]	-0.304	0.458	-0.66	0.507
Habitat [Open]	-0.421	0.458	-0.92	0.358
Region [Desert] × Season [Cool]	0.617	0.643	0.96	0.337
Region [Alpine] × Season [Cool]	1.701	0.644	2.64	0.008*
Region [Desert] × Habitat [Open]	-2.320	0.643	-3.61	<0.001*
Region [Alpine] × Habitat [Open]	-2.869	0.644	-4.46	<0.001*

compared to warm seasons in the Forest (mammals: $p = 0.013$; birds: $p < 0.001$) and Desert (mammals and birds: $p < 0.001$) bioregions, but scavenging times were similar across seasons for the Alpine bioregion (mammals: $p = 0.115$; birds: $p = 0.358$) (Figure 3.3). For mammals, scavenging time was similar across habitats for all bioregions (Alpine: $p = 0.576$; Forest: $p = 0.247$; Desert: $p = 0.606$), while for birds scavenging time was similar across habitats in the Alpine ($p = 0.507$) and Desert ($p = 0.488$) bioregions, but was higher in the open compared to the closed habitat in the Forest ($p = 0.002$) (Figure 3.3). Almost all scavenging recorded by reptiles were in the Forest bioregion (98.1% of total time spent scavenging across the three

bioregions), with all events occurring in the cool season. In the Forest bioregion, for reptiles, there were no differences in scavenging times across habitat (p = 0.936) (Figure 3.3).

Dingoes, red foxes, birds of prey, and corvids all spent more time scavenging carcasses in cool compared to warm seasons, but dingoes and foxes didn't differ in terms of their scavenging activity across habitat types while birds of prey and corvids spent more time scavenging carcasses in open compared to closed habitats (Table 3.3). P*ost hoc* Holm-Bonferroni log-rank tests showed that dingoes scavenged for longer in the Forest compared to the Desert (p < 0.001) and the Alpine compared to Desert bioregions (p = 0.005) (Figure 3.4). On the other hand, red foxes, birds of prey, and corvids generally scavenged for longest in the Desert bioregion, with all three species/groups scavenging for longer in the Desert compared to the Alpine bioregion (foxes: p < 0.001; birds of prey: p = 0.032; corvids: p = 0.008), and foxes and corvids also scavenging for longer in Desert compared to the Forest bioregion (foxes/corvids: p < 0.001) (Figure 3.4). Dingoes spent longer feeding in the cool season in the Forest bioregion (p = 0.035) and did not feed in the warm season in the Desert but fed on carcasses for longer in the warm season in the Alpine bioregion (p = 0.008) (Figure 3.4). Foxes spent longer feeding on carcasses in the cool season in the Desert bioregion (p < 0.001), and they fed only in the cool season in the Forest bioregion (Figure 3.4). Both birds of prey and corvids fed on carcasses for longer in the cool season in the Forest and Desert bioregion (all p values < 0.001), and birds of prey also spent longer feeding on carcasses in the cool season in the Alpine bioregion (p < 0.001), while corvids spent longer scavenging on carcasses in the warm season in this bioregion (p = 0.016) (Figure 3.4). For dingoes, scavenging time was similar across habitats for all bioregions, while there was some evidence for foxes scavenging longer in the open in the Desert bioregion (p = 0.018) and for birds of prey in the open in the Alpine bioregion (p = 0.008) and for both birds of prey and corvids in the Forest bioregion (p = 0.001) (Figure 3.4).

Table 3.3. Results of the generalised linear models (GLMs), testing for differences in carcass use (i.e. total scavenging time) at carcass by Dingoes (A), red foxes (B), birds of prey (C), and corvids (D) across different bioregions, seasons, and habitats. Asterisk indicates significant (p ≤ 0.05) results.

Variables	Estimate	Std. error	z-value	p
(A) Dingoes				
(Intercept)	4.215	0.617	6.84	<0.001*
Region [Desert]	-2.375	0.809	-2.94	0.003*
Region [Alpine]	-0.763	0.807	-0.95	0.344

Season [Cool]	1.027	0.469	2.19	0.029*
Habitat [Open]	0.804	0.806	1.00	0.319
Region [Desert] × Habitat [Open]	-1.171	1.145	-1.02	0.307
Region [Alpine] × Habitat [Open]	-0.808	1.148	-0.70	0.482
(B) Red foxes				
(Intercept)	-1.322	0.684	-1.93	0.053
Region [Desert]	3.910	0.679	5.76	<0.001*
Region [Alpine]	-1.995	0.789	-2.53	0.011*
Season [Cool]	5.161	0.618	8.35	<0.001*
Habitat [Open]	0.048	0.588	0.08	0.936
(C) Birds of prey				
(Intercept)	-0.389	0.798	-0.49	0.626
Region [Desert]	2.411	1.097	2.20	0.028*
Region [Alpine]	-0.599	1.159	-0.52	0.605
Season [Cool]	4.494	0.884	5.08	<0.001*
Habitat [Open]	2.859	0.884	3.24	0.001*
Region [Desert] × Season [Cool]	-2.387	1.237	-1.93	0.054
Region [Alpine] × Season [Cool]	-0.420	1.271	-0.33	0.741
Region [Desert] × Habitat [Open]	-0.172	1.237	-0.14	0.889
Region [Alpine] × Habitat [Open]	0.724	1.272	0.57	0.569
(D) Corvids				
(Intercept)	2.891	0.388	7.45	<0.001*
Region [Desert]	1.827	0.546	3.34	0.001*
Region [Alpine]	2.922	0.547	5.34	<0.001*
Season [Cool]	2.847	0.446	6.39	<0.001*
Habitat [Open]	0.995	0.446	2.23	0.026*
Region [Desert] × Season [Cool]	-0.606	0.629	-0.96	0.335
Region [Alpine] × Season [Cool]	-3.548	0.633	-5.60	<0.001*
Region [Desert] × Habitat [Open]	-0.492	0.629	-0.78	0.434
Region [Alpine] × Habitat [Open]	-1.624	0.633	-2.56	0.010*
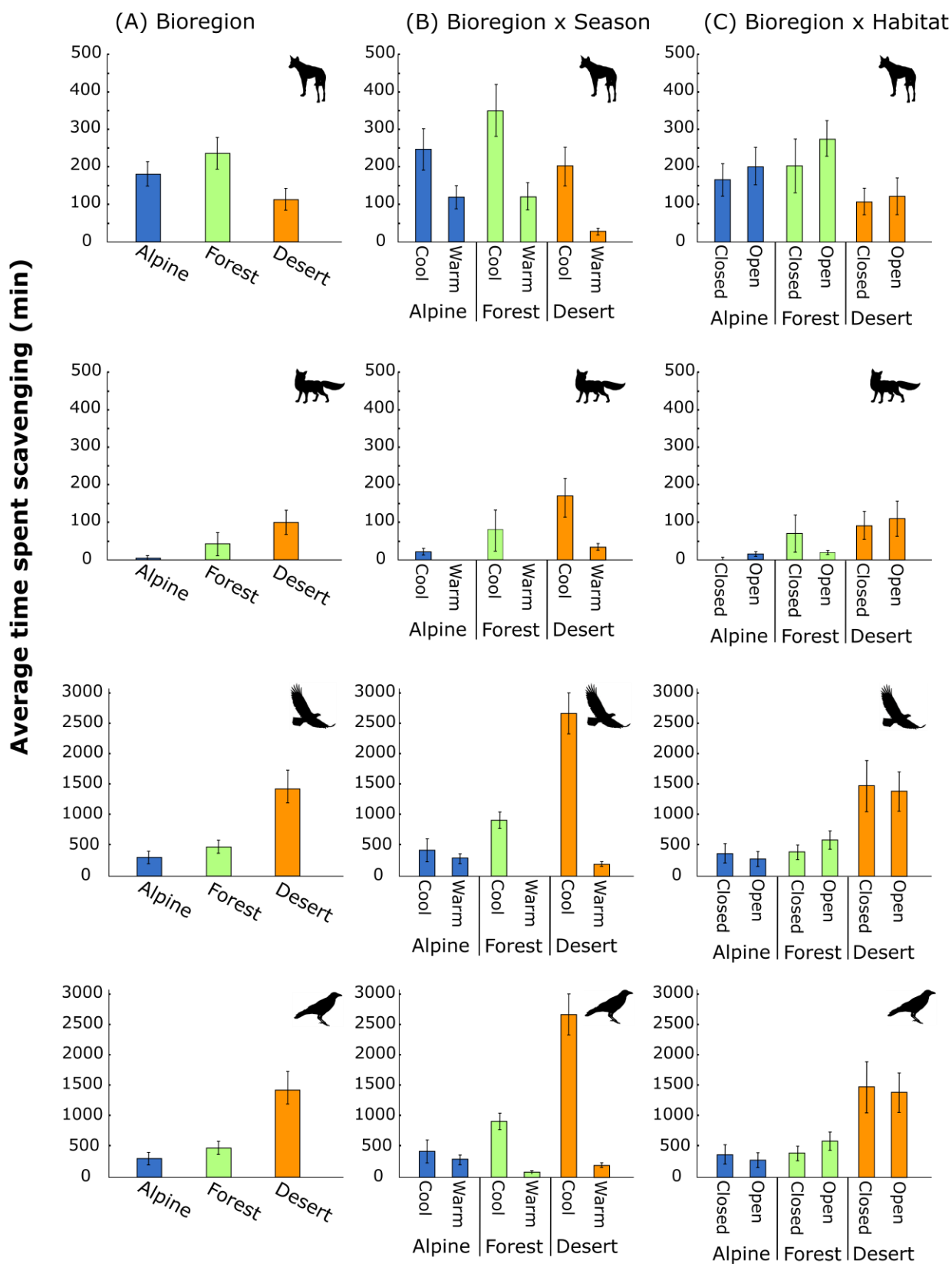
Figure 3.4 Average time (± standard error) spent scavenging by dingoes, red foxes, birds of prey and corvids across different bioregions (A), different seasons within different bioregions (B) and different habitats within different bioregions (C).

3.5 Discussion

Our results highlight the highly variable nature of vertebrate scavenging and the importance of context dependency at local and biogeographic scales in terrestrial ecosystems. They also add novel information on the carrion-associated vertebrate communities that characterise key Australian bioregions. Twenty-seven species were recorded using carrion resources across the three focal bioregions, far exceeding numbers recorded in any previous Australian mainland study (e.g. Brown et al. 2015; Forsyth et al. 2014; Read & Wilson 2004). Across regional scales, as anticipated, there was clear variation in carrion-associated vertebrate communities (*Prediction 1*), although the most common animals that scavenged remains such as corvids, red foxes, dingoes, and wedge-tailed eagles, were generally present in every bioregion. Seasonal variation also played a strong role in shaping scavenger communities and, as predicted, vertebrate carcass use generally differed across seasons with most scavenging activity occurring during cooler seasons (*Prediction 2*). There was, however, some seasonal variability across the three bioregions, for the different animal groups examined. For example, while most mammals and birds scavenged more in cool seasons across the three bioregions, in the Alpine bioregion dingoes and corvids were more active in the warm. Finally, we also saw some variation in vertebrate carcass use across habitats, and there was variation in the effects of habitat on different species (*Prediction 3*), but there was also variation across the bioregions. For example, while birds of prey used carcasses more in open habitats in the Forest and Alpine bioregions, and corvids and foxes in the Forest and Desert bioregions, respectively, their use of carcasses was not affected by habitat in any of the other study bioregions. We expand upon our findings against our three predictions below and discuss how multi-scale environmental context shapes the use of carcass resources by a variety of different taxa, as well as the impacts that scavenging and carrion resources can have on ecosystems more broadly.

3.5.1 Prediction 1: variation in scavenger community structure is most pronounced across different bioregions

As predicted, the greatest variation in scavenger community composition occurred between bioregions. Indeed, our multivariate analyses showed clear separation between the scavenger communities recorded across the three bioregions, and bioregion explained > 4.6 times more variation in scavenger guild dissimilarity than season and > 9.8 times more than habitat. Part of this variation can be explained by the presence or absence of species in each of the study bioregions. Different geographic bioregions are generally characterised by different climatic

conditions and habitat types, which along with other factors, influence the potential pool of species that is available to scavenge (Mittelbach and McGill 2019). Common brush-tailed possums, for example, were observed on carcasses in the Forest and Alpine bioregions, but not in the Desert bioregion, probably due to water limitation and a lack of suitable trees for shelter and breeding in the arid zone (Kerle et al. 1992). Further, feral pigs were found scavenging in the Alpine bioregion only, where open grasslands provide optimal grazing habitat (Saunders 1993). The Desert bioregion, on the other hand, provides less attractive habitat for the pig (Dexter 1998, Wardle et al. 2015), and while suitable habitat existed in the Forest bioregion, the high surrounding cliffs that characterise the study area, coupled with the heavy persecution of the animal in the area (e.g. via baiting, shooting, and poisoning) may have prevented its spread into the bioregion. Finally, reptiles were observed scavenging only in the Desert and the Forest bioregions, probably because the cooler temperatures in the higher altitude sub-alpine Alpine bioregion provided less favourable conditions for cold-blooded animals (Hamilton et al. 2021).

Most species recorded during our study were, however, observed scavenging across all bioregions. This was unsurprising, as our study bioregions were situated on the same continent, and certain animal groups and species are generally more likely to scavenge (DeVault et al. 2003). However, there were still differences in carcass use across bioregions for these species. Variation in scavenger community structure was therefore not related solely to whether a species resided in the bioregion. Instead, it probably also reflected variables such as the local abundances, as well the dietary habits and scavenging efficiency (i.e. ability to locate and consume carcasses) of the species present. For example, corvids (Australian ravens, little ravens, and little crows), and to a lesser extent, wedge-tailed eagles, were often recorded in high abundances at carcass sites in each bioregion. Corvids are some of the most common scavengers, not only in Australia (Read and Wilson 2004, Rees et al. 2020), but also globally, especially where vultures are absent (DeVault et al. 2003, Mateo-Tomás et al. 2015). Eagles also take advantage of carcass resources and readily exploit hunter-kills (Selva et al. 2005, Mateo-Tomás et al. 2015). In our study, corvids and birds of prey including wedge-tailed eagles scavenged most frequently in the Desert study bioregion. In arid environments where animal densities are usually low and resources sparse, birds might have an advantage as scavengers because their capacity for flight allows them to efficiently search large areas (Schmidt-Nielsen 1972).

For mammalian scavengers, dingoes and red foxes were the most frequent carcass visitors across all sites. Interestingly, like birds, scavenging by foxes was most common in the Desert bioregion, while dingoes used carcasses most frequently in the Forest and Alpine bioregions. Globally, scavenging by canids is common (Wirsing and Newsome 2021) and dingoes and foxes have been recorded scavenging previously in temperate and arid systems in Australia (Read and Wilson 2004, Allen 2010, Forsyth et al. 2014, Rees et al. 2020). The infrequent scavenging by dingoes in the Desert bioregion probably reflected their low densities at the time of study, resulting from the reduced productivity and resources that followed bioregional droughts. Extended drought periods in the Simpson Desert generally result in low animal densities, with dingo populations typically far lower than those of smaller predators like foxes and cats (Greenville et al. 2014). The lower dingo densities in the Desert bioregion may, however, also explain why foxes used carcasses more frequently here. Lower densities or absence of larger mammalian predators such as the dingo may encourage reduced competition for carrion resources (DeVault et al. 2011). Finally, feral cats, while common in the Forest and Alpine bioregions, frequented carcasses only in the Desert bioregion. This again probably reflected reduced resource availability in the arid zone (especially as our study was conducted during a dry period); cats often show a preference for live prey (Paltridge et al. 1997), but carcasses could support feral cats in the arid zone, especially when alternative resources are sparse.

Of note, we also recorded variation in the total number of species using carcasses across the three study bioregions. Specifically, we observed more scavenging species in the temperate environment of the Forest bioregion, compared with the desert and sub-alpine environments of Desert and the Alpine bioregions (Forest: 18 species; Desert and Alpine: 13 in each). Similarly, we also found higher average scavenger species abundance in the Forest compared to the Alpine bioregion. These findings support previous studies, which indicate that species richness, and scavenger species richness specifically, may be lower in more extreme biomes, including low productivity environments (Field et al. 2009, Mateo-Tomás et al. 2015).

3.5.2 Prediction 2: carcass use differs seasonally, with most scavenging occurring in cooler seasons

Our study revealed that season was an important factor affecting scavenging patterns and that, in general, cooler seasons facilitated greater overall carcass use as well as average scavenger species richness and abundance. Indeed, birds and mammals, and especially birds of prey,

showed greatest carcass use in cooler seasons. This result is in line with previous studies examining the effects of seasonality on vertebrate scavenger assemblages (Selva et al. 2005, Turner et al. 2017) and probably reflects the reduced activity of insects and microbes during cooler periods. Lower insect and microbe activity may result in greater carcass persistence times, meaning that carcasses are accessible for scavenging animals for longer periods. Supporting this interpretation, we generally observed reduced insect presence on carcasses (see: Thesis Chapter 2), and slower carcass decomposition, during cooler compared to warmer seasons (carcass persistence averaged across all bioregions ± s.e. cool: 13.3 ± 1.4 days, warm: 6.7 ± 0.5 days). Apart from being outcompeted by insects and microbes, these vertebrate species may have also been less active in the warmer periods to preserve water and prevent overheating during times of high temperature (Cook 2012), especially in the Desert bioregion where temperatures can reach upwards of 40-50°C. Additionally, the reduced presence of scavengers in warmer periods (when most rapid carcass decomposition occurs) may have resulted from their preference for fresher carcasses, in the earlier stages of decomposition (Field and Reynolds 2013). Finally, it is also possible that these animals showed a stronger preference for feeding on carcasses during the cool season, as alternative food may have scarcer than in the warm period (Needham et al. 2014). Surveys of landscape productivity and food availability that are conducted concurrent to carcass studies would help provide support for or against this possibility.

When examining how season differed within the study bioregions, we did, however, observe some variability in the results. Increased scavenging by varanids in warmer periods was unsurprising, as reptiles are ectotherms and tend to be most active in warmer seasons. It was also interesting that varanids were the most frequent scavengers at carcasses in certain bioregions. For example, 90% of carcasses in the warm season in the Forest were scavenged by these animals. Such high presence of reptiles is important to note, as scavenging by reptiles is not commonly reported (but see T. DeVault & Krochmal 2002), and globally reptiles are often dismissed as opportunistic or otherwise unimportant scavengers (Mateo-Tomás et al. 2015). However, like these studies we probably also underestimated reptile activity on carcasses. Our cameras traps were programmed to detect motion by thermal activity and were therefore not optimised for detecting smaller reptiles (Meek et al. 2014). We also observed similar overall average species richness across seasons in the Alpine bioregion, while average species richness was always higher in the cool season in the Forest and Desert bioregions. This finding may reflect differences in the average temperatures, and corresponding insect and

microbial activity and carcass persistence, experienced across seasons in each study bioregion. Indeed, while the two different study seasons in the Forest and Desert bioregions averaged maximum and minimum temperatures that differed by 11-14°C across the two seasons, in the Alpine bioregion temperature differences were less than 6°C (see section 3.7 Supplementary Information: Figure S1). Further, carcass persistence was longer in the warmer season in the Alpine bioregion compared to both the Forest and Desert bioregions (Figure 2.6).

3.5.3 Prediction 3: there is habitat variation in the use of carcasses by vertebrates, with the effects of habitat on carcass use varying across different animal groups and species

Perhaps unsurprisingly, habitat had the smallest influence on scavenger species composition, and most vertebrate species used carcasses similarly across both the closed and open habitat types. While carcasses were spaced by at least 1 km during each study period, the two habitats were in close proximity of each other (generally 50–100 m apart). In general, most of the scavenging animals recorded were relatively mobile and able to move between both habitats in search of food. Habitat preferences likely did still play a role carcass discovery and use for some species (Hager et al. 2012). For example, brush-tailed possums were typically recorded on carcasses only in closed habitats due to their requirement for trees for foraging and breeding, and their preference for foraging in areas adjacent to their den (Ji et al. 2003). Further, there was also evidence that some animals, particularly birds of prey, spent more time using carcasses in open habitats in the Desert and Forest bioregions. Carcasses may have been encountered more often in the open due to the higher visibility of carcasses in that habitat type. This is supported by the fact that birds and especially birds of prey are predominantly biased to visual detection of food resources (Pardo-Barquín et al. 2019). Further research into the effects that specific micro- and macrohabitat vegetation and landscape characterises have on scavenging patterns would be beneficial to achieve greater understanding of the effects of habitat across the three study bioregions (e.g. Pardo-Barquín et al. 2019).

3.5.4 Conclusions and implications

Our study contributes to understanding of the use of carrion resources by a variety of different vertebrate scavengers in various environmental contexts. It also has important implications for building knowledge around some of the wider impacts that scavenging, and carcasses may have on ecosystems. Particularly, it elicits the question: if scavenging is highly variable across different seasons and habitats within and between bioregions, then do the associated ecosystem

services provided by scavengers vary similarly too? For example, differences in dingo scavenging between the Alpine and Forest bioregions and the Desert bioregion may influence regional carcass removal rates and nutrient cycling. This species is not only capable of consuming large volumes of meat (Corbett and Newsome 1987) but also of breaking apart bones that birds and smaller mammals cannot. The frequent use of carcasses by transitory bird species (i.e. little crows) in the Desert bioregion may also have implications for nutrient dispersal, as birds can travel long distances from centralised resources to deposit faeces (Uriarte et al. 2011). The extensive use of carcasses by red foxes across all bioregions and feral cats in the Desert bioregion means that carcasses may influence the impacts of invasive species on vulnerable animals in these locations (Abernethy et al. 2016). For example, predation by invasive species may be increased or redirected if carcasses bolster predator numbers or shift predator activities to certain locations (Read and Wilson 2004). Alternatively, these invasive species may also provide important carrion removal services, especially in locations where larger scavenging animals, such as the dingo, may be absent or reduced in the environment as a result of human persecution (e.g. lethal control) (Glen et al. 2007, DeVault et al. 2011). Carcasses may also influence the impacts of invasive species in other ways, for example, by redirecting grazing and other forms of environmental destruction to areas where carcasses are present. This was observed incidentally in the Alpine bioregion, where scavenging feral pigs dug up the area surrounding experimental carcasses, but these effects deserve greater focus in future studies.

Several prior studies explore the impacts of scavengers on surrounding ecosystems (e.g. Cortés-Avizanda, Carrete, et al. 2009; Cortés-Avizanda, Selva, et al. 2009), but have focused largely on native predator-prey interactions and have incorporated little consideration of environmental drivers and different spatial and temporal scales. We therefore support further studies that address these gaps, including those that target systems where invasive facultative scavengers are abundant. Studies should also focus on assessing key services that scavengers provide, such as nutrient dispersal, cycling and carcass removal, and should do so in the context of a range of different environmental drivers. Finally, we support further development of large-scale multi-system and standardised approaches to surveying global scavenger assemblages (e.g. see Newsome et al. 2021). While our study provides one of the most extensive surveys of vertebrate scavengers, covering multiple bioregions, seasons and habitats and including over one hundred large (~30 kg) animal carcasses, it still represents only a few snapshots in time and space. Further research should incorporate larger temporal and spatial scales in carrion and

scavenger community surveys. This includes surveys conducted over multiple seasons, across multiple years, and that span multiple bioregions and continents, across environmental gradients such as productivity and altitudinal gradients. Only then will we improve understanding of the different local and regional drivers that shape scavenger communities and the services they provide, disentangle complex interactions, and build a framework that reflects global scavenging trends.

3.5.5 Acknowledgements

3.6 References

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3.7 Supplementary Information

Table S1 Percentage (%) frequency of occurrence of vertebrate scavenger species observed visiting kangaroo carcasses across bioregions (Alpine, Forest, Desert) and seasons (warm, cool) based on carcass trials completed between March 2018 and August 2019, in Australia. Dominant bird, mammal and reptile species for each site and season shown in bold.

Species	Alpine		Forest		Desert		Overall % occurrence
	Cool (n = 19)	Warm (n = 20)	Cool (n = 20)	Warm (n = 20)	Cool (n = 20)	Warm (n = 20)	(n = 119)
Birds							
Corvid species (*Corvus* spp.)	100.0	80.0	100.0	55.0	100.0	95.0	88.2
Raven species (Corvus mellori or C. coronoides)	100.0	80.0	100.0	55.0	60.0	50.0	73.9
Little crow (Corvus bennetti)	0.0	0.0	0.0	0.0	100.0	95.0	32.8
Wedge-tailed eagle (*Aquila audax*)	47.4	20.0	75.0	15.0	90.0	40.0	47.9
Australian magpie (*Gymnorhina tibicen*)	5.3	15.0	50.0	45.0	5.0	5.0	21.0
Willie wagtail** (Rhipidura leucophrys)	0.0	0.0	0.0	10.0	85.0	5.0	16.8
Pied currawong (Strepera graculina)	10.5	5.0	55.0	5.0	0.0	0.0	12.6
White-winged Chough** (*Corcorax melanorhamphos*)	0.0	0.0	30.0	10.0	0.0	0.0	6.7
Black kite (Milvus migrans)	0.0	0.0	0.0	0.0	20.0	0.0	3.4
Pied butcherbird (Cracticus nigrogularis)	0.0	0.0	20.0	0.0	0.0	0.0	3.4

Brown falcon (*Falco berigora*)	0.0	0.0	0.0	0.0	15.0	0.0	2.5
Grey butcherbird (*Cracticus torquatus*)	0.0	0.0	15.0	0.0	0.0	0.0	2.5
Brown goshawk (Accipiter fasciatus)	5.3	0.0	5.0	0.0	0.0	0.0	1.7
White-Faced heron (Egretta novaehollandiae)	0.0	0.0	10.0	0.0	0.0	0.0	1.7
Kookaburra** (Dacelo novaeguineae)	5.3	5.0	0.0	0.0	0.0	0.0	1.7
Indian myna* (Acridotheres tristis)	0.0	0.0	0.0	5.0	0.0	0.0	0.8
Grey goshawk (Accipiter novaehollandiae)	0.0	0.0	5.0	0.0	0.0	0.0	0.8
Magpie lark** (Grallina cyanoleuca)	0.0	0.0	5.0	0.0	0.0	0.0	0.8
Little eagle (Hieraaetus morphnoides)	5.3	0.0	0.0	0.0	0.0	0.0	0.8
Mammals							
Red fox* (Vulpes vulpes)	52.6	50.0	100.0	40.0	75.0	75.0	65.5
Dingo (Canis dingo)	31.6	80.0	95.0	100.0	60.0	0.0	61.3
Common brushtail Possum (Trichosurus vulpecula)	52.6	35.0	45.0	0.0	0.0	0.0	21.8
Feral pig* (*Sus scrofa*)	63.2	50.0	0.0	0.0	0.0	0.0	18.5
Feral cat* (*Felis catus*)	5.3	0.0	0.0	0.0	35.0	15.0	9.2
Reptiles							
Lace goanna (*Varanus varius*)	0.0	0.0	5.0	90.0	0.0	0.0	16.0

Sand goanna (Varanus gouldii)	0.0	0.0	0.0	0.0	0.0	15.0	2.5
Military dragon** (Ctenophorus isolepis)	0.0	0.0	0.0	0.0	0.0	5.0	0.8

* Invasive species

** Species suspected to be feeding on arthropods associated with carcasses (e.g. fly and beetle larvae)

Table S2 Table showing the species groups and corresponding species used in scavenger community composition analyses (PERMANOVA, nMDS). Five of these species groups were also used in carcass use analyses (GLMs), including reptiles, dingoes, red foxes, birds of prey and corvids.

Species group	Diet details	Species included
Reptiles	Generalists	Lace goanna, Sand goanna, Military dragon
Suids	Generalists	Feral pig
Dingoes	Apex predator (generalists)	Dingo
Feral cats	Mesopredator (specialist)	Feral cat
Red foxes	Mesopredator (generalist)	Red fox
Corvids	Generalist	Australian raven, little crow
Brushtail possums	Generalist	Common brushtail possum
Birds of prey	Specialist	Wedge-tailed eagle, Black kite, Brown falcon, Brown goshawk, Grey goshawk, Little eagle
Artamids	Generalist	Australian magpie, Pied currawong, Pied butcherbird, Grey butcherbird, Magpie lark
Other birds*	Generalist/mix	Willie wagtail, White-winged Chough, White-Faced heron, Kookaburra, Indian myna

* Mainly observed feeding on insects associated with carrion

Figure S2 nMDS plots showing the similarity of the scavenger communities at kangaroo carcasses across different seasons (cool, warm) and habitats (closed, open) for each bioregion (Alpine, Forest, Desert. Different seasons and habitats within bioregions are grouped either by dotted lines or shaded polygons. See section 3.7 Supplementary information: Table S2 for further details on the groups.
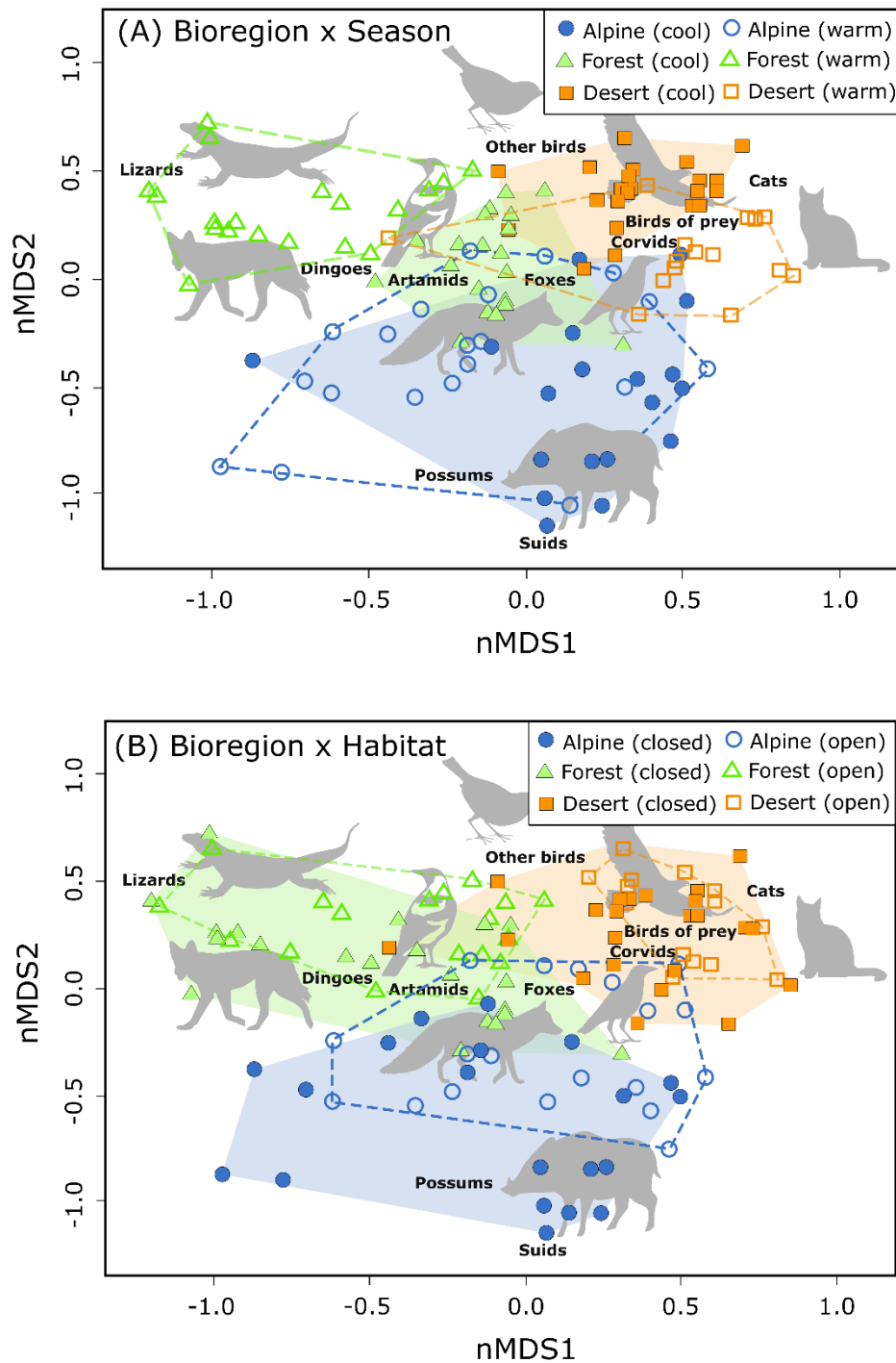
Figure S3 Average time (± SE) until carcass removal (<5% biomass remaining) in warm and cool seasons across the three bioregions.
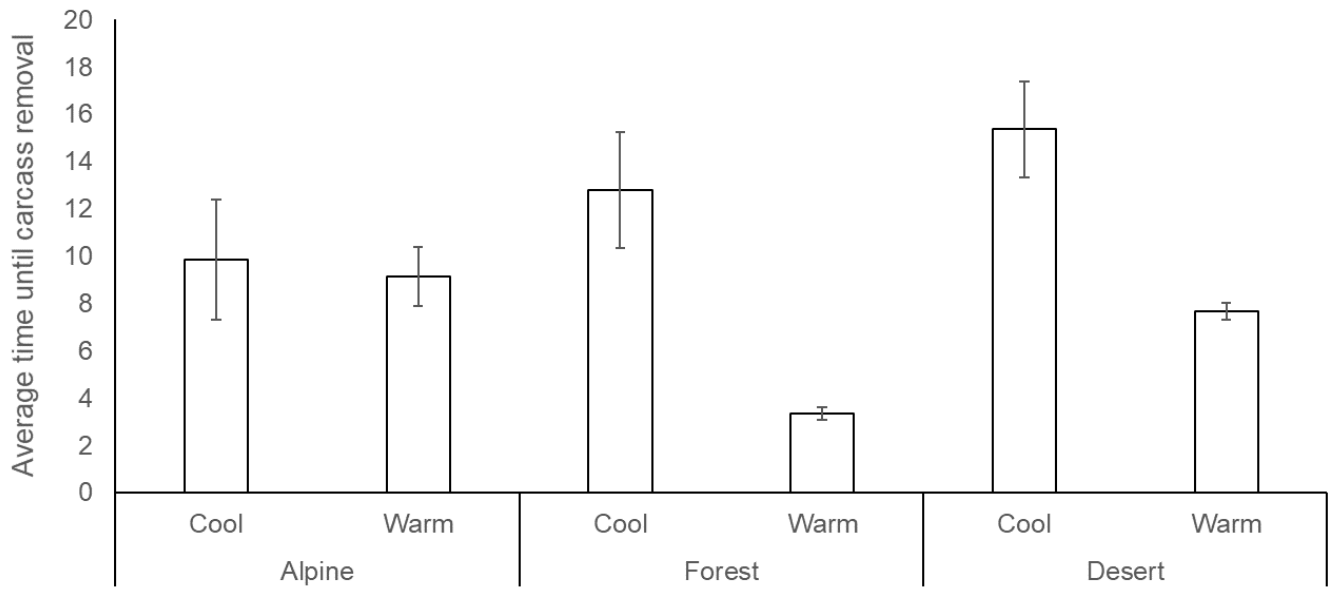
CHAPTER 4

DINGOES DINING WITH DEATH

Dingo visiting a carcass site in Kosciuszko National Park (the Alpine bioregion). Photograph by Emma Spencer.

A version of this chapter was published as Spencer, E. E., and T. M. Newsome. 2021. Dingoes Dining with Death. Australian Zoologist 41:433–51.

My contribution for this paper was very substantial, and included conceptualisation of ideas, leading fieldwork, data collation and analysis, and writing and editing all drafts, in consultation with my co-authors.

4.1 Abstract

Dingoes (*Canis dingo*) are known for hunting and killing animals to meet their energetic requirements, but like almost all predators they also scavenge animal remains. To improve our understanding of dingo scavenging ecology, we investigated the role of abiotic and biotic factors in shaping carcass utilisation by dingoes and further determined whether dingo scavenging influenced carcass persistence in the landscape. To do so, we monitored visitation and scavenging by dingoes using remote cameras positioned on 119 kangaroo carcasses in open and closed canopy habitats and in warm and cool seasons. The carcasses were monitored across multiple study sites, which incorporated forest, alpine and desert ecoregions in Australia. We found that season played an important role in shaping carcass utilisation by dingoes, as well as carcass persistence. Warmer seasons increased the rate of carcass discovery 6.3-fold in the Forest study site and 4.8-fold in the Alpine study site, and also increased the time dingoes spent feeding on carcasses in the Alpine study site. Further, across all study sites, carcasses persisted at least 4.7 times longer in cool compared with warm seasons. On the other hand, carcass utilisation by dingoes was not influenced by habitat, although carcasses were more likely to persist in open compared with closed canopy habitats in the Alpine study site. Finally, our study showed that dingo scavenging may contribute to substantial carcass removal in certain contexts. Indeed, decreased carcass persistence in the Forest study site was evident in the cool season, when dingo scavenging occurred during the first two weeks of monitoring. The variability in results highlights the complexity of patterns in dingo scavenging and, more broadly, of vertebrate scavenging. It emphasises the need to consider multiple abiotic and biotic factors to properly understand the functional roles of different scavenger species. Longer-term studies with additional seasonal replicates may also yield a more detailed picture of the role of dingoes as apex scavengers.

4.2 Introduction

The diet of the dingo (*Canis dingo*), including hybrids (*Canis dingo* x *Canis familiaris*) is well-studied across a range of Australian environments (Doherty et al. 2019). There is substantial variability in the prey species dingoes consume and their dietary habits are often linked to the abundance of prey (Corbett and Newsome 1987). Dingoes typically show preferences for medium to large prey, in particular for macropods (e.g. kangaroos) and rabbits (*Oryctolagus cuniculus*; Whitehouse 1977), although rodents and reptiles can also comprise major dietary components (Paltridge 2002). Across resource-poor landscapes, arthropods, fruits, and

vegetation often supplement their feeding (Spencer et al. 2014), and in human-modified environments, livestock and garbage may feature (Brook and Kutt 2011; Newsome et al. 2014). Further, while dingoes are well known for hunting and killing animals to meet their energetic requirements, they also scavenge animal remains (Brook and Kutt 2011; Davis et al. 2015; Newsome et al. 1983).

In Australia, animal carcasses are abundant. In addition to natural deaths of macropods and other herbivores, millions of carcasses are produced from road-kills or as a result of conservation and agricultural culls (Englefield et al. 2018). In recent times, Australia has witnessed the production of high densities of animal carcasses in localised areas following mass animal mortality events, or "die-offs", which have occurred as a result of heatwaves, droughts, floods, and bushfires. These carcasses may be utilised by dingoes and could provide an important resource when alternative foods are scarce. Indeed, patterns of dingo scavenging may be linked to fluctuations in their preferred prey (Thomson 1992) and, during drought periods, dingoes have been observed feeding on cattle carcasses, and even cannibalising remains of their own (Allen 2010). Carcasses produced via anthropogenic practices such as hunting, and fishing may also provide an important subsidy for dingoes. Dingoes have been recorded scavenging on carcasses of shot deer (Forsyth et al. 2014) and the remains of sea-life left behind by recreational fishers (Déaux et al. 2018).

Apart from the potential benefits of carcass resources to the dingoes themselves, dingo scavenging may accelerate the break-down of carcasses. Dingoes are the largest native terrestrial mammalian carnivore in Australia, and can form packs of more than 10 individuals, making them capable of quickly consuming large prey items (Thomson 1992). The ability of dingoes to rapidly consume carcasses is important, as carcasses may attract and support invasive species (Abernethy et al. 2016) or become a hub for disease spread (Jennelle et al. 2009). Dingo scavenging may also regulate carcass use by smaller scavengers, either by facilitating access to carcass meat by piercing tough animal hides or by provoking behavioural avoidance through fear effects (Cunningham et al. 2018; Wikenros et al. 2014). Evidence for dingoes exerting strong suppressive effects on other species via predation is accumulating (e.g. Glen et al. 2007; Letnic and Koch 2010; Ritchie et al. 2013), but little attention has been paid to understanding the role of dingoes as apex scavengers. This gap in our understanding influences how we think about dingo interactions with other species, including how they influence prey populations, and how they impact the agricultural industry via predation of

livestock. It also affects the ecological value that we place on dingoes; for example, as a contributor to important ecosystem services such as carcass removal.

To improve our understanding of dingo scavenging ecology, it is important to explore the basic abiotic and biotic factors that may influence their use of carcasses. It is well established that temperature affects carcass persistence, with warmer conditions promoting microbial and insect activity, which increases carcass decomposition (Payne 1965; Putman 1978). Carcasses in warmer seasons may also provide stronger olfactory attractants (DeVault and Rhodes 2002). Habitat complexity can further affect carcass detection and rates of scavenging, by changing the visual conspicuousness of carcasses. Carcass detection by vertebrate scavengers at the Savannah River site in South Carolina, USA, for example, was highest in open, clear-cut habitats (Turner et al. 2017). Similarly, in Poland most vertebrates, including free-roaming domesticated dogs, scavenged on ungulate carcasses more in open grassland compared to closed canopy habitats (Selva et al. 2005).

Here we investigate the scavenging patterns of dingoes on hunter-shot kangaroo carcasses at three study sites—an alpine, a forest, and a desert ecoregion—in Australia. Within these study sites we explore the effects of abiotic and biotic factors, including season and habitat, on carcass use by dingoes. To do so, we distributed kangaroo carcasses in warm and cool seasons and across open (i.e. no canopy cover) and closed canopy (i.e. woodland/dune valley) habitats and measured dingo carcass detection rates and scavenging times, as well as rates of carcass persistence. Across all study sites, we predicted that season and habitat would influence carcass use by dingoes. Across all study sites, we predicted that season and habitat would influence carcass use by dingoes. Specifically, we predicted that dingoes would show (1) increased carcass discovery in warmer seasons and in open habitats, and (2) greater foraging activity in cool seasons when competition with insects and microbes is reduced. We also predicted that (3) carcass persistence would be shorter in warmer seasons and as a result of dingo scavenging.

4.3 Methods

4.3.1 Study sites

Our study sites cover two locations in New South Wales and one in Queensland, Australia. These sites were selected as they are home to a moderate-sized population of dingoes and represent diverse habitats. In particular, research was undertaken in the Wolgan Valley in the Blue Mountains, eastern New South Wales (NSW) ("Forest" study site; between August 2017

– February 2018), on the Snowy and Botherum Plains in Kosciuszko National Park, southern NSW ("Alpine" study site; between March 2018 – January 2019) and at Ethabuka Reserve in the Simpson Desert, western Queensland ("Desert" study site; between June – November 2018; Figure 4.1).
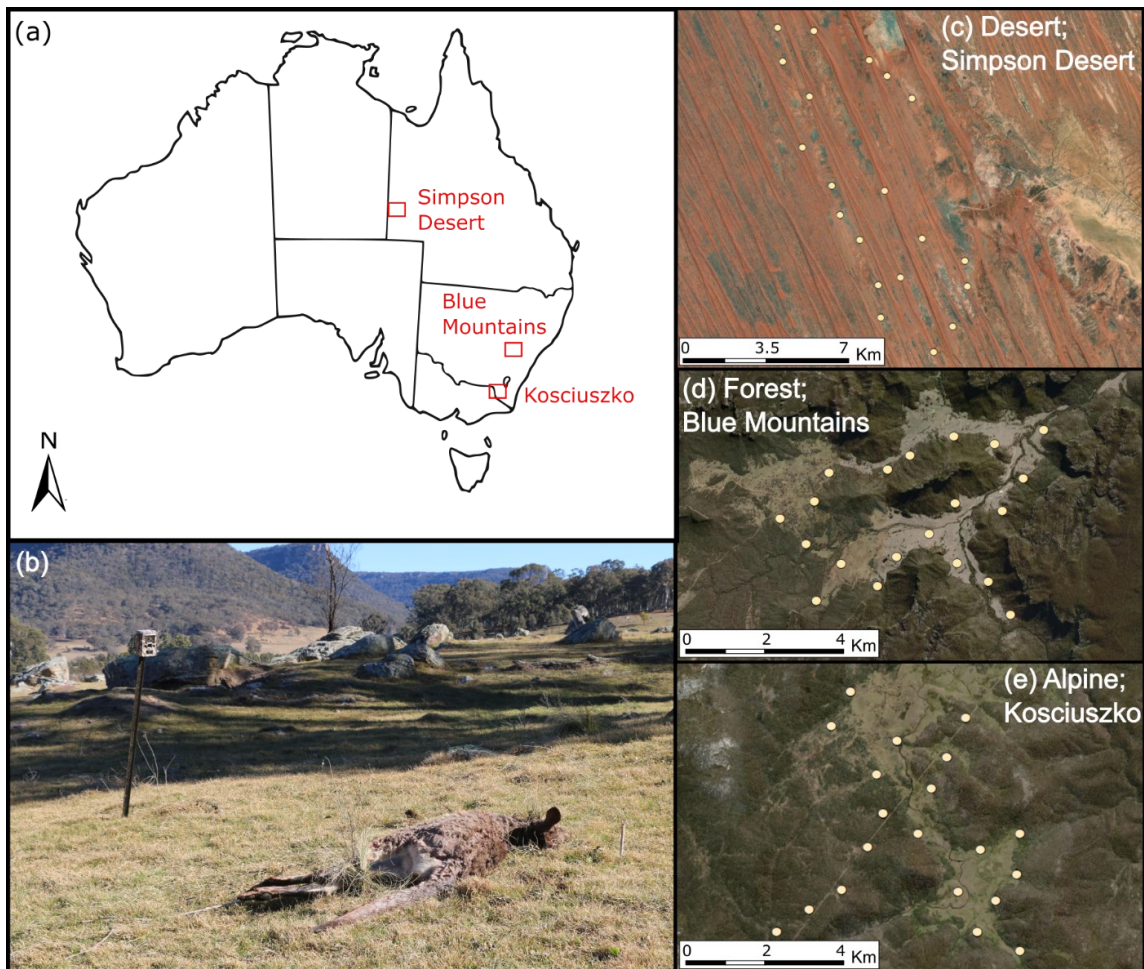
Figure 4.1 Study area map and carcass site set-up; (a) shows the location of the three study sites in Australia (boxes), (b) provides an example carcass site set-up with the remote monitoring camera positioned ~4 m from the staked kangaroo carcass. Satellite images provide examples of carcass site spatial spread in one study season at (c) the Desert study site, at Ethabuka Reserve in the Simpson Desert, western Queensland, (d) the Forest study site, in the Wolgan Valley, in the Blue Mountains, central NSW, and (e) the Alpine study site, at the Snowy and Botherum Plains in National Park, south-eastern NSW. Yellow circles on the satellite images mark the position of monitored kangaroo carcasses.

The Forest study site is approximately 50 km^2 in size (altitude: 540–680 m) and is positioned on the edge of the Greater Blue Mountains National Park. This area contains a mix of open woodland and grassland habitats, with various *Eucalyptus* species (e.g. *Eucalyptus viminalis* and *E. haemastoma*) and a mix of native (e.g. *Austrodanthonia* sp. and *Themeda triandra*) and introduced (e.g. *Microlaena stipoides*) grasses. The climate is temperate, with average maximum temperatures of 27°C recorded in January and 11°C in July (nearest station 30 km away at Lithgow, records from 1878 - 2020; Bureau of Meteorology 2020).

The Alpine study site encompasses approximately 70 km^2 in the eastern section of Kosciuszko National Park (altitude: 1305–1540 m). This area contains sub-alpine and montane forests and open grasslands. The dominant vegetation in the open grasslands is snow grass (*Poa* sp.), with non-native grass species including *Anthoxanthum odoratum* also abundant. Snow gums (*Eucalyptus pauciflora*) were the most common tree species observed in the closed canopy habitat. The average maximum temperature ranges from 23°C in January to –6°C in July (nearest station 20 km away at Perisher Valley, records from 2010 - 2020; Bureau of Meteorology 2020).

The Desert study site is located on the edge of the Simpson Desert and is a conservation property managed by Bush Heritage Australia. This area is approximately 80 km^2, at elevations between 65 and 120 m. The Simpson Desert is a hot desert, characterised by long, parallel sand dunes (Purdie 1984) and the prevailing habitat is hummock grassland dominated by hard spinifex (*Triodia basedowii*) (Wardle et al. 2015). There are differences in vegetation between the sand dune crests and the inter-dune valleys, with the crests lacking any tree cover and the valleys host to stands of gidgee trees (*Acacia georginae*). The climate is arid, with the hottest month, January, averaging maximums of 40°C and the coolest month, June, averaging maximums of 23°C (nearest station 100 km away at Bedourie, records from 1988 - 2020; Bureau of Meteorology 2020).

4.3.2 Carcass monitoring

In each study site, we distributed 20 kangaroo carcasses in both cool (winter and autumn) and warm (summer, spring) periods, with half placed in open and half placed in closed canopy habitats. Our study sites included a mix of grassland (open) and woodland (closed) habitats in the Forest and Alpine study sites, and dune crest (open) and valley (closed) habitats in the Desert study site. Open canopy habitats lacked canopy cover and were at least 50 m from any densely forested or vegetated land. Closed canopy habitats had more than 20% canopy cover.

We tried to ensure that these closed canopy sites were at least 50 m from any open space; however, this was not possible in the Desert study site due to the general sparsity of trees.

In each season, carcasses were separated by at least 1 km to mitigate scent travel between carcasses. We used dead, adult eastern grey kangaroos (*Macropus giganteus*; Forest and Alpine study sites) or dead adult red kangaroos (*Osphranter rufus;* Desert study site) sourced from nearby management culls. Any carcasses displaying evidence of disease (e.g. heavy parasite loads), were not used. Each carcass was placed into the field without freezing within 24 hours (warm period) or 36 hours (cool period) of collection. Scientific licenses/permits were obtained to relocate the kangaroo carcasses (SL 101901 and SPP WA0006737) and research was approved by the University of Sydney Animal Ethics Committee (Project number: 2017/1173).

To allow for ongoing monitoring and detection of dingoes visiting and feeding on each carcass, we fastened a Reconyx PC800 Hyperfire™ camera trap (Professional Reconyx Inc., Holmen, WI, USA) to a free-standing star picket, approximately 3–4 m away from each carcass. Each camera was programmed to take continuous photographs when triggered by thermal movement around the carcass (rapidfire, no wait period). To prevent complete removal of the carcasses from the remote camera monitoring frame, each carcass was secured to the ground by wire attaching the neck and Achilles tendon of the animal to two metal stakes spaced ~0.6 m apart. Cameras were used to monitor carcasses until only skin and bones remained (< 4 months); however, at the Alpine study site carcasses were monitored for only 30 days due to the high risk of camera theft.

4.3.3 Data collection

All photographs were tagged according to each new visitation event by one or more dingoes to a carcass, the number of dingoes present, whether the dingoes engaged in scavenging behaviour or not, and the date and time that the observation was recorded. A visitation event was considered new if it occurred ≥ 10 min from the previous visitation event by the same dingo. Different individual dingoes were identified using markings, size, and sex. We then extracted four values from the images that we tagged including: "presence", "scavenging", "discovery time" and "total feeding time". Presence was calculated as the number of carcasses that dingoes were recorded visiting, and scavenging was the number of carcasses where they were recorded feeding. Discovery time was calculated in decimal hours as the time between when the carcass was first positioned and the arrival of the first visiting dingo. Total feeding time was calculated as the sum of all feeding events at a given carcass for all dingoes. We calculated the duration

of a given feeding event by subtracting the time at the start of the visit from the time at the end of the visit. We rounded all feeding visits to the closest minute; however, for visits less than 30 seconds, we considered the species present for 1 min rather than 0 mins. Using a combination of in-person visual inspection of the carcasses and inspection of camera images, we determined the number of days until complete carcass consumption. A carcass was defined as completely consumed when only skin, hair and/or bone remained.

4.3.4 Statistical analysis

To test each prediction, we ran separate analyses for each study site. This is because our sampling effort differed across study sites (i.e. at the Alpine study site carcasses were monitored for only 30 days, whereas at the Desert and Forest study sites carcasses were monitored until complete decomposition), and because some study sites did not provide enough data points to statistically compare all predictor variables. Before conducting analyses, we also excluded data from one carcass site (from the cool season at the Alpine study site) due to camera theft occurring during the first 3 days of monitoring. We conducted all analyses in R Version 4.0.2 (R Development Core Team 2020).

To determine whether dingoes showed increased carcass discovery in warmer seasons and in open habitats (*Prediction 1*), we performed survival analyses using Cox proportional hazards models on the time taken for carcasses to be discovered in hours ("survival" package). Survival analyses work well with censored data (Hosmer et al. 2008). Carcass discovery data were right-censored because some carcasses were not discovered by dingoes by the end of monitoring periods (i.e. complete carcass decomposition; Forest and Desert study sites, or 1 month post carcass placement; Alpine study site). We ran three separate analyses investigating how long carcass discovery took in each study site. For the Forest (n = 40) and Alpine (n = 39) study sites, season (warm, cool) and habitat (open, closed) were used as the predictor variables. For the Desert study site (n = 40), only habitat (open, closed) was used as a predictor variable, because no dingoes were recorded on the carcasses in the warm period. We tested the proportional hazards assumption by visualising the survival curves and by testing the non-zero slope for the Schoenfeld residuals versus time (Therneau and Grambsch 2000). To visualise the results of these analyses, we separated data into carcasses monitored in warm or cool seasons, and in open and closed canopy habitats and present the Kaplan-Meier estimates of the survival function comparing two survival curves for each study site ("survival", "survminer"

and "ggplot2" packages). Finally, we also present the results of log-rank tests, comparing these survival curves.

To test if dingoes showed greater foraging activity in cool seasons (*Prediction 2*), we used generalised linear models (GLMs) to compare foraging activity for dingoes across season (warm, cool) and habitat (open, closed). Foraging data followed a negative binomial distribution and were zero-inflated. This indicated a two-process mechanism for data generation, which we modelled using hurdle models. For the first model, we conducted a GLM with binomial distribution and a log-link function using whether a dingo fed at a carcass as the response variable. For the second model, we conducted a GLM with negative binomial distribution and a log-link function using how long a dingo fed in minutes, from the non-zero data. For the Forest and Alpine study site, season (warm, cool) and habitat (open, closed) were used as the predictor variables in both models, but for the Alpine study site sparse data precluded inclusion of season from the second stage of modelling. For the Desert study site, only habitat was utilised in the models because no dingoes were recorded on the carcasses during the warm period. We visually assessed model predicted values against the residual values to confirm that each model met their necessary assumptions.

To determine whether carcass persistence would be reduced in warmer seasons and as a result of dingo scavenging (*Prediction 3*), we performed further survival analyses using Cox proportional hazards models on data for the time taken in days for complete carcass decomposition. Carcass persistence data were right-censored because some carcasses were not completely decomposed by the end of monitoring periods (i.e. n = 12 carcasses, during the cool monitoring period in the Alpine study site). We ran separate analyses investigating how long carcass decomposition took in each study site. To create our models, we used a combination of three predictor variables including season (warm, cool), habitat (open, closed) and presence or absence of dingo scavenging during the first two weeks of monitoring (as a binary measure). For the Forest study site, we also included the interaction term between season and dingo scavenging, to examine whether dingo scavenging influenced carcass persistence across different seasons. We did not have enough data to include this term in the Alpine or Desert study site, as only one carcass was scavenged by dingoes in the cool season at the Alpine study site and no carcasses were scavenged by dingoes during the warm season at the Desert study site. Instead, we conducted a second round of analyses for these two study sites, excluding data from the seasons where dingo scavenging was rare or absent. For these analyses, we used habitat (open, closed) and presence or absence of dingo scavenging during the first two weeks

of monitoring (as a binary measure). The presence or absence of dingo scavenging in the first two weeks was used rather than the presence of dingo scavenging across the entire monitoring period, as this is when most carcass biomass was lost. It also enabled us to exclude data where dingoes appeared on mostly-decomposed carcasses to chew on bones and so did not contribute much to the removal of carcass biomass. For all analyses, we tested the proportional hazards assumption, as for analyses conducted for prediction 1. To visualise the results of these analyses, we separated data into carcasses where dingo scavenging was present or absent during the second week of monitoring and where carcasses were monitored in warm or cool seasons and presented Kaplan-Meier estimates of the survival function comparing up to four survival curves for each study site. Again, we also presented the results of log-rank tests that compare these survival curves. For any significant interactions, we calculated the pairwise comparisons between group levels with Bonferroni corrections for multiple testing.

4.4 Results

We conducted successful camera trials on 119 kangaroo carcasses over a total of 9,427 days, collecting and analysing 54,823 images of dingoes, which yielded a total of 540 dingo visitation events (see section 4.8, the Photo Appendix, for further observations and comments on dingo behaviour observed around carcasses during the study).

4.4.1 Prediction 1: Increased carcass discovery in warmer seasons and in open habitats

Across all study sites, a total of 59 (50%) of the 119 carcasses were visited by dingoes, and 42 carcasses (35%) were fed upon by dingoes (Figure 4.2). The Forest study site had the highest carcass visitation (32 carcasses; 80%) and scavenging rates (25 carcasses; 63%) by dingoes (Figure 4.2). Dingoes visited 17 (44%) carcasses and scavenged 11 (28%) carcasses in the Alpine study site (Figure 4.2). In the Desert study site, dingo carcass visitation and scavenging were the lowest of all sites (visitation: 10 carcasses or 25% and scavenging: 6 carcasses or 15%; Figure 4.2). Dingoes generally discovered carcasses in the first 1 to 6 days, with carcass discovery in the Forest study site occurring between days 1 and 34, in the Alpine study site between days 1 and 24 and in the Desert study site between days 3 and 17. It took dingoes an average ($\pm$ se) of 197 $\pm$ 26 hours to discover carcasses, with average carcass discovery times in the Forest study site: 215 $\pm$ 45 hours, the Alpine study site: 158 $\pm$ 33 hours, and the Desert study site: 209 $\pm$ 36 hours (averages based on only those carcasses that were visited by dingoes; Figure 4.3).

In the Forest and Alpine study sites, kangaroo carcasses were discovered more quickly by dingoes in the warm season compared to the cool season (Figure 4.4; Table 4.1). In the warm season compared to the cool, carcasses were discovered by dingoes approximately 6.3-fold faster in the Forest study site, and 4.8-fold faster in the Alpine study site (Table 4.1). For the Desert study site, no carcasses were discovered by dingoes in the warm season (Figure 4.4). Habitat did not influence carcass discovery by dingoes in any study site (Figure 4.4; Table 4.1).
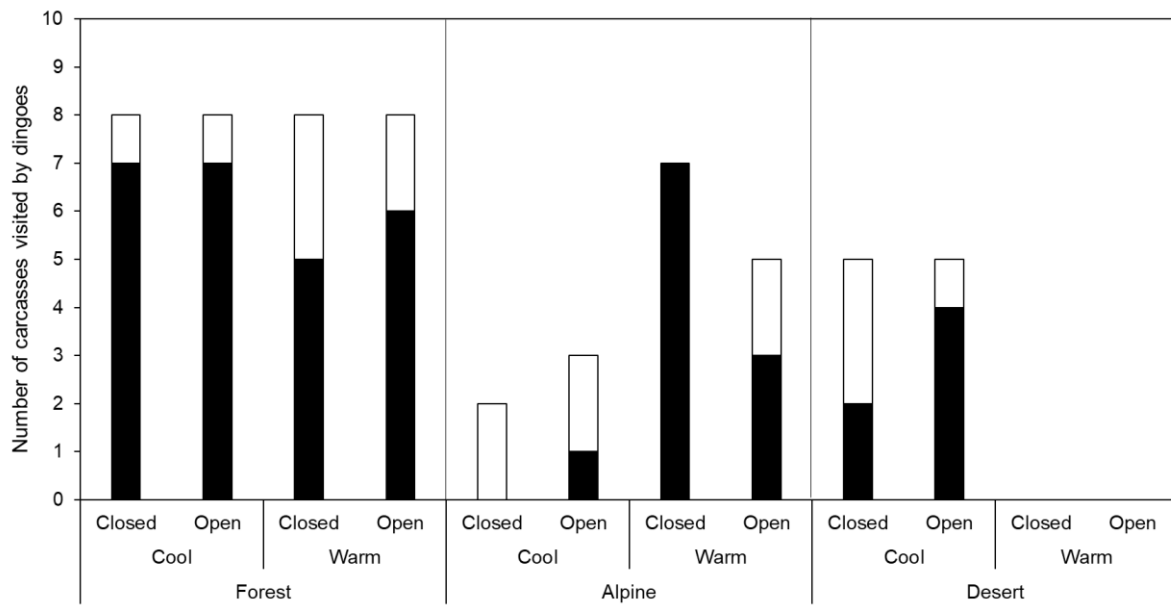
Figure 4.2 Dingo visitation of kangaroo carcasses (n = 119) across cool and warm seasons, open and closed canopy habitats, and in the Forest, Alpine and Desert study sites. The numbers of carcasses visited by dingoes are separated into the carcasses fed upon by dingoes (black bars) and carcasses visited but not fed upon by dingoes (white bars).
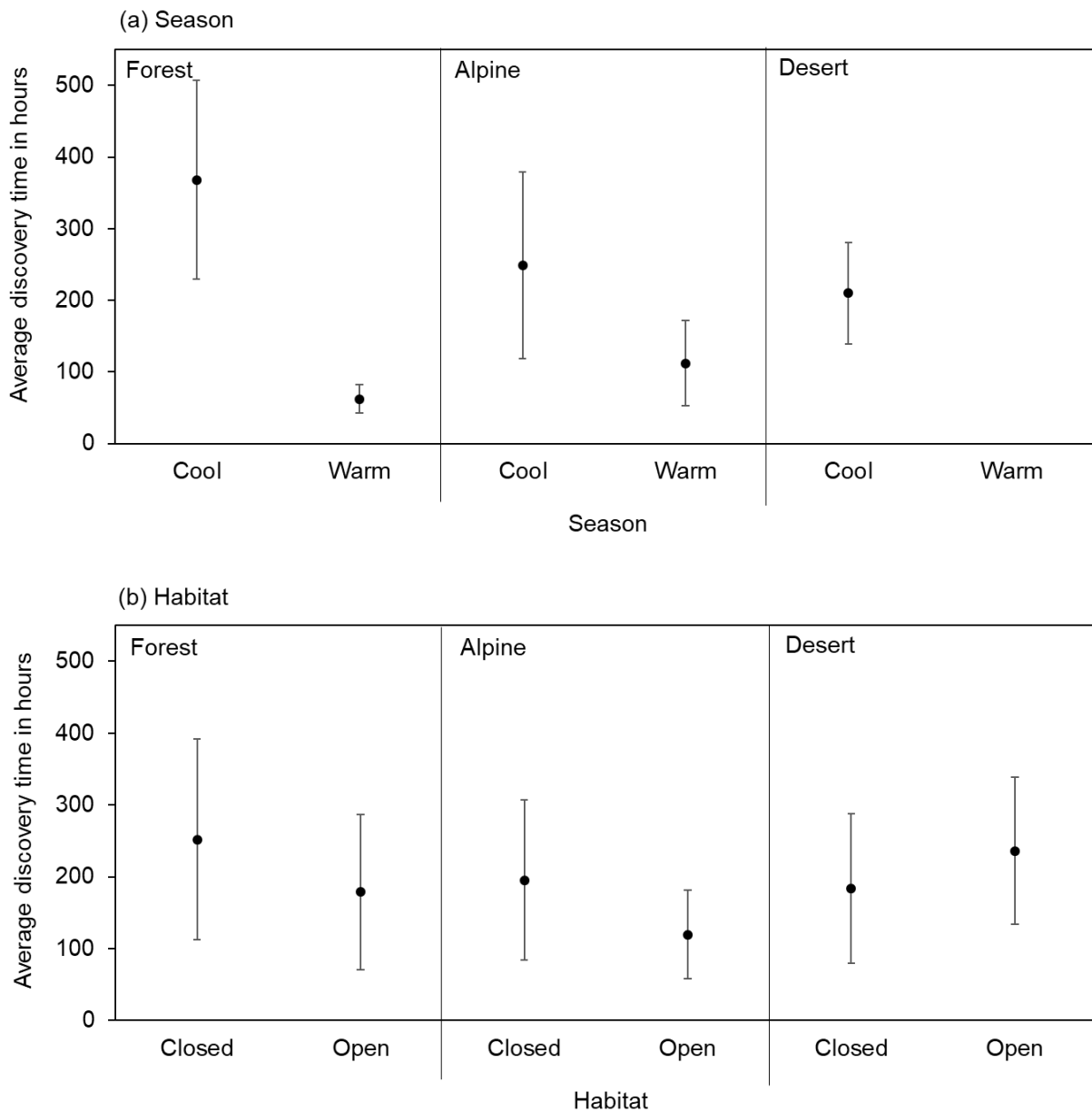
Figure 4.3 The average time in hours (± 95% confidence intervals) it took for carcasses to be discovered by dingoes during different (a) seasons and (b) habitats, across the Forest (n = 30), Alpine (n = 18) and Desert (n = 10) study sites. Averages and confidence intervals consider only those carcasses that were visited by dingoes. No dingoes visited carcasses in the warm period in the Desert study site.
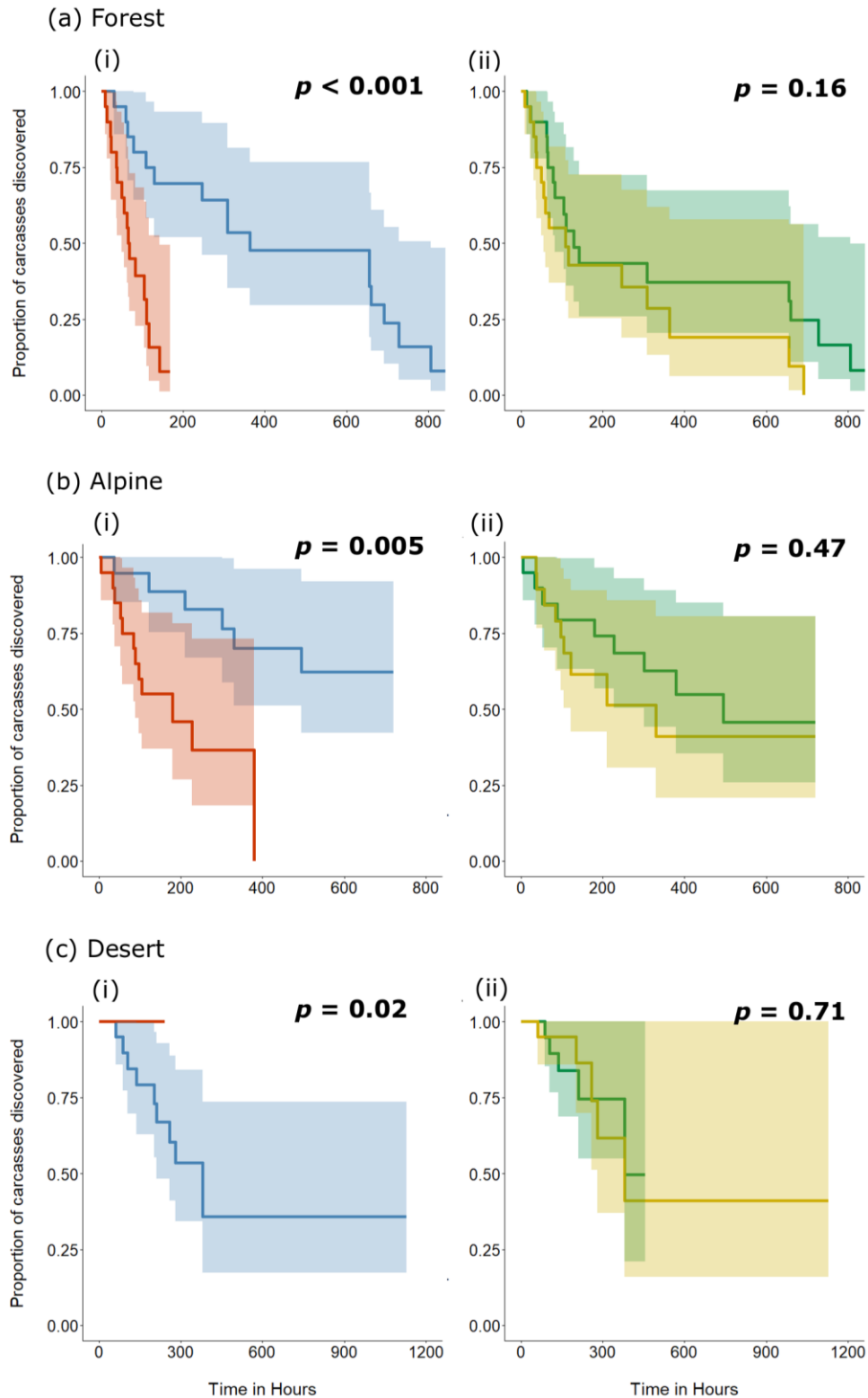
Figure 4.4 Kaplan-Meir estimate of the survival function for carcass discovery time by dingoes, divided into carcasses at the (a) Forest study site (n = 40), the (b) Alpine study site (n = 39), and the (c) Desert study site (n = 40), where (i) seasons were warm (red) or cool (blue), and where (ii) habitats were open (yellow) or closed (green) canopy. Light shading shows 95% confidence intervals. The *p*-values are from the log-rank tests comparing the survival curves.

Table 4.1 Cox proportional Hazards models testing for differences in carcass discovery time in hours across season and habitat in the Forest, Alpine, and Desert study sites, with parameter estimates, Hazard ratios, and associated standard error (SE). No dingoes visited carcasses in the warm period in the Desert study site.

Variables	Estimate	Hazard ratios**	SE	z-value	p	
Forest study site (n = 40)						*
Season	1.842	6.311	0.511	3.61	<0.001*	
Habitat	0.698	2.010	0.378	1.85	0.065	
Alpine study site (n = 39)						
Season	1.578	4.847	0.518	2.72	0.006*	
Habitat	0.552	1.736	0.518	1.07	0.287	
Desert study site (n = 40)						
Habitat	-0.240	0.787	0.639	-0.38	0.707	

Indicates significance; $p < 0.05$. ** Hazard ratios = exp(Estimate) and estimates the magnitude of the effect. Carcasses monitored in the warm season in the Forest study site, for example, were found 6.3 times faster by dingoes than carcasses monitored in cooler months in the Forest study site.

4.4.2 Prediction 2: Greater foraging activity in cool seasons

Dingoes generally fed on carcasses when they visited (~71% of visitations). Feeding in the Forest study site occurred until day 52, and in the Alpine and Desert study site until day 17. Of the carcasses that dingoes fed upon, they spent an average (± se) of 61 ± 11 minutes feeding. They fed on carcasses for an average of 52 ± 14 minutes at the Forest study site, 70 ± 21 minutes in the Alpine study site, and 80 ± 28 minutes in the Desert study site.

There were no associations between the presence of feeding, or the amount of time spent feeding, by dingoes on kangaroo carcasses, in warm and cool seasons or in open and closed canopy habitats at the Forest study site (Figure 4.5; Table 4.2). In the Alpine study site, dingoes fed on more carcasses in the warm compared to the cool season but there were no differences between the presence of dingo feeding across open and closed canopy habitat types (Figure 4.5; Table 4.2). At the Desert study site, dingoes spent longer feeding on carcasses in the closed canopy habitat compared to the open habitat (Figure 4.5; Table 4.2).
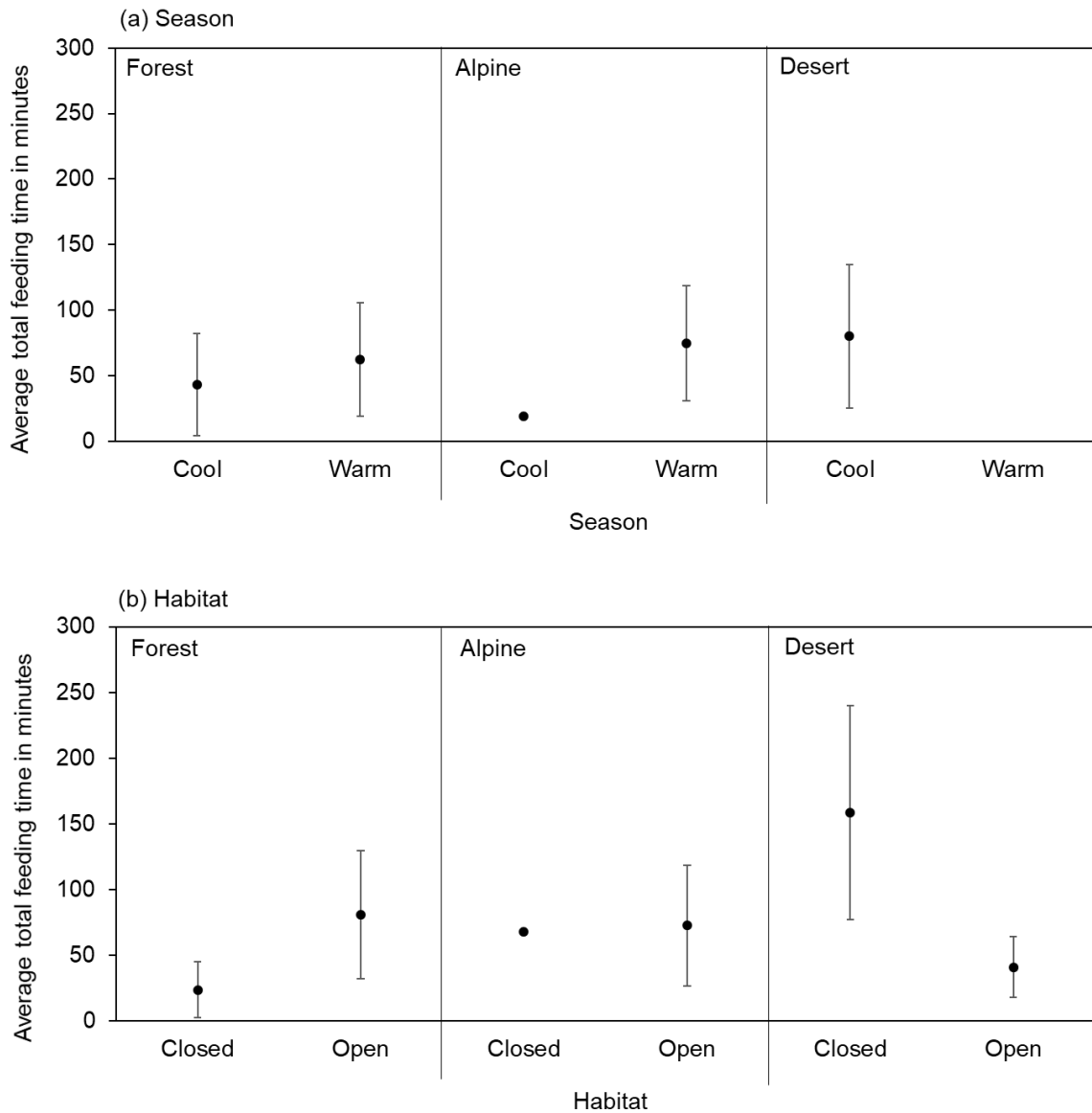
Figure 4.5 The average time in minutes (± 95% confidence intervals) dingoes fed on carcasses during different (a) seasons and (b) habitats, across Forest (n = 24), Alpine (n = 11), and Desert (n = 6) study sites. Averages and confidence intervals consider only those carcasses that were visited and fed upon by dingoes. No dingoes visited carcasses in the warm period in the Desert study site.

Table 4.2 Results of the hurdle models, testing for differences in the total time in minutes dingoes spent feeding at the Forest (n = 40), Alpine (n = 39), and Desert (n = 40) study sites. Tables show results of the: (a) generalised linear model (GLM) with binomial distribution testing whether dingoes fed at carcasses, and (b) GLM with negative binomial distribution testing how much time dingoes spent feeding at carcasses that they decided to feed from. No dingoes visited carcasses in the warm period in the Desert study site.

Variables	Estimate	SE	t-value	p
(a) Presence of feeding				
Forest study site				
Intercept	0.740	0.582	1.27	0.204
Season	-0.648	0.664	-0.98	0.329
Habitat	0.219	0.662	0.33	0.741
Alpine study site				
Intercept	-2.517	1.057	-2.38	0.017*
Season	3.029	1.150	2.64	0.008*
Habitat	-1.025	0.860	-1.19	0.233
Desert study site				
Intercept	-2.197	0.745	-2.95	0.003*
Habitat	0.811	0.932	0.87	0.384
(b) Time spent feeding				
Forest study site				
Intercept	2.575	0.719	3.58	<0.001*
Season	0.224	0.749	0.30	0.765
Habitat	1.314	0.745	1.76	0.078
Log(theta)	-1.498	0.779	-1.92	0.054
Alpine study site				
Intercept	4.183	0.443	9.44	<0.001*
Habitat	0.066	0.730	0.09	0.928
Log(theta)	-0.302	0.519	-0.58	0.560
Desert study site				
Intercept	5.066	0.269	18.81	<0.001*
Habitat	-1.352	0.337	-4.02	<0.001*
Log(theta)	1.975	0.649	3.05	0.002

* Indicates significance; $p < 0.05$.

4.4.3 Prediction 3: Reduced carcass persistence in warm seasons and where dingoes scavenge

Carcasses persisted for an average (± se) of 16 ± 4 days, with complete carcass decomposition taking between 2 and 66 days (Figure 4.6). In the Forest study site, carcasses persisted for an average (± se) of 19 ± 4 days (range 3 – 66 days; Figure 4.6). In the Alpine study site, carcasses persisted for an average (± se) of 16 ± 5 days (range 2 – 30 days; keeping in mind that carcass monitoring was capped at 30 days at this study site; Figure 4.6). In the Desert study site, carcasses persisted for an average (± se) of 14 ± 4 days (range 3 – 49 days; Figure 4.6).

Across all study sites, kangaroo carcasses persisted at least 4.7-fold longer in the cool seasons compared to warm seasons (Table 4.3; Figure 4.7; Figure 4.8a; Figure 4.9b). Dingo scavenging during the first two weeks of carcass monitoring reduced carcass persistence by 1.1-fold in the Forest study site (Table 4.3). At this study site, the interaction between season and dingo scavenging was also significant (Table 4.3; Figure 4.7). The post-hoc adjusted pairwise analyses indicated that in the cool period, carcass persistence was lower where dingoes scavenged in the first two weeks, compared to carcasses that were not scavenged by dingoes during this time (Bonferroni adjusted pairwise log rank test: $p = 0.016$). On the other hand, for the warm season, dingo scavenging during the first two weeks of monitoring was not found to influence rates of carcass persistence (Bonferroni adjusted pairwise log rank test: $p = 0.196$). At the Desert and the Alpine study sites, there was no difference in carcass persistence between carcasses where dingo scavenging was present or absent in the first two weeks (Table 4.3; Figure 4.8b; Figure 4.9b). This was the case when all seasons were considered, or when only the warm or the cool season was considered in the Alpine and Desert study sites, respectively (Table 4.3; Figure 4.8b; Figure 4.9b). Finally, in the Alpine study site, carcasses were 4.1-fold more likely to persist in open compared with closed canopy habitats, and there were no differences in carcass persistence times across habitats in the Forest or the Desert study site (Table 4.3).
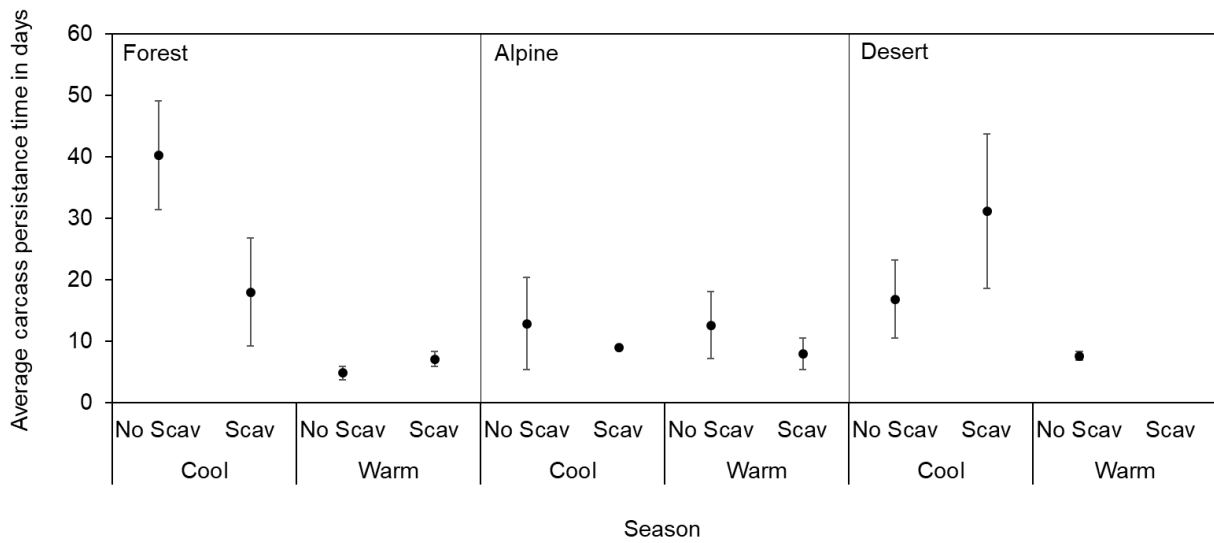
Figure 4.6 The average time in days (± 95% confidence intervals) that carcasses persisted during different seasons and where dingo scavenging was present or absent during the first two weeks of carcass monitoring in the Forest (n = 40), Alpine (n = 28), and Desert (n = 40) study sites. Averages and confidence intervals consider only those carcasses that reached complete decomposition (i.e. 11 carcasses from the cool season in the Alpine study site were excluded from these calculations). No dingoes visited carcasses in the warm period in the Desert study site.

Table 4.3 Cox proportional Hazards models testing for differences in carcass persistence time across season, habitat and presence or absence of dingo scavenging during the first two weeks of carcass monitoring in the Forest, Alpine, and Desert study sites, with parameter estimates, Hazard ratios, and associated standard error (SE).

Variables	Estimate	Hazard ratios**	SE	z-value	P
Forest study site, both seasons (n = 40)					
Season	4.664	106.012	0.857	5.44	<0.001*
Habitat	0.104	4.967	0.360	0.29	0.773
Dingo scavenging	1.603	1.109	0.575	2.79	0.005*
Season × Dingo scavenging	-2.698	0.067	0.752	-3.59	<0.001*
Alpine study site, both seasons (n = 39)					
Season	2.028	7.596	0.650	3.12	0.002*
Habitat	1.421	4.142	0.478	2.98	0.003*

Dingo scavenging	0.895	2.447	0.529	1.69	0.090
Alpine study site, warm season only (n = 20)					
Habitat	2.490	12.060	0.810	3.07	0.002*
Dingo scavenging	0.906	2.475	0.574	1.58	0.115
Desert study site, both seasons (n = 40)					
Season	1.548	4.702	0.472	3.28	0.001*
Habitat	0.069	1.071	0.336	0.21	0.837
Dingo scavenging	-0.952	0.386	0.538	-1.77	0.077
Desert study site, cool season only (n = 20)					
Habitat	-0.347	0.707	0.475	-0.73	0.465
Dingo scavenging	-0.975	0.377	0.547	-1.78	0.075

* Indicates significance; $p < 0.05$. ** Hazard ratios = exp(Estimate) and estimates the magnitude of the effect. Carcasses monitored in the cool season in the Forest study site, for example, were 106.0 times more likely to persist for longer than carcasses monitored in warmer months in the Forest study site.
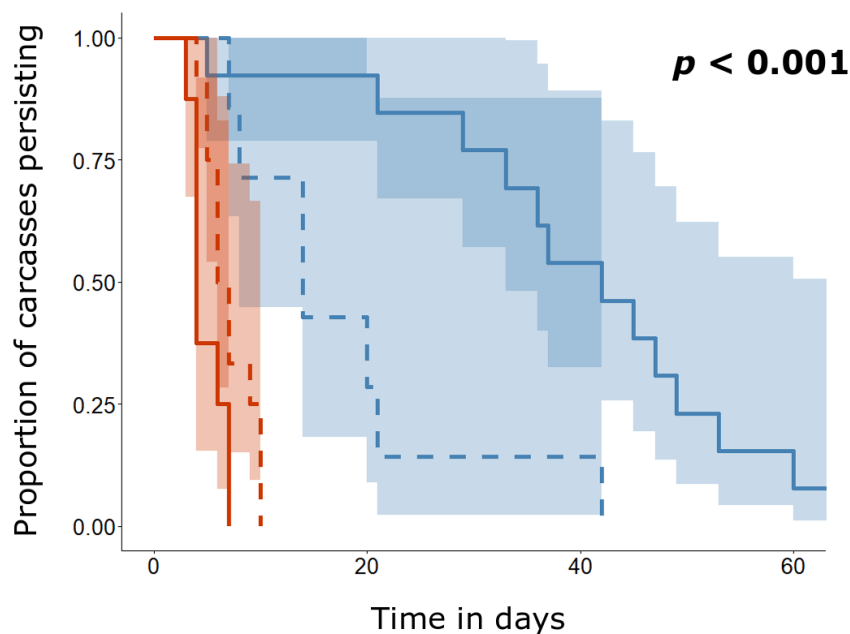
Figure 4.7 Kaplan-Meir estimate of the survival function for carcass persistence, divided into carcasses at the Forest study site, where seasons were warm (red) or cool (blue), and dingo scavenging was present (dashed line) or absent (solid line). Light shading shows 95% confidence intervals. The *p*-values are from the log-rank tests comparing the survival curves.
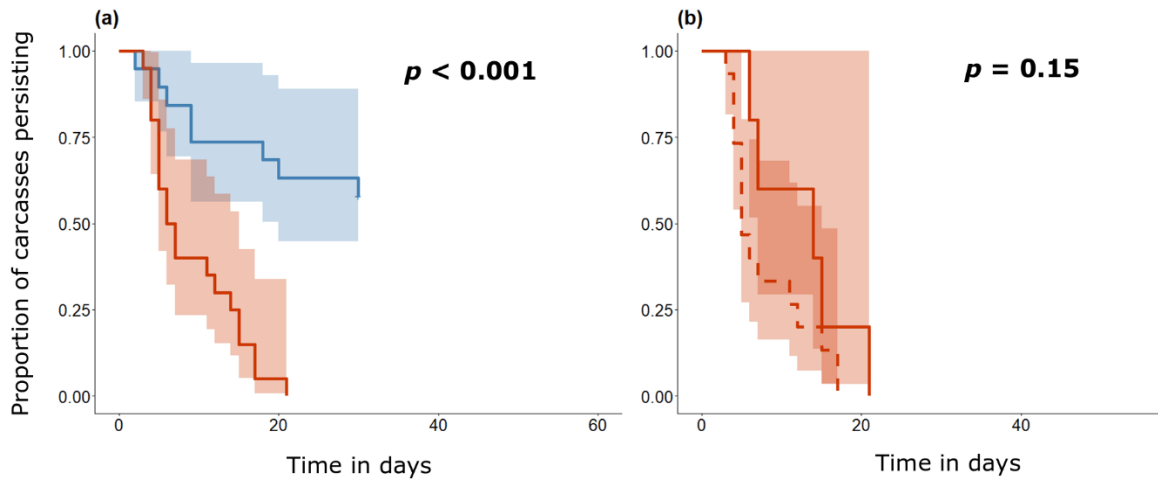
Figure 4.8. Kaplan-Meir estimate of the survival function for carcass persistence, divided into carcasses at the Alpine study site, across (a) warm (red) or cool (blue) seasons, and (b) in the warm season only, when dingo scavenging was present (dashed line) or absent (solid line). Light shading shows 95% confidence intervals. The *p*-values are from the log-rank tests comparing the survival curves.
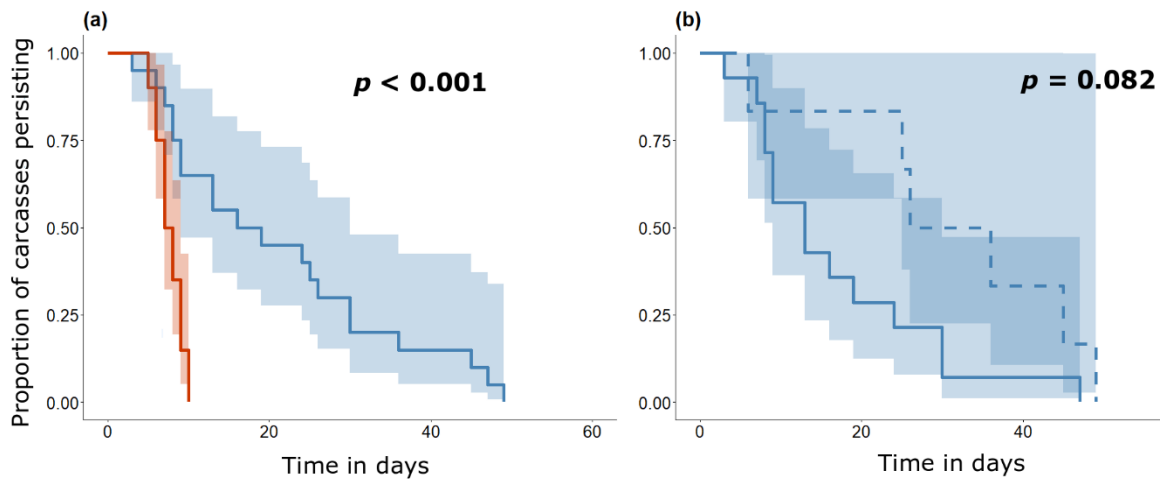
**Figure 4.9.** Kaplan-Meir estimate of the survival function for carcass persistence, divided into carcasses at the Desert study site, across (a) warm (red) or cool (blue) seasons, and (b) in the cool season only, when dingo scavenging was present (dashed line) or absent (solid line). Light shading shows 95% confidence intervals. The *p*-values are from the log-rank tests comparing the survival curves.

4.5 Discussion

We present the single largest study examining patterns of dingo scavenging in Australia to date. It has revealed widespread carcass use by dingoes, which foraged at carcasses across nearly every season and habitat studied. It also indicated substantial variation in dingo scavenging across different Australian ecoregions. For example, in the Forest and Alpine study sites dingoes detected carcasses more quickly in the warmer season, but in the Desert study site carcasses were detected by dingoes only in the cool season. Further, foraging activity by dingoes was increased in warmer seasons, but only in the Alpine study site, and closed canopy habitats saw increased foraging activity, but only in the Desert study site. Finally, our study showed that dingo scavenging may contribute to substantial carcass removal in certain contexts. Indeed, decreased carcass persistence in the Forest study site was evident in the cool season, at carcasses where dingo scavenging occurred during the first two weeks of monitoring. We expand upon our findings in relation to our initial predictions and discuss potential management implications of the study.

4.5.1 Prediction 1: Greater carcass discovery in warmer seasons and in open habitats

Carcass discovery by dingoes was primarily influenced by season, with dingoes generally discovering carcasses at a greater rate in warmer seasons in support of prediction 1. Against this prediction, however, open habitats did not increase carcass detection by dingoes at any study site. Rather than relying on visual identification of the carcasses, dingoes probably use decomposition odour to detect carcass resources across the different habitat types. Odour is a dominant stimulus used by mammals to detect carcasses and other food resources (DeVault and Rhodes 2002; Henry 1977) and, while the propagation of odour cues may decrease in complex habitats (Verheggen et al. 2017), these cues were probably still strong enough to be detected by dingoes at a distance. Forsyth et al. (2014) found that dingoes readily discovered ungulate carcasses in forested habitats, suggesting that dingoes there were relying on odour cues to detect carcasses. Studies with other canid species such as red foxes (*Vulpes vulpes*) and wolves (*Canis lupus*) have also shown even carcass visitation across open grassland and woodland habitats (Selva et al. 2003).

Higher temperatures generally increase microbial activity on carcasses (Payne 1965; Putman 1978), which in turn enhances decomposition odour. Increased odour driven by warmer temperatures probably explains why dingoes showed greater rates of carcass discovery in the

Forest and Alpine study sites during the warm season. It is also probable that seasonal differences in carcass discovery were influenced by local dingo densities at the time. Animal density is an important factor influencing scavenging efficiency (Cunningham et al. 2018; Huijbers et al.; Morales-Reyes et al. 2017; Ogada et al. 2012). At the Desert study site, low dingo density may explain why we observed no dingo scavenging during the warmer period, against prediction 1. Supporting this idea, 10 camera traps monitoring roads during our study also failed to detect any dingo activity during the warmer study period. In arid regions, animal population densities are typically low, especially compared to those of the more productive temperate regions. This can lead to reduced scavenger diversity and to fewer carcasses being scavenged. In the Sonoran Desert, in the USA, for example, only four scavenging species were recorded, and they scavenged only 40% of bird carcasses monitored (Rogers et al. 2014). Similarly, at our Desert study site, there were relatively few individual dingoes observed visiting carcasses (~3 individuals observed on our carcass cameras), and dingoes detected only 25% of carcasses. In contrast, in more productive areas, including the Forest study site, high dingo densities (~14–18 individuals observed on our carcass cameras) explain why so many carcasses were detected by dingoes (80% of carcasses monitored). Dingo numbers are also unlikely to change dramatically across seasons in these more productive areas, explaining why dingoes detected the same number of carcasses between seasons at the Forest study site (16 carcasses during both the warm and cool seasons). Compared to the Desert study site (warm: 0 carcasses detected by dingoes, cool: 10 carcasses detected by dingoes), where mammalian predator home ranges are often large (Newsome et al. 2017), in temperate forest regions dingoes often have smaller and more stable home ranges, as they need not travel as far in search of food (Harden 1985).

4.5.2 Prediction 2: Greater foraging activity in cool seasons

Dingoes did not increase their foraging activity in cool seasons, against prediction 2. Their rapid discovery of carcasses in the warm season may have enabled them to effectively compete with other scavengers and decomposers including microbes and insects during this time. Further, their tendency to return to carcasses to scavenge bones and dried skin (which decomposed or were consumed by insects more slowly than the carcass flesh) allowed them to continue feeding on carcasses in the warm period even when the majority of carcass biomass had been removed.

Foraging activity by the dingo was likely dependent on the availability of alternative resources in the surrounding environment and by dingo dietary preferences. Previous studies have shown that animals increase their consumption of carcasses during seasons when live prey populations are reduced, such as following winter snows (Olson et al. 2016; Selva et al. 2005). Similarly, while scavenging by dingoes has been recorded during drought periods, they may consume less carrion biomass when other prey is readily available (Allen 2010; Doherty et al. 2019). This is because, despite being opportunists, dingoes still hold preferences for certain prey types, such as macropods (Robertshaw and Harden 1986; Whitehouse 1977), and foraging preferences probably also extend to capturing live prey over scavenging. In the Forest study site, food availability probably was relatively constant over the warm and cool study seasons, explaining why dingoes fed evenly at carcasses across both time periods. Supporting this hypothesis, while we did not conduct counts, we did note highly abundant kangaroo and wallaby populations across both seasons at this study site. In the Alpine study site, on the other hand, lower food availability in the warm season may explain why dingoes increased their foraging activity on carcasses during this time (December 2018). This could have reflected the dynamics of their preferred prey; indeed, kangaroo and wallaby numbers could have been suppressed following the winter snow that fell from April to September. It is also possible that dingoes had access to other carcasses in the cool season. Pig (*Sus scrofa*) and deer (*Cervus* spp.) culls were carried out by the National Parks and Wildlife Service during this time (March 2018) and resulted in the production of carcasses in the study site. Finally, this result might have further been a function of our sampling method. At the Alpine study site, during the cool season, 12 carcasses persisted past the one-month monitoring period. Dingo scavenging may have occurred after we removed the monitoring cameras.

4.5.3 Prediction 3: Reduced carcass persistence in warm seasons and where dingoes scavenge

Season was an important determinant of carcass persistence, with carcass biomass decomposing rapidly in warmer seasons at all study sites. This result supported part of our third prediction that carcasses would persist for shorter times in warmer seasons and can probably be attributed to increased insect and microbial activity on carcasses as a result of warmer temperatures (Putman, 1978). Also supporting our third prediction, in the Forest study site, we found a relationship between the presence of dingo scavenging and a decreased probability of carcass persistence. Reduced carcass persistence has been associated with the presence of obligate scavengers such as turkey vultures (*Cathartes aura*) and black vultures (*Coragyps*

atratus; Hill et al. 2018), but also with top carnivores, such as the Tasmanian devil (*Sarcophilus harrisii*; Cunningham et al. 2018). Our results suggest that like these animals, dingoes could play an important role in carrion removal, although their role is likely to vary according to other factors, such as season. Indeed, in the Forest study site dingo scavenging reduced carcass persistence only during the cool season. Similarly, no effect of dingo scavenging was found during the warm season in the Alpine study site, even though dingoes fed frequently on the kangaroo carcasses. These findings were unsurprising, as vertebrates often play a greater role in carcass removal when temperatures are cooler and competition with insects and microbes is reduced (DeVault et al. 2003). In the Desert study site, on the other hand, scavenging did not influence carcass persistence in the cool season. Variation in the foraging efficiencies of individual dingoes could explain these location-based differences. Dingoes in the Desert study site, for example, often spent substantial time chewing bones to remove the tails from kangaroo carcasses. In the Forest study site, on the other hand, there were several cases where dingoes primarily targeted the stomach area and rump meat, which led to faster biomass loss compared to when they spent time chewing on bones.

It is also important to consider that our results on the effects of dingo scavenging on carcass persistence may have represented a correlative effect. Indeed, we did not consider the impacts of scavenging by other species at any of our study sites. Aside from the impacts of insects and microbes, especially in the warmer seasons, carcass persistence would have likely been affected by smaller scavenging species, along with other dominant scavengers. These animals may have avoided feeding on carcasses visited frequently by dingoes (i.e. due to fear effects). Conversely, dingo scavenging could also facilitate feeding by these animals. Smaller scavengers may associate with larger species that inadvertently provide food (Stahler et al. 2002), and scavenging communities frequently show nested patterns on carcasses where highly efficient scavengers are present (Sebastián-González et al. 2016). In the Alpine study site, another dominant scavenger, the feral pig, was also recorded frequently on carcasses and in the Forest and Desert study site, red foxes, and wedge-tailed eagles (*Aquila audax*) were also recorded frequently on carcasses. Future studies should therefore focus on teasing out the relative effects of dingoes and other major scavengers on carcass persistence.

4.5.4 Study implications and future research

Several important points emerge from our study that could be useful in future research on dingo scavenging ecology. First, in agreement with previous studies on vertebrate scavenging and

carcass persistence (e.g. Forsyth et al. 2014; Selva et al. 2005; Turner et al. 2017), seasonal effects have been revealed as important in contributing to patterns in dingo scavenging and carcass decomposition. Seasonal changes in carrion utilisation, presumably driven by temperature but also by scavenger population densities, may not only affect how quickly dingoes detect carcasses, but also whether any carcasses are detected by dingoes in the first place and the effects they have on carcass removal. This could be an important consideration in certain regions, such as deserts, where lower animal densities may reduce carcass detection and therefore use. Similarly, prey availability may also differ across seasons, and this could influence how much dingoes feed on carcasses. Thus, surveying prey populations (e.g. macropods and rabbits) during different seasons would benefit future studies. Second, while some factors such as habitat might not always appear important to dingo scavenging or carcass persistence, the effects they have will likely differ with study location, and habitat factors should still be considered in future studies. Third, while not as important as season in determining how long carcasses persist, dingo scavenging may help to accelerate carcass decomposition. Fully teasing out the role of dingoes in accelerating decomposition, however, will depend on simultaneous analysis of dingo and insect use of carcasses, as well as carcass use by other vertebrate scavenger species. Longer term studies with additional seasonal replicates will also yield a more detailed picture of the role of dingoes as apex scavengers.

Finally, it is important to consider that we conducted our study during periods when food resources were readily available. During drought, dingoes may rely on carcasses far more than we observed. Similarly, other weather extremes such as high rainfall events or wildfire might change how they interact with carcasses; for example, by either reducing their use of carcasses as alternative prey resources increase or decrease, or by increasing or decreasing their use as dingo densities and/or competition change. We therefore suggest that, along with incorporating habitat and seasonal factors, surveying prey populations and conducting longer-term studies, future work should consider how dingo scavenging changes across periods of high and low productivity. Further studies should also consider whether regular carcass production (i.e. especially via anthropogenic practices such as culling) influences dingo scavenging and, following this, the number or activity of dingoes in an environment. Understanding whether anthropogenically produced carcasses sustain dingoes through droughts, and whether they focus dingo activity or increase dingo populations in certain areas, will ultimately lead to better-informed land management strategies.

4.6 Acknowledgements

4.7 References

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4.8 Photo Appendix

A1 In most cases, dingoes visited carcasses alone or in pairs. Occasionally, however, dingoes were observed around carcasses in large numbers. This image shows a dingo pack investigating a kangaroo carcass at the Forest study site, in the Wolgan Valley, NSW. Ten individuals are pictured here but using sequential pictures we were able to determine that at least 13 individuals were present in the surrounding area.

A2 Dingoes often fed preferentially on kangaroo tails (top images). This preferential feeding behaviour was most prominent at the Desert site in the Simpson Desert, QLD, where dingoes sometimes removed the tail for a 'take-away meal' (bottom image).

A3 Dingo scavenging may lead to rapid removal of carcass biomass. This image shows two dingoes, which consumed this 30 kg kangaroo carcass over three days in the Alpine study site, in Kosciuszko National Park, NSW.

A4 Carcasses are used as a source of sustenance by dingoes, but they may also be a social point of interest. This image shows a female dingo scent marking around a kangaroo carcass at the Desert site, in the Simpson Desert, QLD.

A5 Apart from scent marking, dingoes were also occasionally recorded rolling in the grass or sand surrounding carcasses. This image shows a dingo rolling in a kangaroo carcass at the Forest study site, in the Wolgan Valley, NSW.

A6 Dingoes were commonly observed howling at carcass sites. Occasionally, after howling, additional dingoes would appear at the carcass site to scavenge. These images show a dingo howling at a carcass site at the Alpine study site in Kosciuszko National Park, NSW.

A7 Dingoes were rarely observed at carcass sites when other species were present. In this image, a dingo pup is pictured at a kangaroo carcass with an Australian raven (*Corvus coronoides*), at the Forest study site, in the Wolgan Valley, NSW.

A8 Dingoes are apex predators, but they often showed vigilance behaviour when visiting carcasses. Some of this behaviour may have occurred due to detection of the wildlife camera, but they may also be responding to the presence of other dingoes, humans and other large animals that may be present at the study sites (e.g. feral pigs). This image shows two dingoes displaying vigilance behaviour around a kangaroo carcass at the Alpine study site, in Kosciuszko National Park, NSW.

A9 Dingoes may interact with insect scavengers at carcass sites. In these images, a dingo displays behaviours indicative of disturbance or interference by swarming European wasps (i.e. snapping at wasps around its head) at the Alpine study site in Kosciuszko National Park, NSW.

CHAPTER 5

CARCASSES ATTRACT INVASIVE SPECIES AND INCREASE ARTIFICIAL NEST PREDATION IN A DESERT ENVIRONMENT

Red fox (*Vulpes vulpes*) steals an artificial egg from a nest. Photograph by Emma Spencer.

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My contribution for this paper was very substantial, and included conceptualisation of ideas, leading fieldwork, data collation and analysis, and writing and editing all drafts, in consultation with my co-authors.

5.1 Abstract

In addition to feeding on animal remains, many scavengers also function as predators. Carcasses may therefore affect local animal communities by attracting facultative scavengers and increasing predation risk for other species in the vicinity of the carcasses. This risk may be elevated in low productivity environments, especially where humans increase carcass production and where facultative scavengers include invasive species. In June and October 2018, we monitored experimentally placed red kangaroo (*Osphranter rufus*) carcasses and artificial bird nests in two different habitats in the Simpson Desert, Australia, to identify the nest predators attracted to the carcasses, and to determine how carcasses affect overall and predator-specific nest predation. We modelled our nests to approximate those of the ground nesting little buttonquail (*Turnix velox*) and the endangered night parrot (*Pezoporus occidentalis*). Native *Corvus* spp. and then invasive red foxes (*Vulpes vulpes*) were the top carcass visitors and nest egg predators. Carcass presence and open habitat increased overall nest predation and fewer artificial parrot nest eggs were depredated compared to those of quail. Open habitat and carcass presence only increased predator-specific nest predation by foxes, but corvid nest predation was highest in June 2018, and for the artificial quail nest types. Foxes were the main predator of eggs from night parrot nests. Our study shows that carcass provisioning by humans may have indirect, deleterious effects on ground nesting birds, and indicates that foxes might pose a greater threat to night parrot populations than previously recognised.

5.2 Introduction

Carrion, or decomposing animal necromass, is a key component and driver of ecosystem structure and functioning (DeVault et al. 2003, Wilson and Wolkovich 2011, Barton et al. 2013). It is produced in all biomes and provides a nutrient-rich resource that supports a range of vertebrate, invertebrate and microbial species. Among vertebrates, vultures are especially important scavengers, contributing to ecosystem functioning via the dispersal of carrion nutrients and by removing carrion, which otherwise may act as a hub for disease spread (Kane et al. 2015, Di Vittorio et al. 2018, Hill et al. 2018). As 'obligate scavengers', vultures feed almost exclusively on carrion. Most carnivorous vertebrates, however, will scavenge on animal remains (DeVault et al. 2003). These 'facultative scavengers' can remove carrion and return nutrients from carcasses to the environment via their faeces (Cunningham et al. 2018). But, in

addition to fulfilling a role as carrion removalists, many facultative scavengers also function as predators.

Because nearly all vertebrate predators engage in scavenging behaviour, it follows that where there are animal carcasses there may also be predator effects (Schmitz et al. 2000, Wilson and Wolkovich 2011, Pereira et al. 2014). Carcass provisioning often mediates the activity of both predators and their prey in the vicinity of the resource. For example, anthropogenic provisioning of ungulate carcasses increases predator activity, with red foxes (*Vulpes vulpes*) aggregating in the vicinity of hunter-provided ungulate carcasses and their potential prey— brown hares (*Lepus europaeus*) and red squirrels (*Sciurus vulgaris*)—decreasing their activities correspondingly (Cortés-Avizanda et al. 2009b). Similarly, a natural mass die-off of reindeer in Norway led to locally increased corvid (common raven *Corvus corax* and hooded crow *C. cornix*) activity and reduced rodent activity (Frank et al. 2020). Studies have also linked the natural provisioning of carcasses in snow seasons (i.e. due to winter die-offs) when alternative resources are scarce, to increased or stabilised predator populations. During winter, in Scandinavia, red fox scavenging of ungulates may increase and stabilise fox populations (Needham et al. 2014). Coyotes (*Canis latrans*) too depend on winter scavenging, with the availability of elk carrion increasing both coyote litter size and pup survival (Crabtree and Sheldon 1999). Collectively, these studies indicate that carrion resources could increase predation risk for some animal communities.

In arid and low productivity regions animal carcasses may provide particularly valuable resources for scavengers (Rogers et al. 2014) and, in addition to natural deaths, could be produced frequently as a result of culling or hunting by humans. In Australia, for example, camels, feral goats, and pigs are targeted for commercial use and to reduce perceived competition with livestock. Kangaroos also are culled in large numbers (Lunney 2013). Harvesters sometimes remove parts of the carcasses they produce, but often whole carcasses are left to rot in-situ following culls and remain available as carrion. By attracting facultative scavengers, these practices could have deleterious effects on native prey species (Salo et al. 2007).

In arid Australia, many ground nesting birds are threatened and in decline (Reid and Fleming 1992). Habitat loss and fragmentation are important contributors to this decline, but ground nesting birds are also threatened by high nest predation rates from invasive predators including the red fox and feral cat, *Felis catus* (Reid and Fleming 1992, Smith et al. 1994, Woinarski et

al. 2017). Ground nesting birds may also be vulnerable to nest predation by native predators such as goannas (*Varanus* spp.) and corvids (e.g. Australian raven; *Corvus coronoides*). If these invasive and native species feed on animal remains, carrion resources may influence nest predation. There are, however, few studies that explore the impact of carcasses on ground nesting birds (i.e. Cortés-Avizanda et al. 2009a, Rees et al. 2015), and none have been conducted in arid environments. Previous research on facultative vertebrate scavenging of kangaroo carcasses in arid regions does suggest that carrion can become a hub of activity for native and invasive predator species (Read and Wilson 2004). Provisioning kangaroo carcasses is therefore likely to increase localised risks of nest predation.

Environmental factors such as habitat and nest-site characteristics influence nest predation risk. Nest predation is often higher in open habitats, whereas nests that 'hide' eggs (e.g. dome nests) usually see reduced predation rates (Hausmann et al. 2005, Noske et al. 2008, Newmark and Stanley 2011). Further, risk of nest predation may vary with predator species. For example, as visual predators, birds might be hindered by structurally complex habitats (Fernández-Juricic et al. 2004). Conversely, many mammals may locate nests successfully in complex habitats when using odour to detect food (Conover 2007). Identification of dominant nest predators is thus integral to disentangling the relationships between factors such as habitat and nest survival (Benson et al. 2010, Chiavacci et al. 2014, Reidy and Thompson 2012). As scavenger assemblages vary widely by region and habitat (Mateo-Tomás et al. 2015, Turner et al. 2017), predator-specific predation on nests in proximity to carrion resources may also vary.

In this study, we monitored facultative scavengers feeding on experimentally provisioned kangaroo carcasses and depredating artificial bird nests in the Simpson Desert, central Australia. We monitored artificial nests in open and closed canopy habitats and using model nests of two species of ground dwelling birds—the little button quail (*Turnix velox*) and the endangered night parrot (*Pezoporus occidentalis*)—identified how nest predation varied between different predator groups. We predicted that: 1) artificial nest predation would be greatest in the presence of and at closer proximities to carcasses, and that 2) nest predation would be higher in open habitats and at open nest types (i.e. artificial little button quail nests) where nest eggs are visible to predators. We also predicted that 3) habitat and nest type would have a greater effect on nest predation by birds compared to nest predation by mammals, due to the greater reliance of birds on visual cues to find food. We use our results to discuss how carcass visitation and nest predation vary across species and highlight potential indirect threats of carcasses to ground nesting birds.

5.3 Material and methods

5.3.1 Study system

This study was conducted at Ethabuka Reserve, a conservation property managed by Bush Heritage Australia on the edge of the Simpson Desert, central Australia (Figure 5.1a). No obligate scavengers occur in this region (or, more generally, in Australia), but there are several facultative native avian, mammalian and reptilian predators like the dingo (*Canis dingo*), wedge-tailed eagle (*Aquila audax*), perentie (*Varanus giganteus*), sand goanna (*Varanus gouldii*) and several *Corvus* spp. (including the Australian raven, little crow *C. bennetti* and Torresian crow *C. orru*). Invasive facultative scavengers include the red fox and feral cat. The study area covers 80 km² and is a hot desert, characterised by long, parallel sand dunes (Purdie 1984). The climate is arid, with the hottest month, January, averaging 40°C and the coolest month, June, averaging 23°C (nearest station Bedourie 1988 - 2020; Bureau of Meteorology 2020). While the Simpson Desert experiences irregular periods of high rainfall and primary productivity, monitoring in our experiment took place during a dry time of low productivity. The sand dune crests, and inter-dune valleys have different vegetation, with the crests lacking trees and the valleys hosting stands of gidgee trees (*Acacia georginae*). The prevailing habitat is hummock grassland dominated by needle-leaved spinifex (*Triodia basedowii*; Wardle et al. 2015), although the inter-dune valleys in our study had sparse spinifex cover. Both the dune crests and inter-dune valleys hosted singular or clumped stands of shrubs such as *Acacia ligulata*, *Eucalyptus pachyphylla, Dodonaea viscosa, Grevillea stenobotrya*, and *Grevillea juncifolia*.

5.3.2 Field methods

5.3.2.1 Site set-up and carcass provisioning

We conducted our experiments in June and October 2018 (Australian winter and spring, respectively), to account for seasonal differences. Eighty sites were established, split evenly across the two study periods, and generally alternating between carcass 'present' (n = 40) and carcass 'absent' (n = 40) sites (Figure 5.1b). Within each study period, sites were spaced ~0.50 km (range: 0.49 – 1.68 km) apart, with distances of about 1 km (range: 0.91 – 2.59 km) between each carcass 'present' site. These distances were chosen to minimise carcass scent travel between sites, such that scavengers would have to actively forage and seek out carcass sites rather than being able to move quickly from one site to another. Carcass-present and absent
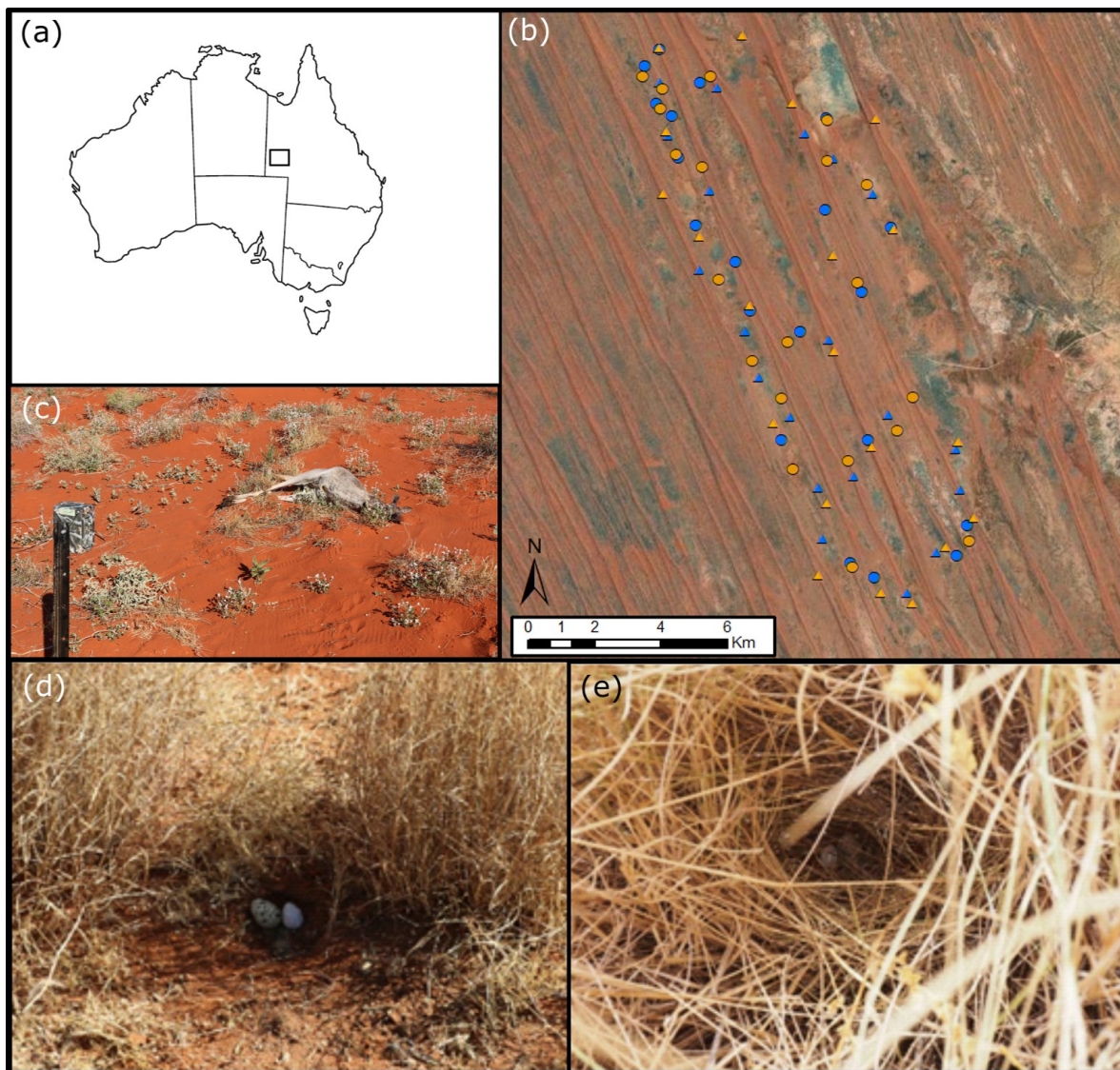
Figure 5.1. Study area map and site set-up; (a) shows the location of the study area, at Ethabuka Reserve in the Simpson Desert, western Queensland in Australia, (b) satellite image of carcass (triangles) and control (circles) site spatial spread at the study area in June 2018 (blue) and October 2018 (orange), (c) provides an example carcass site set-up with the remote monitoring camera positioned ~4 m from the staked kangaroo carcass, (d) shows the artificial nest design for little buttonquails (*Turnix velox*) and (e) shows the nest design for night parrots (*Pezoporus occidentalis*).

sites were also split evenly between dune crest and valley habitats. We classed dune crests as "open" and the inter-dune valleys as "closed" habitats. Open habitats were devoid of tree cover, while closed habitats were sparsely populated by gidgee trees.

The centre point of both carcass-present and absent sites was marked with a single black 1 m high stake (Figure 5.1c). At carcass-present sites, we placed a single red kangaroo (*Osphranter*

rufus) carcass (mean 25 kg +/- 0.5 s.e) sourced from pre-planned local culls, and as such were not killed for the purpose of this study. Any carcass displaying evidence of disease (e.g. heavy parasite loads) was not used. Following collection, carcasses were placed in the field without freezing within 24 h (June) or 36 h (October) of collection. Scientific licenses were obtained to relocate and monitor the carcasses (SL WA0006737), and all research was approved by the University of Sydney Animal Ethics Committee (Project number 2017/1173).

5.3.2.2 Artificial nests

Artificial nests were installed on NW–SE transects in both carcass-present and absent sites, following the direction of the sand dunes. Transects were designed to intersect either the central carcass subsidy, or the stake used to mark each carcass-absent site. In June 2018, 6 quail nests (see design below) were positioned at 10 m, 30 m, and 50 m along the transect such that each distance was sampled in both the NW and SE direction (total of 240 quail nests in June 2018). In October 2018, this method was replicated, with the addition of two parrot nests (see design below) set up 10 m on either side of the centre points in the carcass-present and absent sites. Parrot nests were set up only in dune crest sites, as these nests were constructed within spinifex hummocks only found consistently in the dune crest habitat (total of 240 quail and 40 parrot nests in October 2018).

We modelled artificial nests to replicate those of two species of ground nesting birds in the region. The first nest model mimicked the nest of the little buttonquail (hereafter 'quail' nests), while the second mimicked a night parrot nest ('parrot' nests). Little buttonquails are commonly sighted in our study area and build their nests on the ground in grassland, usually at the edge of small shrubs and overhanging grasses. In contrast, night parrots build their nests in the centre of dense shrubs and, in particular, large partially dead spinifex hummocks (Murphy et al. 2017). While night parrots have not been sighted in our study area, they have been recorded in nearby areas with comparable habitats (Murphy et al. 2017); as an endangered species, they provide a relevant conservation model to work with (Murphy et al. 2018).

Artificial quail nests were positioned no more than 5 cm from the base of spinifex hummocks, small shrubs, low lying gidgee trees or logs, by creating a small indent (~10 cm diameter) in the ground with the palm of a hand (Figure 5.1d). Artificial parrot nests were placed in spinifex hummocks (1–4 m diameter) using a broom handle to force a 15 cm wide hole in the hummock. A broom pole was then used to create a small chamber (<30 cm deep and wide) at the base of the plant where the roots enter the sand (Figure 5.1e). Each nest contained 1 artificial egg, made

from plasticine modelling clay, and coated with Plasti-dip™, and 1 commercial quail egg, collected fresh and then refrigerated until use. Nests were also scented with ~5 g of feathers and droppings collected from domestically reared quails (Game Farm Pty Ltd., Galston NSW). The quail egg, droppings and feathers were used as attractants. Quail droppings were replenished at any sites where eggs remained 6 days after placement. We used latex gloves smeared in quail droppings to reduce human scent on nests and, when possible, human footprints were smoothed using a rake to minimise any obvious pathways in the sand that might lead predators to the nests. A GPS unit (Garmin GPSMAP 64sc) was used to mark each nest site.

All nests were set out between ~11 am and 8 pm, 1 day after carcass placement to ensure that scents associated with transporting the carcasses were kept separate from the nest sites. When setting the nests, we ensured that any nearby scavengers and predators, especially corvids, were flushed before starting, to ensure that they would not be able to watch nest placement. As nest placement took ~15 mins per site, it was not expected that this had any significant impact on scavengers using the carcass sites.

5.3.2.3 Carcass and nest site monitoring

To allow ongoing monitoring and detection of scavengers visiting the carcasses, a remote camera (Reconyx Hyperfire PC800) was positioned on the stake marking the centre of each site, 3–4 m from the kangaroo carcass (Figure 5.1c). The camera was programmed to take continuous photographs when triggered by thermal movement around the carcass (rapidfire, no wait period). To prevent removal of carcasses from the camera monitoring frame, carcasses were secured to the ground by wire attaching the neck and Achilles tendon of the animal to two metal stakes spaced ~0.6 m apart. We monitored carcasses over the same period we monitored nests (14 days). We examined all photographs collected by the cameras and tagged them by the animal species present in the frame and whether it was engaged in scavenging or not. We then examined the tagged images and compiled a list of all vertebrate species observed feeding on at least one carcass. Species that we suspected to be feeding on insects on the carcass, but not the carcass itself, were included on this list.

Nests were monitored in the landscape for 14 days, as little buttonquails and other ground nesting birds in the region generally hatch in an equivalent time (Higgins et al. 1990). Every two days, we visited each nest and recorded evidence of predation. Sites where either clay or quail eggs had been bitten into or removed were considered depredated. The plastic-coated clay

enabled identification of species attempting to depredate the eggs (i.e. from the tooth or beak marks in the clay) and helped to minimise the scent of the clay, which has been linked to higher rates of predation (Purger et al. 2012). In addition to the plastic-coated clay eggs, identification of nest predators was aided by smoothing sand around the nest site and through the use of remote cameras (Reconyx Hyperfire PC800), which were placed 3 m away from select nests at carcass and control sites and programmed to take pictures continuously when any animal motion was detected (79 nests were monitored by cameras). As camera placement may influence nest predation rates, cameras were hidden in adjacent vegetation and set on nests at random sites (Richardson et al. 2009). No cameras were placed on artificial parrot nests.

When reviewing the carcass and nest site camera images, differentiating corvid species was challenging. In most cases, we could identify Australian ravens by their larger size and stature, smaller group numbers and long throat hackles that form a layered beard. We identified crows by their thinner appearance, smaller throat hackles, white feather bases and generally larger group numbers. While both little crows and Torresian crows occur in our study area and are difficult to differentiate without hearing their calls, we are fairly confident that all crows appearing in our camera images were little crows. This assumption is based on the fact that no Torresian crows were detected in the field during the two two-week periods of fieldwork carried out as part of this study (i.e. based on calls), or by concurrent bird surveys carried out in the study area and surrounding region (pers. comm. Ayesha Tulloch). Further, continuous bird surveys in the region typically only place Torresian crows in the area following high rainfall events and we conducted our study during a dry period. At nest sites, corvid predation events could only be specified to species when using camera images (and not by prints in the sand or beak marks in the clay eggs).

5.3.3 Data analyses

We used R version 4.0.2 for all statistical analyses (R Development Core Team 2020).

5.3.3.1 Nest predation rates

To determine if rates of artificial nest predation were increased by carcass proximity and provisioning (Prediction 1) and in open habitats and nest types (Prediction 2), we used generalized linear mixed-models with binomial distributions (Package: lme4; Bates et al. 2015). For this, the nest was checked for evidence of predation and the status or response of each nest at the end of a 2-day interval was recorded, so the data used were either 0 = survived,

or 1 = depredated. The results of our analyses therefore provided the probability of nest predation over two-day intervals. Due to different sampling methodology used for parrot and quail artificial nest types, we ran three separate analyses. The first incorporated data collected from all artificial quail nests (n = 480; hereafter "Quail dataset"). The second incorporated data collected from all artificial parrot nests (n = 40; hereafter "Parrot dataset"). The third incorporated data from all parrot nests and for a subset of quail nests (n = 80; hereafter "Parrot-quail dataset"). We used both parrot and quail nests for the third analysis, as we wanted to evaluate potential differences between the two nest types. The Parrot-quail dataset included artificial parrot and quail nests that were monitored in October 2018, positioned in open habitats, and at 10 m from the centre point of carcass-present and absent sites. This ensured that we had a balanced design (i.e. 40 parrot and 40 quail nests).

For the Quail dataset, we first tested for a camera effect on nest predation rates because the remote cameras used to monitor a selection of these nests might have elevated nest visibility and therefore predation rates (Richardson et al. 2009). We then analysed nest survival over the 2-day interval as a function of carcass presence (*present or absent*), habitat type (*open or closed*), study period (*June or October*) and nest distance (*10m, 30 m, 50m*). We also tested the two-way interactions between carcass presence and nest distance to determine whether carcass proximity influenced nest predation. We included site as a random factor in the model to account for the potential non-independence of nests within the 80 sites. For the Parrot dataset, we analysed nest survival as a function of carcass presence (*present or absent*), and for the Parrot-quail dataset, we analysed nest survival as a function of nest type (*parrot or quail*). For both analyses, site was incorporated as a random factor. Contrasts between rates of nest predation across different nest distances were calculated using Tukey's tests for *post hoc* analysis (Package: emmeans; Lenth 2019).

5.3.3.2 Predator-specific nest predation

To assess whether habitat and nest type had a greater effect on nest predation by birds than nest predation by mammals (Prediction 3), we used generalized linear models with a Poisson distribution to model the total count of nests depredated after 14 days by the different predator groups and by the carcass provisioning, habitat and nest type factors examined. As we were most interested in comparing mammalian and avian predators and because nest predation by reptile species was rare (<10 cases), we only counted nests that were depredated by corvids or foxes. The corvid group included both little crows and Australian ravens. No other birds or

mammals were included in analyses, as none were observed depredating nest eggs. Again, we analysed the three datasets (Quail, Parrot and Parrot-quail) separately.

For the Quail dataset, we analysed the total counts of nests depredated by the fox and corvid predator groups separately, at sites with different carcass provisions (*present or absent*), habitat types (*open or closed*) and across the two study periods (*June or October*). For the Parrot dataset, we analysed the total number of parrot nests depredated by foxes across carcass-present and absent sites. We only tested total counts of the nests depredated by the fox predator group due to insufficient data for the corvids (corvids depredated only 2 parrot nests). Finally, for the Parrot-quail dataset, we analysed total counts of the nests depredated by the fox and corvid predator group separately, as a function of nest type (*parrot or quail*).

5.4 Results

5.4.1 Carcass visitation

We monitored 40 kangaroo carcasses over 560 observation days during June and October 2018 and recorded 19 non-herbivorous species visiting them (see section 5.8 Supplementary Information: Figure S1). Guild composition comprised mammalian (n = 4), avian (n = 12) and reptilian species (n = 3). Birds were the most frequent visitors, attending 97.5% of carcasses (n = 39), mammals visited 95.0% of carcasses (n = 39) and reptiles 30.0% (n = 39). Of all species, the little crow visited the most carcasses (95.0%; n = 38), followed by the red fox, wedge-tailed eagle, Australian raven, willie wagtail (*Rhipidura leucophrys*) and dingo (fox: 72.5%, n = 29, eagle: 65.0%, n = 26, raven: 45.0%, n = 18, willie wagtail: 45.0%, n = 18, dingo: 30.0%, n = 12). Little crows, red foxes and ravens visited relatively similar numbers of carcasses across both study periods, but more wedge-tailed eagles were observed in June than October, and no dingoes were observed in October (see section 5.8 Supplementary Information: Figure S1).

5.4.2 Nest predation rates

Of the 480 artificial quail nests monitored, 86.0% (n = 413) were depredated during the 14-day monitoring period (Figure 5.2; Figure 5.3). This included 95% (n = 228) of artificial nests at carcass-present sites and 77.1% (n = 185) at carcass-absent sites. For the Quail dataset we recorded no camera effect on nest predation rates (Z = 1.85, P = 0.065). Nest predation rates increased in the presence of carcasses and in open habitat (Figure 5.2a,b; Table 5.1). *Post hoc* contrasts indicated that rates of nest predation were higher at 10 m compared to 50 m from the

centre of the site (Z = 3.59, P = 0.001) and higher at 30 m compared to 50 m (Z = 2.50, P = 0.033), but revealed no differences in nest predation rates for nests at 10 m compared to 30 m (Z = 1.10, P = 0.513). There was no effect of study period or of the interaction term carcass presence × nest distance (Table 5.1). Of the 40 artificial parrot nests, 52.5% (n = 21) were depredated, with 75% (n = 15) of nests depredated at carcass-present sites and only 30% (n = 15) at carcass-absent sites (Figure 5.2c; Figure 5.3b). For the 40 quail nests that we compared with the parrot nests, 97.5% (n = 39) were depredated (Figure 5.2d; Figure 5.3b). For the Parrot dataset, nest predation was higher at carcass present sites and for the Parrot-quail dataset, nest predation was higher for the quail nest type (Figure 5.2c,d; Figure 5.3b; Table 5.1).

5.4.3 Predator-specific nest predation

Avian nest predators visited 69.0% (n = 285) of the depredated quail nests (n = 413) and 9.5% (n = 2) of the depredated parrot nests (n = 21; Figure 5.3). Camera monitoring indicated that little crows contributed most to predation on quail nests (see section 5.8 Supplementary Information: Figure S2). Red foxes were the only mammalian nest predators, visiting 23.7% (n = 98) of the depredated quail nests (n = 413) and 76.2% (n = 16) of the depredated parrot nests (n = 21; Figure 5.3). Reptiles, notably sand goannas (*Varanus gouldii*) and centralian blue-tongued skinks (*Tiliqua multifasciata*), accounted for 5.8% (n = 24) of all quail nest predation events (n = 413) and 4.8% (n = 1) of all parrot nest predation events (n = 21; Figure 5.3). We could not identify nest predators on 18 occasions (Figure 5.3).

For the Quail dataset, corvids depredated more nests during the June compared to October but showed no difference in nest predation according to carcass presence or habitat (Figure 5.3; Table 5.2). Nest predation by foxes was similar across study periods but was higher at carcass-present compared to carcass-absent sites and in open compared to closed habitat (Table 5.2). For the Parrot dataset, foxes depredated more parrot nests at carcass-present than absent sites (Figure 5.3; Table 5.2). Corvids depredated only two parrot nests, both at sites with a carcass (Figure 5.3). For the Parrot-quail dataset, corvids depredated more quail compared to parrot nests, while foxes showed no difference in the number of quail and parrot nest depredated (Figure 5.3; Table 5.2).
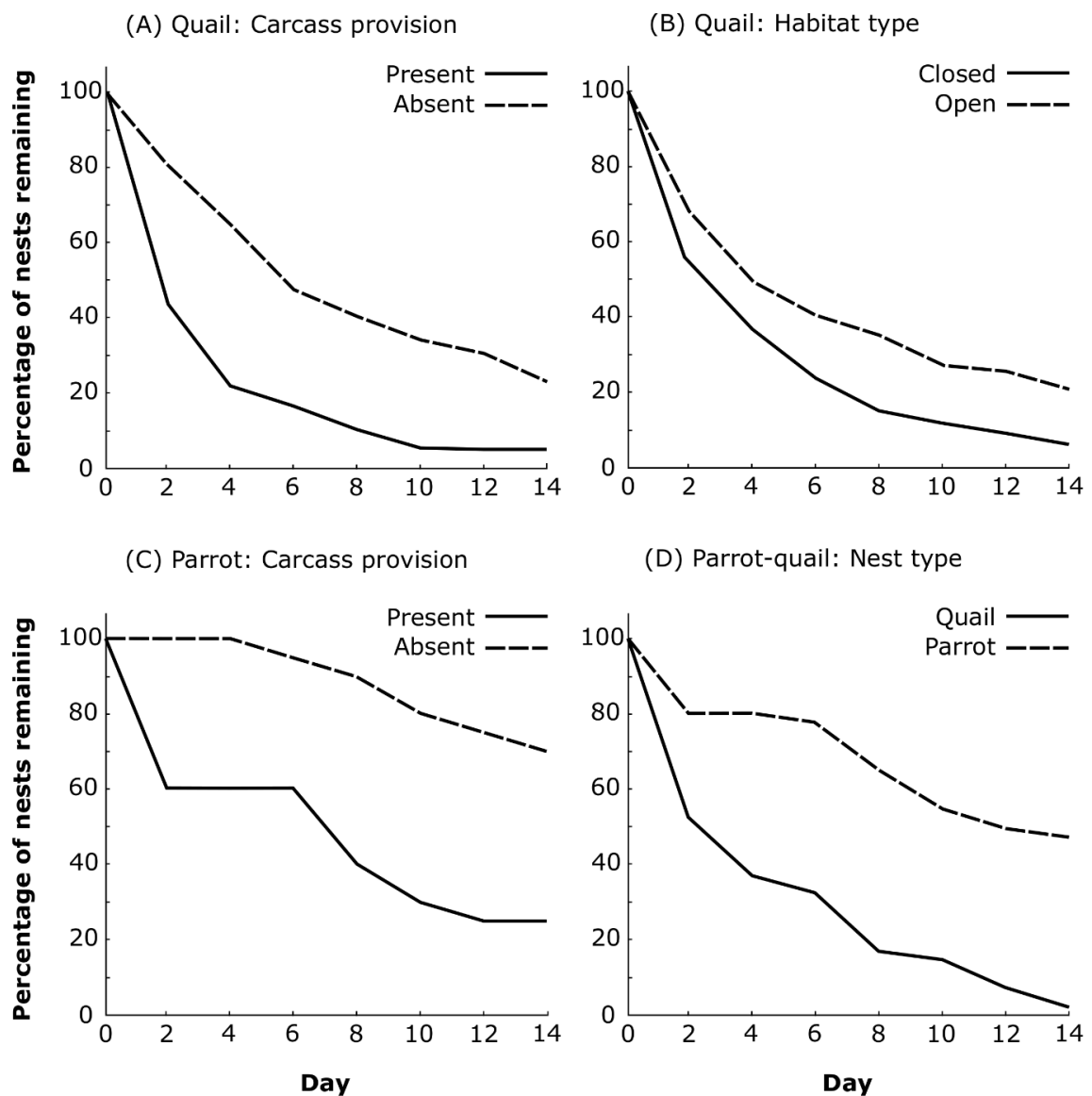
Figure 5.2 Percentage of nests remaining over the 2-week experimental period for artificial quail nests (n = 480) over sites with different (A) carcass provisioning and (B) habitat types, for artificial parrot nests (n = 40) with different (C) carcass provisioning, and for the combined artificial parrot and an equal subset of quail nests (n = 80) over different (D) nest types. Artificial nests were checked over 2-day intervals.
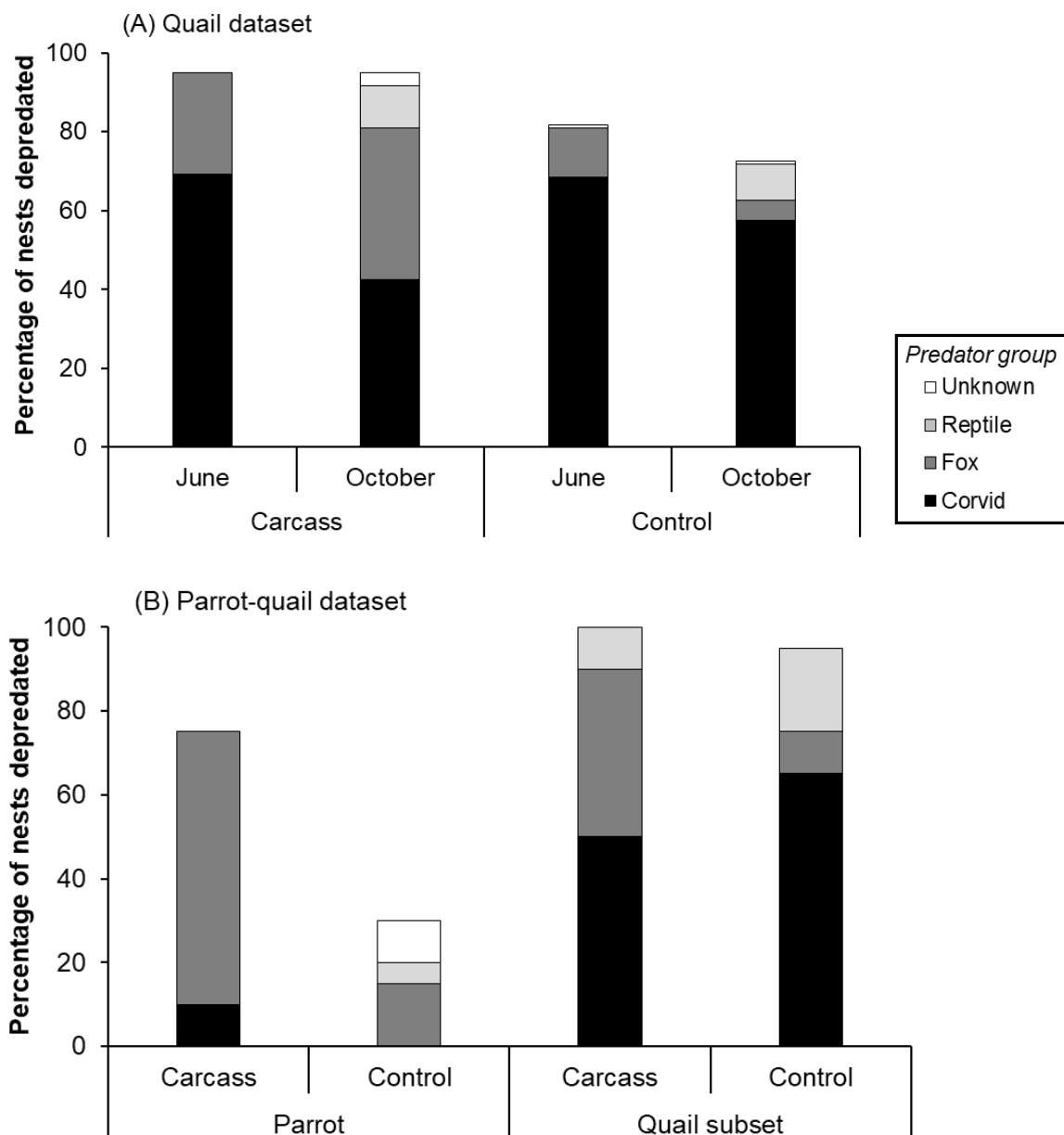
Figure 5.3 Percentage of nests depredated by different species or species-groups during two study periods (June and October) in 2018. Includes data from all (A) quail nests (n = 480) and (B) parrot nests (n = 40) and an equal subset of quail nests (n = 40). As footprints and egg indentations cannot provide positive identification of different corvid species (i.e. little crows; *Corvus bennetti* and Australian ravens *Corvus coronoides*), these species were groups as "corvid." Reptile species were grouped due to their small contribution to nest predation and include the centralian blue-tongued skink (*Tiliqua multifasciata*) and the sand goanna (*Varanus gouldii*).

Table 5.1 Parameter estimates and standard errors for the logistic-exposure models predicting nest predation for artificial quail and parrot nests over two-day intervals. For Nest distance, the reference value was set to 50 m. Parameters marked by asterisks are significant at α = 0.05.

Variables	Estimate	SE	Z	P
Quail dataset (n = 480)				
Intercept	-2.287	0.441	-5.19	< 0.001*
Carcass (present)	1.931	0.475	4.07	< 0.001*
Habitat (open)	1.144	0.429	2.67	0.008*
Study period (June)	0.702	0.426	1.65	0.099
Nest distance (10 m)	0.479	0.225	2.12	0.034*
Nest distance (30 m)	0.233	0.228	1.02	0.308
Carcass (present) × Nest distance (10 m)	0.343	0.361	0.95	0.343
Carcass (present) × Nest distance (30 m)	0.432	0.358	1.21	0.228
Parrot dataset (n = 40)				
Intercept	-3.367	0.635	-5.31	< 0.001*
Carcass (present)	2.182	0.840	2.60	0.009*
Parrot-quail dataset (n = 80)				
Intercept	-2.137	0.397	-5.38	< 0.001*
Nest type (quail)	2.123	0.382	5.56	< 0.001*

Table 5.2 Model parameter estimates and standard errors for the generalised linear model predicting the proportion of nests depredated by foxes and corvids, for the Quail, Parrot and Parrot-quail datasets. Parameters marked by asterisks are significant at α = 0.05.

Variables	Estimate	SE	z-value	p
Quail dataset (n = 480)				
Corvid				
Intercept	3.390	0.124	27.27	< 0.001*
Carcass (present)	-0.119	0.119	-1.01	0.314
Habitat (open)	0.134	0.119	1.13	0.261
Study period (June)	0.319	0.120	2.65	0.008*
Fox				

Intercept	1.381	0.274	5.04	< 0.001*
Carcass (present)	1.299	0.246	5.28	< 0.001*
Habitat (open)	0.588	0.211	2.79	0.005*
Study period (June)	-0.123	0.202	-0.606	0.545
Parrot dataset (n = 40)				
Fox				
Intercept	1.099	0.577	1.90	0.057
Carcass (present)	1.466	0.641	2.29	0.022*
Parrot-quail dataset (n = 80)				
Corvid				
Intercept	0.693	0.707	0.98	0.327
Nest type (quail)	2.443	0.737	3.31	< 0.001*
Fox				
Intercept	2.773	0.250	11.09	< 0.001*
Nest type (quail)	-0.470	0.403	-1.17	0.244

5.5 Discussion

Our findings indicate that carrion in Australian arid environments attracts a range of facultative scavengers that could cause cascading predation effects on ground nesting birds. Corvids were the dominant predators of artificial quail nests, while foxes were the dominant predators of artificial night parrot nests. This is one of very few studies to investigate nest predation in arid Australia (but see Noske et al. 2008) and it provides the only record of extensive nest predation by an invasive species (i.e. the red fox) in response to carcass provisioning. We found support for our first two predictions that artificial nest predation would increase near kangaroo carcasses and in open habitats and nest types. Our third prediction that nest predation by birds would be influenced more by habitat and nest type compared to nest predation by mammals received partial support. Specifically, nest predation by corvids but not foxes was influenced by nest type, with corvids depredating more quail nests compared to parrot nests and red foxes depredating both nest types evenly. On the other hand, only nest predation by foxes was influenced by habitat, with foxes depredating more nests in open than closed habitats and corvids depredating nests evenly across habitat types. We also found differences in the effects of carcasses on nest predation by birds and mammals, with foxes depredating more nests where carcasses were present and corvids showing similar nest predation rates regardless of carcass

provisioning. We interpret these findings and explore potential management implications of the study below.

5.5.1 Dominant scavengers and nest-site predators

Kangaroo carcasses attracted 14 scavenger species, but only five (little crow, Australian raven, red fox, sand goanna and centralian blue-tongued skink) were identified as nest predators. Birds – specifically corvids, and largely little crows – were the most frequent scavengers. In other regions of the country (Read and Wilson 2004, Rees et al. 2020) and the rest of the world (DeVault et al. 2003, Mateo-Tomás et al. 2015), birds have been identified as prolific scavengers. In arid environments where animal abundances are usually low and resources sparse, birds might have an advantage as scavengers and nest predators because their capacity for flight enables efficient searching of large areas (Schmidt-Nielsen 1972). After the little crow, foxes appeared most frequently on kangaroo carcasses, and they detected more carcasses than any other bird species including wedge-tailed eagles and Australian ravens. By maintaining large home ranges in arid environments, the fox may be able to compete with bird species that utilise flight to detect resources. Indeed, individual red foxes have been recorded using areas exceeding 500 km^2 in our study region (Newsome et al. 2017).

Our finding that nest predation by corvids did not differ across the open and closed habitats suggests that there were likely other factors, in addition to nest visibility, that were influencing corvid nest detection. For example, the 'closed' dune swales and gidgee woodland may have provided attractive resources not found on the 'open' dune crests. Previous studies show that bird assemblages in arid Australia can be strongly associated with locally dense habitats, including woodland, as these habitats provide important breeding and foraging opportunities (Pavey and Nano 2009). Higher corvid activity in the closed habitat may have then increased the probability of corvids detecting nests here, despite these nests being less visually conspicuous than those in the open habitat. It is also possible that corvids detected nests equally across habitats because the closed habitat in our study may have still allowed flying birds a clear line of site to the nests. Although the 'closed' dune valleys provided more complex structure than the treeless 'open' dune crests, tree presence was relatively sparse in the valleys and ground cover was similar across both habitats. The finding that red fox nest predation increased in open habitats can be explained by the fact that mammals in this region, including the red fox, may preferentially travel along dune crests (Mahon et al. 1998). This behaviour

could have therefore increased the probably that foxes encountered carcasses and nests in our 'open' sites.

Birds' reliance on sight could, nonetheless, explain why corvids were more active predators of the 'open' quail nest type, while foxes were the dominant predators of the 'closed' parrot nest type. The parrot nests were placed in hummocks of needle-leaved spinifex (*Triodia basedowii*), which provide dense cover that would prevent easy detection of eggs by visually hunting predators. Another possibility is that corvids were unable to access nests within spinifex hummocks. *T. basedowii* leaves that are tightly rolled, stiff, sharply pointed and densely packed, making them impenetrable for many species. Corvid tracks in the sand circled repetitively around several parrot nests, suggesting that corvids had detected the nests but were unable to access the eggs. Red foxes, on the other hand, were able to locate eggs regardless of nest type, potentially using their keen sense of smell and ability to penetrate spinifex to access the eggs by forcing their head through, or by digging under, the hummocks (Supplementary information: Figure S3).

5.5.2 Effect of carrion on nest predation

Carcasses increase predation risk by attracting scavengers that function also as predators. This may lead to decreased abundances and foraging activities by prey (Cortés-Avizanda et al. 2009b, Steinbeiser et al. 2017) or, as our findings show, increased rates of nest predation. By monitoring eggs in nests at different distances from the kangaroo carcasses, we showed that nests less than 50 m from carcasses were most likely to be depredated. Previous research has shown elevated artificial nest predation in Mediterranean steppe (Cortés-Avizanda et al. 2009a) and in temperate beach environments (Rees et al. 2015). As in these studies, by the end of our monitoring (14 days), we recorded almost complete depletion of artificial nests near carcasses (95% of quail nests were removed in both June and October 2018). We also recorded high quail nest predation at sites where carcasses were absent (nests depredated in June: 82%, October: 73%). While little research has been conducted on nest predation in arid Australia, studies on ground nesting birds in other deserts have found similarly low nest success (<20%; Mezquida and Marone 2001).

The high nest predation rates we observed may have arisen in part from our study design. Our nests were artificial and therefore not directly comparable to natural nests. Artificial nests may invite higher rates of predation than natural nests, for example, because they lack an incubating adult to defend or camouflage the eggs from predators (Major and Kendal 1996, Wilson et al.

1998, Burke et al. 2004). It is also possible that the spacing of our carcasses (~ 4 carcasses per km^2) elevated predation risk at sites without carcasses; the distances of ~500 m between carcass-present and absent sites may not have been sufficient. Indeed, Cortés-Avizanda et al. (2009) observed increased nest predation of nests up to ~500 m from carcasses. Finally, it is possible that corvids learnt to use and associate 'human' cues to detect nests, such as the stakes marking the control and carcass sites. This possibility is backed up by our finding that nest discovery increased similarly at closer proximity to the centre of control sites and that corvids contributed to nearly all quail nest predation at carcass-absent sites.

The study period differences for corvids could be explained by changes in daily activity of corvids with season. Birds were less active in October and probably exhibited restricted foraging activity due to the high temperatures experienced at this time (Figure 2.6). Animals expend water when travelling (Goldstein & Bradshaw 1998, Giladi & Pinshow 1999, Porter et al. 2000) and higher temperatures increase water loss. As birds are most active by day, they probably restricted their activity to preserve water and prevent overheating during times of high temperature (Cook 2012). Another possible explanation for the seasonal difference in nest predation is that corvids were less abundant in the region during October. The main carcass scavenger and nest predator was the little crow, which is nomadic (Rowley and Vestjens 1973). This suggests the importance of replicating studies on carcasses and nests in multiple seasons and years, as temporal changes such as droughts and rains in arid regions could reduce the generality of inferences made over short periods.

5.5.3 Management implications

Carcasses are often overlooked in management, perhaps because they are considered as spatially patchy resources that provide only short bursts of nutrients into ecosystems. But when present in excessive or unnatural quantities, such as following culling, or when utilised by invasive scavengers, they may impose substantial negative effects on local communities. We have shown that carcasses increase the probability of local nest predation by birds and attract invasive red foxes. The red fox's ability to access our artificial parrot nests is especially concerning. Night parrot populations occur predominantly where red foxes are scarce or absent (Murphy et al. 2018), and our data suggest that the lack of nest predation by red foxes could be a factor. Our carcasses also attracted invasive feral cats (23% of carcasses; see section 5.8 Supplementary Information: Figure S1) which have been linked to declines and extinctions of birds and mammals in central Australia (Dickman 1996). Cats typically prefer live prey, but

carcasses could support feral cats in the arid zone, especially when alternative resources are low. In turn, this could impose negative effects on the animals they depredate. Although feral cats did not depredate the nests in our study, they may impose higher predation risk for ground nesting birds, and particularly for night parrots, at other life stages (i.e. fledglings and adults; pers. comm. Nick Leseberg; Woinarski et al. 2017).

One solution to reduce the negative impacts of carcasses on bird nests is to remove them from the landscape. This may be necessary if carcasses are in abundance following sustained culling activities (Newsome et al. 2015). However, if carcass numbers are not in excess, any carcass removal requires consideration of the positive effects that these resources provide. Indeed, native scavengers such as wedge-tailed eagles, sand goannas and dingoes used carcasses in our study and their populations could be affected by carcass removal. There are several alternative management options. First, carcasses could be moved from areas that provide animal refuge or important nesting habitat, especially when animals are breeding and producing young. Second, concurrent control of invasive species that utilise carrion, including the red fox and feral cat, could be conducted during times of culls or when there are abundant carcass resources. Third, management of carcasses (i.e. carcass disposal) could focus on periods when native animal populations are low and particularly vulnerable to predation. In arid environments this includes the early stages of drought, when prey numbers are declining but predator numbers are still high (Letnic and Dickman 2006).

Whatever the case, the question of whether to remove carcasses could be determined by monitoring scavenger use of carcasses in the landscape (e.g. using remote cameras), and by quantifying and tracking changes in carcass numbers so that baseline carcass biomass loads are established (Barton et al. 2019). At present, carcass monitoring is not part of management programs in Australia, or elsewhere (Olea et al. 2019). Carcasses are, however, used to provide supplementary feeding resources for translocations of small native carnivores in Australia (e.g. see Robinson et al. 2020) and land managers on agricultural properties and on conservation reserves (e.g. Ethabuka Reserve, managed by Bush Heritage Australia) have proposed the use of carcasses to manipulate native and introduced predator populations. Our study shows that there is a risk of perverse outcomes on ground nesting birds, such as the endangered night parrot. For this reason, use of carcasses in food supplementation and predator manipulation requires further investigation, and we suggest that carcasses should be monitored to determine appropriate management actions. Overall, our paper adds to the growing body of knowledge

about the ecological role of carcasses in the landscape and suggests a greater need to consider how their presence has negative effects on native species under some circumstances.

5.6 Acknowledgements

5.7 References

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5.8 Supplementary Information
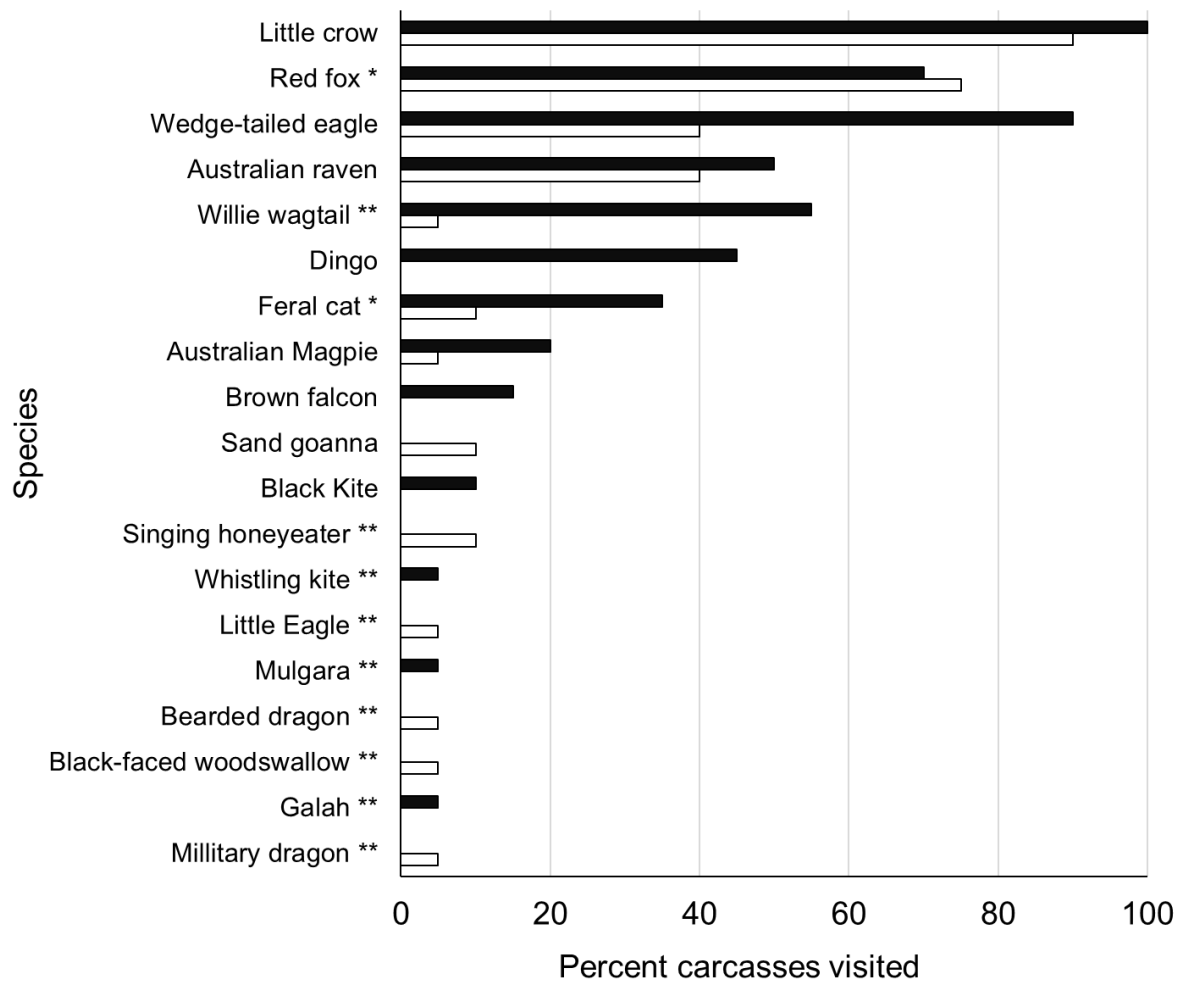
Figure S1 Number of carcasses visited by vertebrates over two two-week periods, during June (closed bars) and October (open bars) 2018. Herbivorous vertebrate species were not included in this list. Single asterisks indicate introduced species, double asterisks indicate species that were not observed directly scavenging on the carcasses. Latin names are as follows: little crow *Corvus bennetti*, red fox *Vulpes vulpes*, wedge-tailed eagle *Aquila audax*, Australian raven *Corvus coronoides*, willie wagtail *Rhipidura leucophrys*, dingo *Canis dingo*, feral cat *Felis catus*, Australian Magpie *Cracticus tibicen*, brown falcon *Falco berigora,* sand goanna *Varanus gouldii*, black kite *Milvus migrans*, singing honeyeater *Lichenostomus virescens*, whistling kite *Haliastur sphenurus,* little eagle *Hieraaetus morphnoides*, mulgara *Dasycercus* sp., bearded dragon *Pogona vitticeps*, black-faced woodswallow *Artamus cinereus*, galah *Eolophus roseicapilla* and military dragon *Ctenophorus isolepis*.
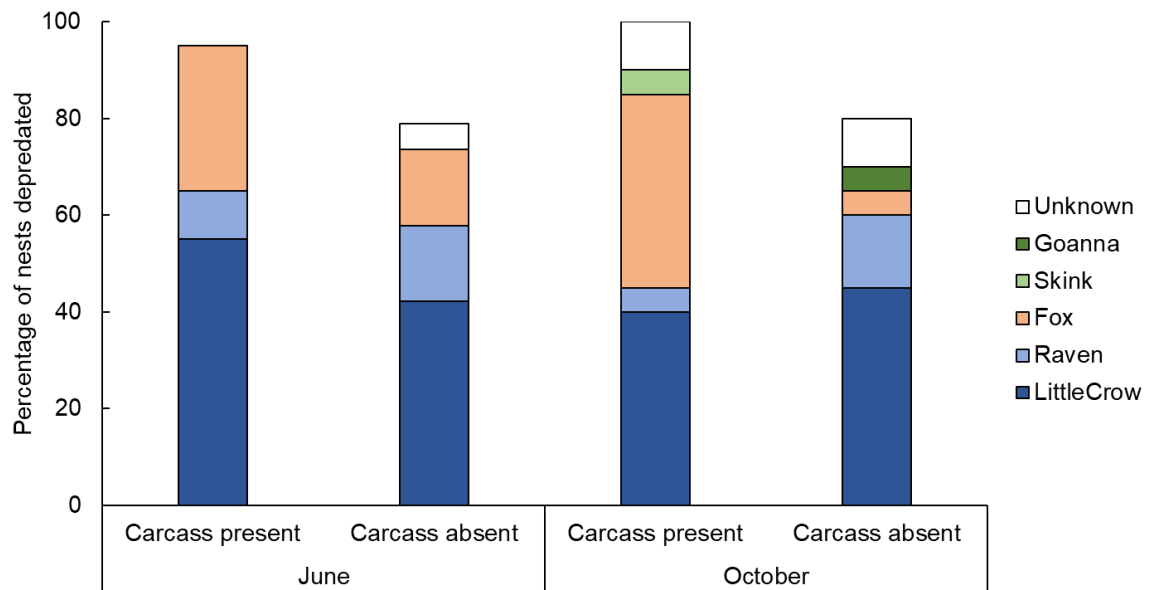
Figure S2 Percentage of nests depredated by different species during the two study periods (June and October) in 2018. Includes data from remote cameras monitoring a subsection of quail nests (n = 79). Latin names are as follows: little crow *Corvus bennetti*, Australian raven *Corvus coronoides*, red fox *Vulpes vulpes*, centralian blue-tongued skink *Tiliqua multifasciata* and sand goanna *Varanus gouldii*.

Figure S3 Image displays an opening made by a red fox in a needle-leaved spinifex hummock (*Triodia basedowii*), where an artificial parrot nest was positioned.

Table S1 Total foraging time on carcasses (monitored for 14 days) by red foxes and corvid species, collected using cameras positioned on carcasses monitored across two study periods and in open and closed habitat types in the Simpson Desert, QLD Australia.

Study period	Habitat	Corvid total foraging time (hr)	Red fox total foraging time (hr)	Total foraging time (hr)
June 2018	Closed	420.1	36.4	456.5
	Open	453.8	48.5	502.3
Total		873.9	85.0	958.9
October 2018	Closed	32.1	8.7	49.8
	Open	72.3	12.5	85.3
Total		105.0	21.2	126.2

CHAPTER 6

INVASIVE EUROPEAN WASPS ALTER SCAVENGING DYNAMICS AROUND CARRION

European wasps (*Vespula germanica*) feeding off the remains of an eastern grey kangaroo (*Macropus giganteus*). Photograph by Emma Spencer.

A version of this chapter was published as Spencer, E.E., P.S. Barton, W.J. Ripple, and T.M. Newsome. 2020. Invasive European Wasps Alter Scavenging Dynamics around Carrion. Food Webs 24: e00144.

My contribution for this paper was very substantial, and included conceptualisation of ideas, leading fieldwork, data collation and analysis, and writing and editing all drafts, in consultation with my co-authors.

A summary of this chapter was also published as a popular science article for the Conservation (Appendix C).

6.1 Abstract

European wasps (*Vespula germanica*) have invaded parts of North and South America, Australia, and New Zealand. They are opportunistic predators and scavengers that can disrupt food webs and species interactions, but their role in food webs associated with carrion is poorly understood. In this study we examined wasp abundance at 20 vertebrate carcasses in south-eastern Australia. We also collected data on the abundance of blowflies and the occurrence and behaviour of vertebrate scavengers at the same carcasses. Wasps arrived within minutes of deploying fresh carcasses and were approximately 4.3 times more abundant in forest compared with grassland habitats. Wasps killed and mutilated native blowflies and may have prevented them from ovipositing on carcasses, as we subsequently found that these carcasses were devoid of fly larvae. European wasps also appeared to interfere with dingoes (*Canis dingo*) feeding on carcasses, based on observations from cameras showing dingoes snapping their heads in the air and then retreating from the carcasses suddenly. The other major vertebrate scavenger in the system, feral pigs (*Sus scrofa*), did not show similar behavioural responses. Although we observed European wasps feeding on carcasses, carcass mass loss was slow. This could be a direct result of European wasps suppressing flies and potentially excluding dingoes from accessing carcasses. We conclude that European wasps may alter the way energy flows through scavenging food webs, which could have cascading impacts on ecosystem dynamics and services, although manipulative experiments would help to further evaluate these possibilities.

6.2 Main body

Invasive species have the capacity to cause severe environmental degradation by altering species dynamics and ecosystem processes (Salo et al. 2007). Such effects are well documented among invasive vertebrates, with hundreds of extinction events now recognized (Doherty et al. 2016). Less well known are the effects of invasive insects, with research efforts historically focusing on a select few areas and taxa (Kenis et al. 2009). Invasive insects have the capacity to alter ecosystems via their effects on food webs and species interactions. This might occur through similar mechanisms as invasive vertebrates, such as through changes to herbivory (Jenkins 2003), predation or parasitism (Boettner et al. 2000; Snyder and Evans 2006), or through more complex mechanisms such as competition, disease transmission or pollination disruption (Council 2002; Desurmont et al. 2014). However, invasive insects have very different biology (e.g. seasonal life cycles) to most invasive vertebrates, and they might be causing damage in ways we do not easily see or fully appreciate. This may especially be true

if the invasive insects are also alien species that have unique adaptations that give them an advantage over native species.

A highly successful invasive alien insect in Australia is the European wasp (or German wasp; *Vespula germanica*). The European wasp is native to Europe, Northern Africa, and parts of Asia, but has been introduced to other countries including North and South America, Australia, and New Zealand (Akre et al., 1989; Edwards, 1978). It is a social wasp, and an opportunistic generalist that utilizes both visual and olfactory cues to detect prey, and often returns to patches that have previously yielded high foraging success (Moreyra et al. 2007). Worker adult European wasps can specialize on different foraging tasks (Hurd et al. 2007), and therefore have different trophic positions in food webs. One distinct role of mature workers is foraging for protein, and can include directly preying on other insects, or scavenging meat from dead animals (Richter 2000). Although there is recognition of the ecological impacts of wasps in areas they have invaded (e.g. Beggs 2001; Cook 2019; Haupt 2015; Kasper et al. 2004), very little is known about the role of wasps in scavenging and carrion food webs (e.g. Archer and Elgar 2003; Wilson et al. 2010).

European wasps could disrupt food webs around carrion in their invaded range by consuming co-occurring insects directly, or by competing with both vertebrate and insect scavengers for the carcass resources. Similar impacts have been observed with their successful invasion of beech (*Nothofagus*) forests in New Zealand, and the wasps' monopoly of honeydew resources. Not only has their dominance of this resource lead to substantial negative impacts on vulnerable insect and bird species that rely on honeydew, it also supports high wasp densities, which drastically increases wasp predation of insect species in the area (Beggs 2001). Like New Zealand, European wasps in Australia lack any natural predators, and, due to their comparatively broad diet, they may also outcompete other native predators such as the common paper wasp (*Polistes humilis*; Kasper et al. 2004). The distinct behaviour and foraging ecology of European wasps and their status as an "apex" insect in Australia, therefore, means they have the potential to monopolize carrion and outcompete other scavengers around this focal food resource.

As part of a study investigating vertebrate and insect scavenging on carrion across Australia, we observed carcass visitation by European wasps and recorded some of the impacts that they were having on co-occurring scavenger species. Specifically, we examined the relationship between European wasps and blowflies (family: Calliphoridae) and determined whether

vertebrate scavengers were being influenced by wasp presence. Blowflies are an important scavenger that encourages rapid decomposition of carcasses via the larvae (i.e. maggots) they produce on decaying flesh (Benbow et al. 2019; Payne, 1965; Putman, 1978). Similarly, many vertebrates are considered efficient scavengers (DeVault et al. 2003) and as such, carcass decomposition may be delayed if these animals are deterred from feeding. Evidence of deterrence effects of wasps on scavenging flies and vertebrates may indicate potential cascading effects on food web dynamics around carrion.

Direct observations while monitoring 20 experimentally positioned eastern grey kangaroo (*Macropus giganteus*) carcasses (30.6 ±1.2 kg) in Kosciuszko National Park, south-eastern NSW (Figure 6.1), in March and April 2018, indicated that European wasps were congregating in large numbers around the animal carcasses. The carcasses were placed 1 km apart in forested (n=10) and grassland (n=10) habitats, and European wasps were present at all carcass sites. In some cases, individual carcasses attracted wasp swarms that we visually estimated to be in the thousands. Elevated wasp activity following carcass placement was also noticeable in the surrounding landscape. At ~80% of carcasses, wasps appeared rapidly, typically within the first 1 to 3 minutes of carcass placement. Wasps were observed feeding off the carcass meat (collecting and carrying it off for larvae in their nests), but even after 30 days of monitoring, some carcasses remained quite intact (e.g. 8 out of 20 carcasses had > 90% biomass remaining).
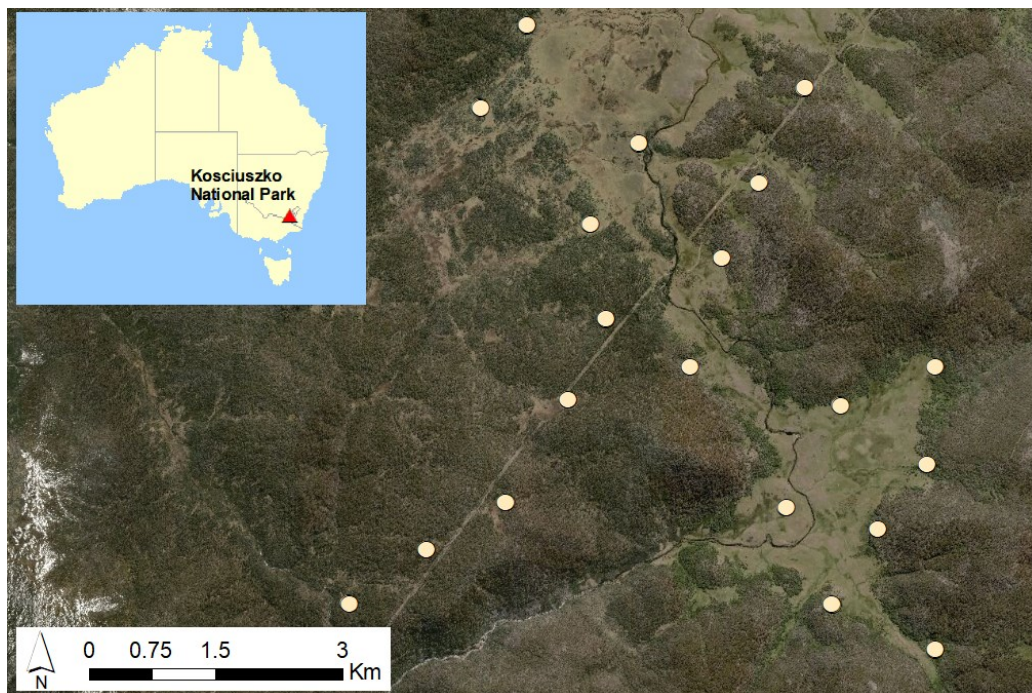

Figure 6.1 Map of the study area in Kosciuszko National Park, Australia, with positioning of eastern grey kangaroo carcasses displayed (yellow circles).

We estimated wasp and fly activity on each carcass using two pitfall traps (i.e. 120 mL jars filled half-way with a preservative fluid, ethylene glycol, and buried flush with the ground). This method was utilized to form part of the larger study comparing general insect (i.e. beetle, fly and ant) activity and has been used successfully to compare insect succession on animal carcasses in previous Australian studies (e.g. Barton and Evans 2017). Two of these traps were set approximately 20 cm from the top (i.e. mouth) and bottom (i.e. anus) of the carcass for 3 days at a time, directly after the carcass was positioned (days 1 - 3) and also two weeks after the carcass was laid (days 15 - 17). We identified and counted the number of European wasps and blowflies captured in traps. As we were interested in direct evidence of predation, we also counted the number of blowflies with any obvious signs of predation, including mutilation or removal of part or all of their abdomen and thorax, or decapitation. We used these more extreme signs of predation as we couldn't definitively identify flies that had been stung but not fed upon or mutilated by wasps, and because flies may have lost limbs or wings while trying to escape from the pitfall traps. As such, it is likely that we underestimated the cases of predation events on flies.

Our comparison of European wasp and blowfly captures across the different habitats (forested and grassland) and time periods (days 1 - 3 and days 15 - 17) revealed differences between blowfly and European wasp activity on the carcasses (Figure 6.2), with more wasps compared to flies captured in the later time period (total wasp: fly ratio = 819:19) compared to the earlier period (total wasp: fly ratio = 247:164; PERMANOVA: $F_{1,36}$ = 22.200, p = <0.001, using 999 random permutations). For the blowfly, a difference between time periods was detected, with more flies captured in the earlier period compared to the later period (GLM: Z = -4.273, p =
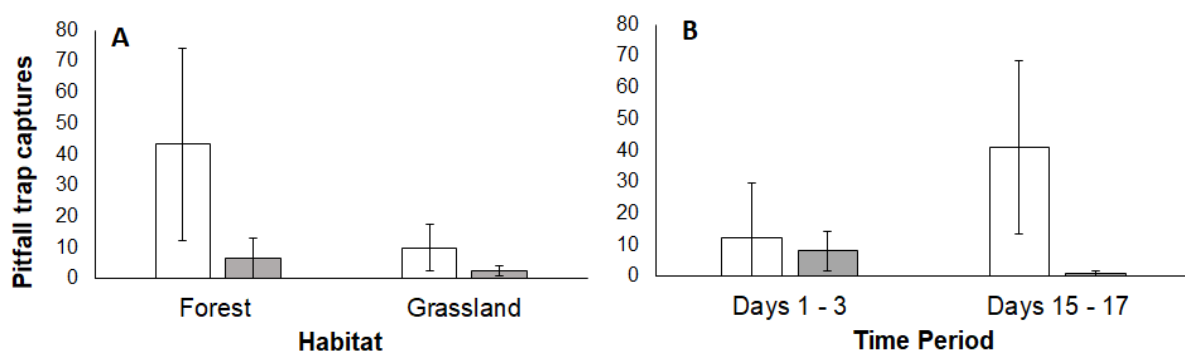

Figure 6.2 The average number of European wasps (open bars; ± 95% CI) and blowflies (grey bars; ± 95% CI) caught in traps set in forest and grassland habitat types (A) and in earlier (days 1 - 3) and later (days 15 - 17) sampling periods (B), in Kosciuszko National Park, Australia.

0.018). For the wasp, a difference between both habitat and time period was found, with more wasps captured in the forest habitat compared to the grassland habitat (GLM: $Z = -3.708$, $p =$ <0.001) and with more wasps captured in the later time period compared to the earlier period (GLM: $Z = 3.217$, $p = 0.001$; for further information on the statistical methods and results see section 6.6 Supplementary Information: Table S1). The eastern golden-haired blowfly (*Calliphora stygia*) was the most commonly identified blowfly species in our traps, comprising 91% of blowflies (Diptera: Calliphoridae) trapped.

When we examined the overall relationship between wasp and blowfly abundance, we did not find a relationship between the number of blowflies and the number of European wasps captured in traps ($F_{1,38} = 2.771$, $p = 0.104$;   a). However, when sorting through traps we identified many blowflies with evidence of mutilation by the wasps (Figure 6.3; Figure 6.4). In total, 18 (11%) blowflies were mutilated and only blowflies of the species *C. stygia* were mutilated. Fly mutilation was also only present at sites where wasps appeared in traps, and there was a significant positive linear relationship between wasp presence and the proportion of mutilated blowflies ($F_{1,23} = 10.07$, $p = 0.004$). Direct observations of predation were also made in the field; when blowflies and wasps were present, flies attempting to reach the carcass were rapidly attacked and subdued by wasps in all observed instances (~35 instances). We also didn't find any fly larvae (i.e. maggots) in, under or on top of the carcass for up to one month following carcass placements, despite checking the orifices and lifting the carcasses on multiple occasions to check the soil underneath.

We used remotely-triggered Reconyx PC800 Hyperfire™ camera traps (Professional Reconyx Inc., Holmen, WI, USA) to monitor large vertebrate scavenger activity on carcasses over a 30-day period, which included the period of time when we sampled flies and wasps. Camera traps were set to take continuous photographs each time the camera was triggered (i.e. rapid fire, no wait period). After tagging all the images to species level, we focused on the responses by dingoes (*Canis dingo*) and feral pigs (*Sus scrofa*) as they are the largest vertebrate scavengers present in the area. We noted where there was any evidence of feeding or scavenging behaviours being disrupted by counting when a dingo or pig snapped their jaws or swung their heads in the air and then retreated from the carcass suddenly.

Figure 6.3 Plots showing the relationship between the number of European wasps caught in traps and the number of blowflies (A) and the proportion of mutilated blowflies (B) caught in traps in Kosciuszko National Park, Australia.

Figure 6.4 Two eastern golden-haired blowflies (*Calliphora stygia*) captured in pitfall traps with mutilation evident in the form of decapitation (i.e. removal of their heads).

Our camera traps captured 221,078 photos of vertebrate animals visiting the carcasses. Dingoes were captured visiting 25% of the carcasses and were identified in 1890 photos, while pigs visited 60% of carcasses and appeared in 139,323 photos. Of these images, we counted 20 instances where dingoes were clearly disturbed or interrupted by wasps around carcasses. For the dingo, two individuals were recorded snapping at the air and then rapidly backing off from carcasses during 4 separate feeding bouts (i.e. separated by > 4 hrs.; e.g. Figure 6.5). In all cases, the individuals were solitary, and they each appeared on different carcasses. The first individual fed on 3 separate occasions on a carcass in the grassland habitat, while the second fed on a carcass in the forest habitat, on one occasion. These feeding bouts all occurred during the day (between 8 am and 6 pm) when high wasp activity was obvious in the sequence of camera images, although dingoes did visit and feed on carcasses at night. Feral pigs scavenged heavily during both the day and night and appeared on carcasses where high wasp activity was obvious. Pigs did not appear to be affected by wasps, and they only displayed head swinging and jaw snapping behaviours in response to other visiting pigs (e.g. Figure 6.5).

Our study shows that European wasps can be abundant scavengers that detect carcasses with a high efficiency. Wasps visited all 20 carcasses, appearing at carcasses rapidly and swarming in large numbers. We did not, however, find a relationship between the number of flies and wasps in pitfall traps, which suggests that flies were not avoiding carcasses where wasps were more abundant. Instead, variation in blowfly numbers among carcasses is likely due to differences in odour cues, which can be moderated by prevailing winds and vegetation or other barriers (Verheggen et al. 2017). This is probably also the case for wasps, although they may select

carcasses based on their nest location, as workers rarely travel more than 200 m from their nests when foraging (Perrott, 1975). While flies did not avoid carcasses where wasps were abundant, our findings did show that there is a potential for fly populations to incur sizable, localised impacts where they co-occur in high numbers with wasps. Wasps excluded flies from carcasses through direct predation, attacking flies before they landed on the resource. Wasps also seemed to prevent flies from ovipositing, evident by the absence of blowfly larvae observed during carcass inspections. These observations may explain why many carcasses displayed little to no decomposition after 30 days.
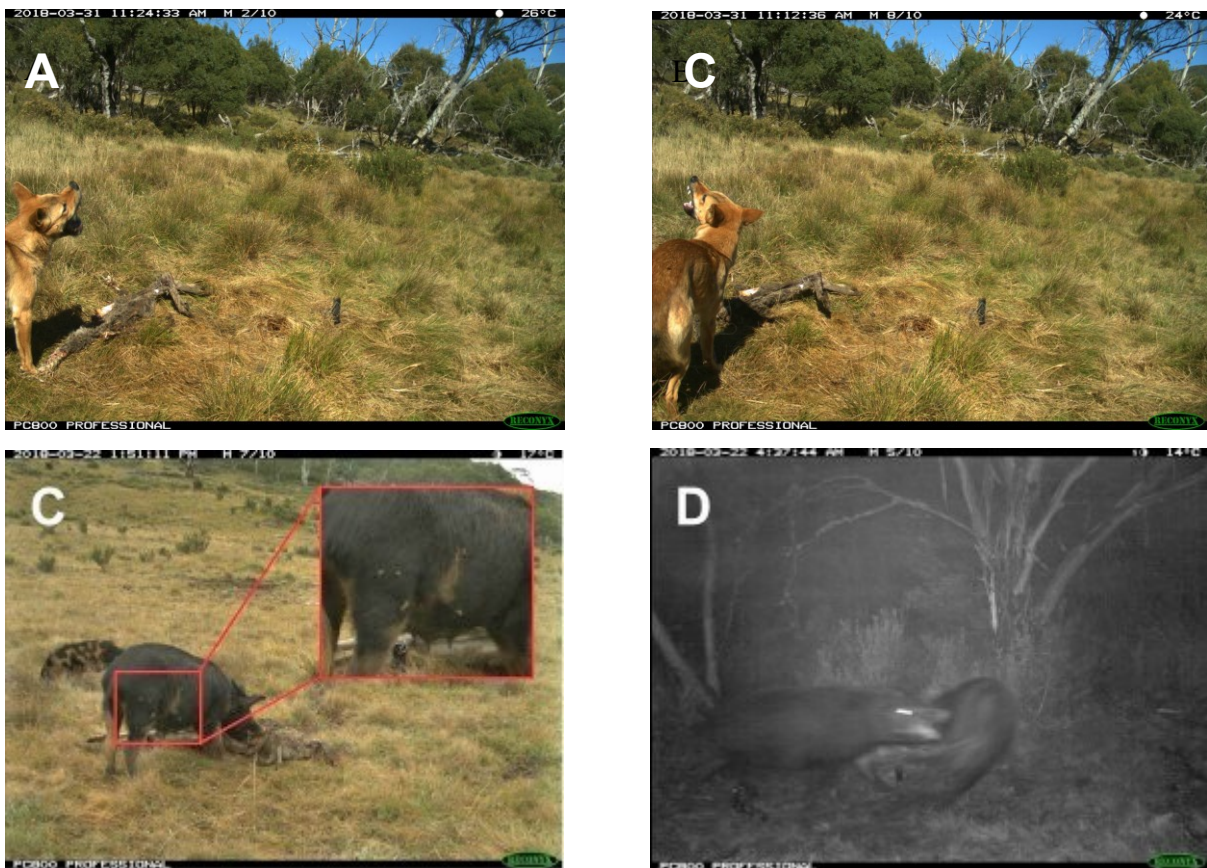
Figure 6.5 A selection of camera trap images where dingoes are displaying behaviours indicative of disturbance or interference by swarming European wasps (i.e. snapping at wasps around their heads; A - B), and where European wasps are pictured landing on feral pigs (C) and where a pig is pictured snapping at and chasing another pig (D).

The cool autumn weather experienced in March (Max:20°C, Min:-3°C) might have also suppressed blowfly reproduction and microbial growth during our study, which in-turn slowed carcass decomposition. Indeed, blowflies and microbes both show greatest activity on carcasses in warmer temperatures and rapid carcass decomposition is strongly associated with high insect and microbial activity (Putman, 1978). Without the wasp, however, we would have likely detected at least some larvae on the carcasses, as the dominant blowfly species observed (i.e. *C. stygia*) is well adapted to Australian subalpine and alpine regions and actively reproduces at low temperatures (Salter, 1946). Along with the effects of temperature on fly activity, blowflies also prefer fresher carcasses as oviposition sites (Putman, 1978). This explanation for the decrease in fly numbers later in the sampling period also fits with general carrion insect succession theory (Benbow et al. 2019). On the other hand, the increase in wasp numbers during this later period probably reflects the wasps' sociality. Social wasps, including the European wasp, may recruit nestmates to food sources over time through processes such as local enhancement (D'Adamo et al. 2000; Parrish and Fowler, 1983; Reid et al., 1994).

The behaviours displayed by dingoes when wasps were present at carcass sites suggest that wasps might also be influencing their scavenging activity. Interference with vertebrate feeding behaviours has been documented when certain species of invasive fire ants (e.g. *Solenopsis invicta*) are present on carcasses (e.g. Antworth et al. 2005), although these behaviours were inferred by comparing biomass loss on carcasses where ants were present or absent. That pigs did not display similar behaviours (perhaps due to their thickened hides; Frädrich, 1974) is worth noting because pigs are a recent (~230 years) invasive animal in Australia and they cause considerable environmental damage through grazing and when they root up the ground (Hone, 1995). Dingoes, on the other hand, are longer established (>4000 years) and are considered Australia's apex predator, helping to regulate the numbers of smaller pests and overabundant herbivores (Letnic et al. 2012). While dingoes prey on on pigs (Newsome et al., 1983; Saunders, 1993) and pigs likely avoid dingoes, the presence of European wasps on carcasses could counter some of these effects, as scavenging pigs are provided a competitive advantage over dingoes. This advantage lends support to the invasional meltdown theory, which suggests that some invasive species will facilitate the success and spread of other invasive species in certain systems (Simberloff and Von Holle, 1999). Prior studies have already established that invasive scavengers may be facilitated by the carcasses of other invasive species (e.g. Abernethy et al. 2016), but virtually nothing is known on whether invasive scavenging insects

facilitate other scavengers. Further, the prospect of an invasive scavenging insect facilitating an invasive scavenging vertebrate is intriguing.

The local interactions we observed could also trigger broader cascading interactions in the surrounding system (see Figure 6.6 for a summary of potential cascading interactions). For the blowfly, their ability to reproduce and their survival may be impeded by wasp presence on carcasses as a result of direct predation. Apart from influencing carcass decomposition rates and nutrient dispersal throughout the landscape, this could lead to cascading effects on other important ecological functions and processes such as pollination. Indeed, in our study region, the blowfly is considered a major pollinator of flowers in alpine areas (Inouye and Pyke, 1988). If wasp numbers are supported by prevalent carcass resources, then pollination in the region may be negatively impacted. Similarly, native vegetation could also be impacted by cascading interactions between wasps, dingoes, and pigs. If wasps deter dingoes but not pigs, this might concentrate the activity of pigs in certain areas (i.e. where carcasses are present) and exacerbate environmental degradation via processes such as grazing and ground rooting. Social wasps such as the European wasp also provide pollination services (Shuttleworth and Johnson 2009) and contribute to carcass scavenging. When exploring potential cascading interactions around carrion, therefore, it is also important that we consider the potential ecosystem services that the wasp may provide, along with any negative impacts.

One key limitation of our study was that it lacked a negative control where carcasses had wasps excluded from feeding. This made it difficult to determine the degree to which European wasps influence insect and vertebrate scavenging and rates of carcass decomposition. Further manipulative experimentation, for example, by excluding wasps from half of the monitored carcasses using wasp-specific poison baits (e.g. Lester et al. 2013) would prove very useful. Pitfall traps can be highly effective at sampling blowflies at carcasses due to their habit of crawling over the carcass and nearby ground to find suitable oviposition sites (Barton et al. 2017). Nevertheless, they could be combined with other forms of collection such as sweep nets, sticky traps, and hand collection (Schoenly et al. 2007). Our sampling methods were originally designed for a larger study investigating the general use of carcasses by different scavenger species across Australia. We did not exclude wasps from any carcasses and chose to use pitfall traps to sample insects, as we had intended to target a broad array of species and did not anticipate the presence of the invasive wasp on carcass resources.
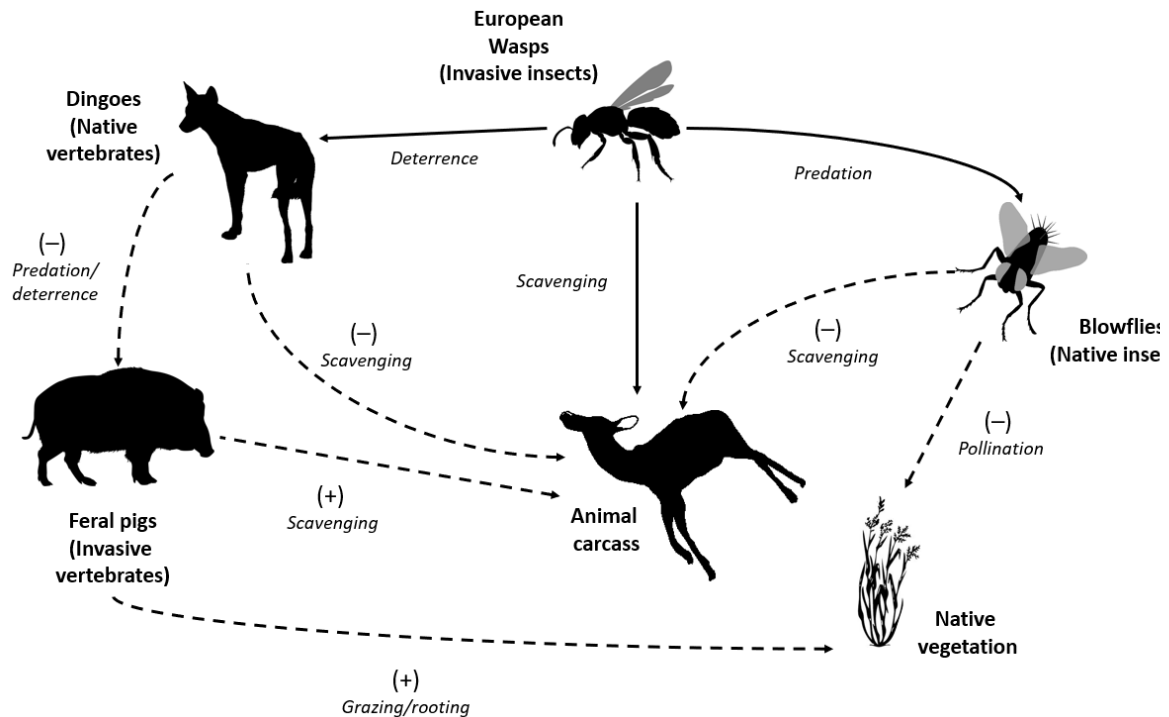
Figure 6.6 Potential interactions between European wasps, blowflies, and native and invasive vertebrate scavengers when European wasps are present in the system. The arrows show the direction of the interactions, and the (–) or (+) signs indicate whether the interaction decreases or increases, respectively, in the presence of wasps. Solid lines indicate direct interactions with the wasp, while dotted lines show the indirect (cascading) effects of wasp presence on other species.

Our findings have broader implications for managing carcass loads in Australian environments. For example, to mitigate the negative impacts of the European wasp, carcass removal could be focused in certain habitats. In our study, wasps showed preferences for carcasses in forest sites, potentially because these habitats provided more options for nesting (e.g. in rotted wood stumps). Managing carcasses may not be as important during seasons with low wasp activity. During these times, dingoes may scavenge more, competing with and repelling feral pigs and potentially other vertebrates such as the introduced red fox (*Vulpes vulpes*). Considering the numbers and sources of animal carcasses is also important when assessing wasp impacts and thus determining whether carcass removal will benefit a system. Mass mortality events resulting from weather extremes, natural disasters (e.g. bushfire and floods), disease or animal culls for pest control, for instance, could attract and support large populations of wasps over vast areas. These populations could then cause substantial impacts that are measurable on the landscape scale, for example, by decimating native pollinator populations or by facilitating pest

scavengers such as the feral pig. To further disseminate these and other impacts, insights into the spatial and temporal use of carcasses by European wasps is required, as are more comprehensive experiments documenting their interactions with a greater range of insect and vertebrate species. Finally, when deciding whether and how to manage carcasses, it is important that the complexity of scavenging food webs is appreciated, especially if our observations of an invasive insect disrupting insect and vertebrate scavengers apply to other regions and scavenger guilds.

6.3 Ethics statement

A Scientific license was obtained to use and relocate the kangaroo carcasses (SL 101901) and research was approved by the University of Sydney Animal Ethics Committee (Project number. 2017/1173). Kangaroos were sourced from pre-planned animal culls in the local area, and as such were not killed for the purpose of this study.

6.4 Acknowledgements

6.5 References

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6.6 Supplementary Information

Table S1 Results of the PERMANOVA and two GLMs, testing for differences between the number of European wasps and blowflies captured in pitfall traps among different habitats (grassland and forested) and time periods (days 1 - 3 and days 15 - 17) in Kosciuszko National Park, Australia. To conduct the PERMANOVA, the number of European wasps and blowflies captured in pitfall traps were the response variables, and habitat and time period were the predictor variables. This analysis was based on Bray-Curtis dissimilarities calculated on wasp and fly count data with a square root transformation and was tested using 999 random permutations. To conduct the two GLMs, the number of European wasps or blowflies captured in pitfall traps was the response variable, and habitat and time period were the predictor variables. As our data were overdispersed, we used negative binomial distribution in the construction of both GLMs. All analyses were conducted using R statistical software v.3.6.1 (R Development Core Team 2019). To execute PERMANOVA and GLMs in R we used the "vegan" and "MASS" packages, respectively.

PERMANOVA (blowfly & European wasp)	df	Sum of Sqs	R^2	F value	P
Habitat	1	0.210	0.034	1.959	0.141
Time Period	1	2.379	0.382	22.200	<0.001 *
Residuals	34	3.643	0.585		
Total	36	6.232	1.000		
GLM (blowfly)	Estimate	Std. Error	Z value	P	
Intercept	4.321	0.739	5.844	<0.001 *	
Habitat	-0.654	0.462	-1.418	0.156	
Time Period	-2.011	0.471	-4.273	<0.001 *	
GLM (European wasp)	Estimate	Std. Error	Z value	P	
Intercept	1.348	0.796	1.694	0.090	
Habitat	-1.780	0.480	-3.708	<0.001 *	
Time Period	1.544	0.480	3.217	0.001 *	

CHAPTER 7
GENERAL DISCUSSION

A large lace goanna (*Varanus varius*) feeding off the remains of an eastern grey kangaroo (*Macropus giganteus*). Photograph by Emma Spencer.

7.1 Overview

Carrion attracts a diverse community of organisms that engage in complex interactions while competing for a shared resource that is generally ephemeral and patchy in nature (Carter et al. 2007, Barton et al. 2013). These interactions are strongly associated with the environmental context in which the carrion resources are situated. Yet there remains a paucity of data on the different environmental drivers directing these interactions, especially across larger regional scales and in Australian environments. There is also poor understanding of how carrion consumers influence surrounding ecosystems via processes linked to decomposition and, in the case of facultative scavengers, via predatory effects (Carter et al. 2007, Wilson and Wolkovich 2011, Barton et al. 2013).

This thesis addressed these gaps, focusing on interactions between carrion resources, the animals that associate with these resources, and the surrounding ecosystems. I monitored insect and vertebrate carrion communities around 120 carcasses in three distinct biogeographic regions in Australia. I identified and compared key members of the insect (Chapter 2) and vertebrate (Chapter 3) carrion communities in each of these bioregions using a standardised approach. I also assessed how their association with carrion across local and regional scales was affected by important environmental variables: season and habitat. To explore interactions between carrion and its consumers, I studied the role that Australia's largest terrestrial apex predator, the dingo (*Canis dingo*), played in carcass removal across the three study bioregions (Chapter 4; Spencer and Newsome 2021). Finally, using two case studies I assessed how carrion communities interact with surrounding ecological communities. In the first case study, I assessed the role of carrion in driving predator-prey interactions between arid-zone predators and ground nesting birds (Chapter 5; Spencer et al. 2021). In the second study, I examined the predatory and competitive relationships between invasive European wasps (*Vespula germanica*) and other co-occurring scavengers in the Australian Alps (Chapter 6; Spencer et al. 2020).

Collectively, the findings of my thesis revealed novel insights into the structure and function of carrion communities across a range of bioregions in Australia. They also help to close important gaps in global understanding of the carrion necrobiome (Benbow et al. 2019). Below I highlight key results, evaluating how my findings have contributed new knowledge on carrion communities in Australia and the role that environmental drivers play in shaping these

communities across local and regional scales. I then go on to identify and discuss key management implications and outline potential next steps for carrion ecology research.

7.2 Key thesis findings

7.2.1 Carrion communities vary across different Australian bioregions

This thesis comprises the most comprehensive, large-scale standardised study investigating both vertebrate and insect carrion communities in Australia to date (but see: Read and Wilson 2004, Cunningham et al. 2018). It has revealed a substantial diversity of taxa that directly associate with carrion as a focal resource. This included at least twenty-seven vertebrate species from sixteen different families (Chapter 3), as well as twenty beetle families and seventeen fly families and a diverse range of wasps and ants (Chapter 2). This is the first time such a high diversity of animals, and this kind of taxonomic breadth, has been demonstrated for carrion communities in Australia. It adds to the growing literature base that supports the important role that carrion resources play to a great number of organisms across a range of geographies (DeVault et al. 2003, Mateo-Tomás et al. 2015).

By conducting standardised surveys across three distinct bioregions, I was able to show how key insects and vertebrates varied in their association with carrion. For example, scavenging by corvids (*Corvus* spp.), wedge-tailed eagles (*Aquila audax*), red foxes (*Vulpes vulpes*), and ants (Formicidae) was common across all bioregions, but these species were most prolific on carcasses in the Desert bioregion, compared to the Alpine and Forest bioregions (Chapter 2 and 3). In contrast, dingoes, flies (Calliphoridae), and beetles (Coleoptera) scavenged carcasses across all bioregions, but they typically visited carcasses in higher numbers in the Alpine and Forest bioregions compared to the Desert bioregion (Chapter 2 and 3). Understanding how animals vary in their association with carrion across a range of different systems is vital, as carrion may provide an important resource contributing to the fitness and reproductive success of these animals but may only do so in certain contexts (e.g. Needham et al. 2014).

Regional variation in carrion community structure and composition may also affect decomposition processes by influencing how quickly carrion is removed from landscapes (Wilson and Wolkovich 2011, Mateo-Tomás et al. 2015). I showed that dingoes can play an important role in carrion removal in Australian environments (Chapter 3 and Chapter 4; Spencer and Newsome 2021). Apex predators are generally capable of quickly consuming large prey items, and so I expected that Australia's largest terrestrial apex predator – the dingo –

would play a particularly important role in accelerating carrion removal. The importance of carrion to other Australian apex predators, including the Tasmanian devil (*Sarcophilus harrisii*) has already been shown (Cunningham et al. 2018), and scavenging by the dingo has been recorded in a few locations (Allen 2010, Forsyth et al. 2014, Déaux et al. 2018). This thesis was, however, the first to show that dingo scavenging, and carcass removal may vary across different biogeographic regions. I found that carrion use by dingoes, and their subsequent role in carrion removal in Australia is highly context dependent, with carcass break-down most strongly influenced by dingo scavenging in the Forest bioregion in the cool seasons (Chapter 4; Spencer and Newsome 2021). This result has implications not only for understanding the contribution that a common Australian vertebrate species has to decomposition, but also adds to our knowledge of the important roles that apex predators, such as dingoes, play in ecosystems (Glen et al. 2007, Ripple et al. 2014).

Aside from contributing to carrion removal, most carrion consumers also engage in predatory foraging behaviours as they hunt for prey in addition to scavenging carrion resources (Moleón et al. 2014, Pereira et al. 2014). The structure and composition of carrion communities may therefore influence predator-prey dynamics, as carcasses bolster predator numbers or redirect their activity to certain locations (Cortés-Avizanda et al. 2009). I showed that carrion can attract nest predators and may increase predation impacts on ground nesting birds up to and potentially beyond 50 m from the resource (Chapter 5; Spencer et al. 2021). I suggested that these predation effects could be substantial if high densities of carcasses are produced long-term (e.g. at roadsides where animal mortality is recorded year-round), or when animals may be vulnerable to predation (e.g. during breeding and nesting seasons).

Predation impacts by carrion-associated animals could further be elevated if invasive predators are present. Invasive predators threaten global biodiversity and have disproportionate effects on Australian native species (Salo et al. 2007, Doherty et al. 2016). I found that invasive predators comprise a large component of carrion communities across Australia (Chapter 2 and 3). Indeed, European wasps and feral pigs (*Sus scrofa*) were frequent visitors of carcasses in the Alpine bioregion, while the feral cat (*Felis catus*) scavenged regularly in the Desert bioregion. Frequent carrion use was also recorded for red foxes across all bioregions. My work further revealed some of the detrimental impacts that carrion-association by invasive predators may have. For example, red foxes comprised the most frequent predator of artificial nests modelled on those of the endangered night parrot (*Pezoporus occidentalis*) in the Desert bioregion (Chapter 5; Spencer et al. 2021). Further, in the Alpine bioregion, European wasps

swarmed carcasses and depredated eastern golden haired blowflies (*Calliphora stygia*), which are considered both important alpine pollinators and carcass 'removalists' (Chapter 6; Spencer et al. 2020). As both the red fox and European wasp consume carrion resources, they may also potentially interact with other members of the native carrion community via competition. This means that invasive predators in Australia could have several cascading impacts within the carrion necrobiome, both as predators and competitors, but also as decomposers.

7.2.2 Multi-scale environmental drivers shape carrion communities

By experimentally positioning carcasses across different seasons and habitats within the three studied bioregions, I demonstrated how different environmental variables influence the complex set of interactions that occur around carrion, across both local and regional scales. I summarised these interactions in three simplified conceptual models, representing each of the study bioregions (Figure 7.1).

Across the different study bioregions, this thesis uncovered several general trends in season and habitat effects on carrion communities. I found that in warmer seasons and closed habitats insect abundances tended to be highest on carrion resources (Chapter 2), while vertebrate scavenging of carcasses was typically most frequent in cooler seasons, and in open habitats, especially for avian species (Chapter 3). However, habitat generally played a lesser role in shaping both insect and vertebrate carrion communities, compared with season (Chapter 2 and 3). This result helps to explain why carcass persistence was strongly affected by season, but less so by habitat (Chapter 4; Spencer and Newsome 2021). In addition, habitat generally played a greater role in shaping carrion communities for vertebrates compared to insects (Chapters 2 and 3). Vertebrates would have been able to easily span the distance between habitats in my study (i.e. between open and closed patches of vegetation). On the other hand, smaller less-mobile insects were likely more restricted by such distances and so their association with carrion was likely linked to habitat preferences. Vertebrate habitat associations were probably also shaped by the visibility of the food resource and search strategy of the scavenger species. Indeed, more visual avian scavengers were generally associated with carcasses in open habitats in the Forest and Alpine bioregions where there was a greater contrast in terms of vegetation complexity between open and closed canopy habitats, at least compared to the Desert bioregion (Chapter 3).

Other key differences in the effects of season and habitat were revealed in this thesis, including across the different study bioregions. This confirms that carrion communities are influenced to
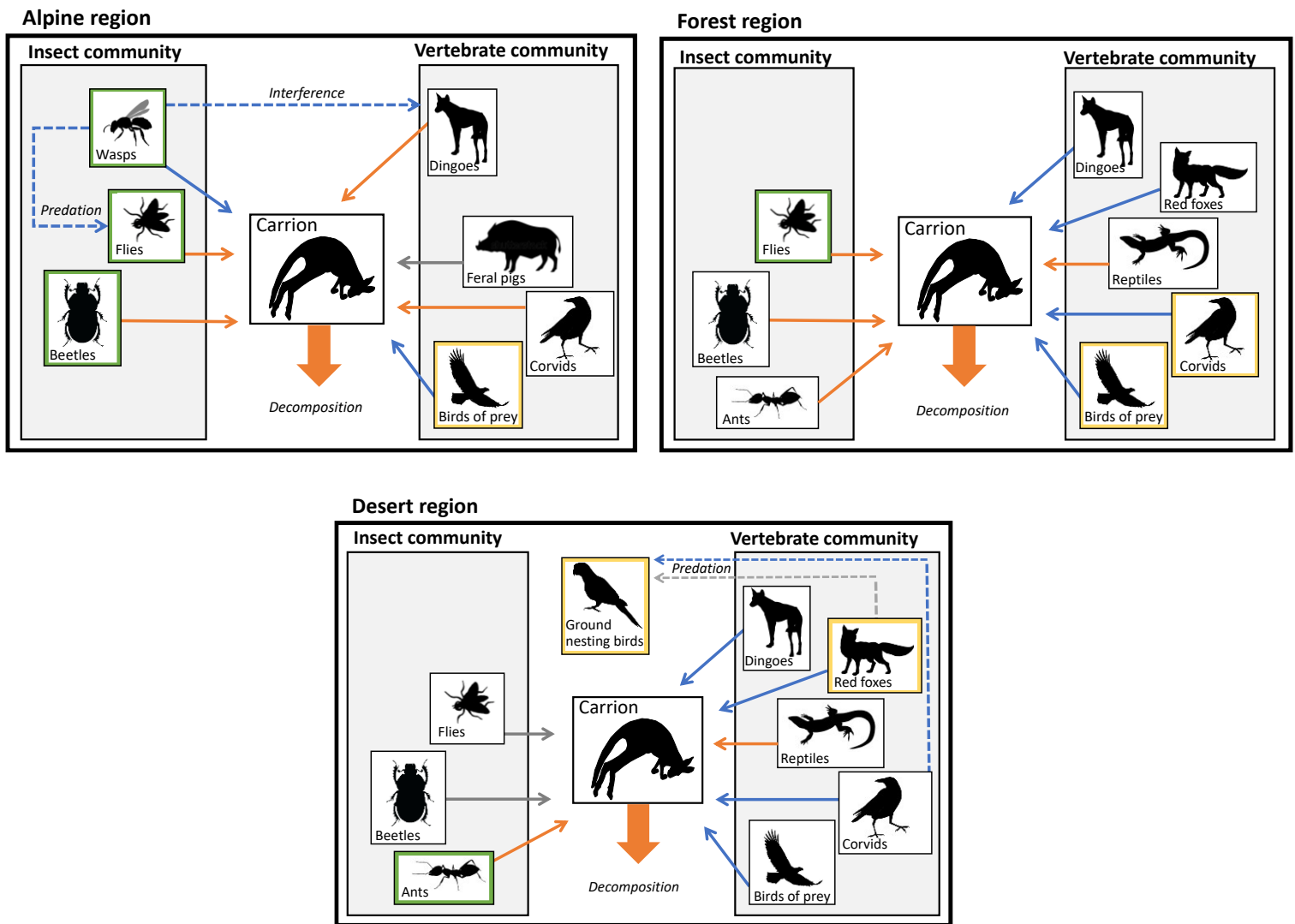
Figure 7.1 Summary of thesis findings on carrion community interactions in the Alpine, Forest and Desert bioregions. These models highlight how carrion community interactions are context-dependent and can change over space (different bioregions) and time (different seasons). Arrow colour indicates whether the relationship was stronger in cooler seasons (blue arrows), warmer seasons (orange arrows), or were similar across both seasons (grey arrows). Coloured outlines around different insects and vertebrates indicate whether their interactions were more likely associated with closed 'treed' habitats (green outline) or open habitats (yellow outline).

different degrees by environmental drivers acting across different scales (Pardo-Barquín et al. 2019). For instance, while warm seasons generally hosted greater insect abundances in the Forest and Alpine bioregions, flies and beetles were similarly abundant across seasons in the Desert bioregion. Similarly, while more vertebrates generally used carcasses in the cool seasons, in the Alpine bioregion feral pigs and red foxes used carcasses equally across seasons,

and dingoes and corvids used more carcasses in warmer seasons. The only consistent trend seemed to be for carcass persistence, which was always fastest in warmer seasons. This result follows the majority of literature investigating the effects of temperature and season on carrion decomposition, which suggests that increased insect and microbial activity in warmer seasons contribute to greater carrion decomposition rates (Carter et al. 2007). However, there are probably other factors at play too. For example, microbial activity might not mirror insect activity across all bioregions, and insect species composition may play a more important role in decomposition than abundance.

7.3 Management implications

7.3.1 Carrion management in Australia

In Australia, carcasses are produced via natural and anthropogenic sources, sometimes accumulating in the environment in large numbers. Most of these carcasses are left to rot *in situ*, although some are removed when they are in proximity to human settlements and release strong odours, or are unsightly and otherwise confronting to people (Tucker et al. 2018), or when they are considered a possible avenue of disease spread (Pandey et al. 2020). In general, however, the overwhelming management sentiment regarding carrion in Australia is: if it impacts or disturbs humans, it needs to be removed. On the other hand, very little consideration has typically gone towards the management of carrion in conservation settings.

This thesis supports the concept that greater emphasis should be placed on considering how carrion is managed across Australia ecosystems. Indeed, I showed that high numbers of invasive predators can use carcasses in Australia, and that these predators can have potentially detrimental effects on co-occurring native animals, including scavengers, pollinators, and endangered species (Chapters 5 and 6; Spencer et al. 2020, 2021). On the other hand, I also showed that a great diversity of native species may benefit from carrion resources as scavengers (Chapters 2 and 3). I even found that some species (e.g. Australian ravens; *Corvus coronoides*) use fur from carrion to line their nests and I observed several animals with young scavenging on carcasses (from brush-tailed possums; *Trichosurus vulpecula*, to dingoes), which indicates that carrion could play a role in increasing breeding success and raising young.

Carrion consumers include important pollinators such as blowflies and apex predators like the dingo (Chapters 2, 4 and 6; Spencer et al. 2020, Spencer and Newsome 2021), meaning carcasses may further play critical roles in supporting important trophic regulators and

ecosystem services (Cunningham et al. 2018). Collectively my findings suggest that a balanced approach to carrion management is required, and that the potential negative impacts that animal carrion may have on surrounding ecosystems should be considered, while also appreciating that carrion removal might have detrimental effects on native scavengers (Barton et al. 2013).

This thesis further supports a need to consider environmental context when determining how to manage carrion in conservation settings. Importantly, carrion community structure, including how carrion is used by native and invasive species, will vary across different locations (e.g. bioregions and habitats), and times (e.g. seasons) (Chapters 2 and 3). It is therefore essential that managers determine how carrion is used by scavengers at a location before they enact any management actions. Similarly, the impacts that carrion have on surrounding ecosystems are likely also to be highly context dependent. For example, certain locations may host populations of endangered species, and these species may be more sensitive to predation at certain times, such as during breeding and nesting periods (Chapter 4; Spencer et al. 2021). Managers should therefore consider the suite of species present at a site, even if they do not actively associate with carcasses.

Finally, it is also important that land managers consider how many carcasses are present or are produced in the environment, as well as the size of these carcasses. This thesis involved use of larger kangaroo carcasses (~30 kg), which may have attracted very different carrion community assemblages compared with, for example, smaller rodent carcasses. Indeed, smaller carcasses attract lower carrion community diversities and provide less biomass and fewer nutrients, compared with medium and larger-sized carcasses (Selva et al. 2003, Moleón et al. 2015). Additionally, if carcasses are produced in large numbers (e.g. as a result of mass mortality events) or are produced in systems frequently, over long periods of times (e.g. like roadkill on country roads, or following regular lethal animal control), this could have substantial effects on scavenger communities and ecosystems (Tomberlin et al. 2017, Fielding et al. 2021). For example, if predator populations increase due to these carrion loads, there is also the possibility of increased predation on live prey, particularly when food subsidies decline (Yirga et al. 2012) or if their prey numbers are low and hyper-predation occurs (Courchamp et al. 2000).

As there is a range of positive and negative effects that carcasses can have on the various components of ecosystems, and because these effects can differ so broadly across different environmental contexts, it is important that carrion management methods are dynamic, and that consideration is given to the potential costs and benefits of alternative measures. For example,

while carcass removal (or burial) may seem like a suitable management option for carcasses attracting or supporting invasive predators, this management action will also permanently remove potentially important nutrients from the system, which could have flow-on effects to native scavengers, detritivores, and even plant communities that draw these nutrients from surrounding soils (Barton et al. 2013). Instead, other methods could be considered to prevent access to carcasses by invasive predators or other unwanted pests, while still allowing nutrients to re-enter systems. For example, carcasses can be fenced off to restrict contact by mammalian invasive predators including foxes and feral cats but allowing insects and avian species to access the resource. Another option involves composting animal remains, which enables the return of nutrients to the soils but prevents most insects and vertebrates from using the resource (Berge et al. 2009, Bonhotal et al. 2014).

Some of the negative impacts relating to carcasses could also be managed by changing how carcasses are produced. For example, carcass production could be limited on roadsides by constructing fences and wildlife crossings or by encouraging changes in human behaviour (e.g. by decreasing vehicle speed limits; Hobday et al. 2008). Further, land managers could change the timing of lethal animal control programs, to limit carcass production and therefore impacts during times when invasive predators are most active or potential prey are most vulnerable. In the Alpine bioregion, where lethal control of invasive herbivores is common, my results indicate that more positive conservation outcomes could be reached by avoiding carcass production in Autumn when European wasps are active (Chapter 6; Spencer et al. 2020). Similarly, encouraging carcass production in warmer periods could help to reduce impacts of invasive mammalian predators, as carcasses decompose quickly for the most part as insects and microbes outcompete vertebrate scavengers (Chapter 4; Spencer and Newsome 2021). Finally, if managing carcasses is difficult, or carcass production (e.g. via animal control or roadkill) cannot be avoided, concurrent management of the impacting species present, such as invasive predators, could also be carried out to counteract any positive effects of carcass subsidies in the environment. Finally, the decision to leave carcasses to rot *in situ* will probably still often be the most suitable management option. For example, carrion produced during summer periods and in areas where larger native animals such as dingoes scavenge frequently (e.g. like in the Forest study bioregion), are likely to disappear quickly with potentially limited effects on surrounding systems (Chapter 4; Spencer and Newsome 2021).

Determining which management methods should be applied when dealing with carrion in ecosystems is difficult, especially as the effects of these methods on carrion communities and

surrounding ecosystems remain virtually unexplored. Monitoring a selection of carcasses and keeping track of potentially vulnerable native species in surrounding ecosystems could ascertain how this resource is used by different species, as well as the species that potentially may be impacted by carcass production. However, due to the complexity of the interactions that occur around carrion, and the fact that there is virtually no understanding of the effects that many of the different potential management methods outlined above have on the necrobiome and surrounding ecosystems, further research is required. I therefore suggest that future studies should work at running a series of experimental trials to weigh up the costs and benefits of specific management actions in Australia.

7.3.2 Managing scavengers

Carrion removal is an important ecosystem service provided by scavengers, as it can help to reduce the potential for disease spill-over and is an essential step in recycling nutrients through systems (Barton et al. 2013, Vicente and VerCauteren 2019). Therefore, how we manage scavengers may have profound effects on ecosystems, especially if these animals contribute to substantial carcass removal. In this thesis, I showed that dingoes were important scavengers in Australian ecosystems, contributing to carrion removal and dispersal of carrion nutrients across landscapes (Chapter 4; Spencer and Newsome 2021). This finding has important management implications, as dingoes are widely persecuted across their range; hunted, baited, shot, and trapped due to their interactions with livestock as an agricultural pest (Archer-Lean et al. 2015). Dingoes play several important roles in ecosystems, as they can suppress overabundant herbivores, and "release" prey populations impacted by mesopredators (Glen et al. 2007). I argue that the role they play as scavengers should also be considered when managing this animal, as their loss in systems could have implications for carcass decomposition and removal in ecosystems. I also support calls to appreciate the importance of apex predators as scavengers more generally (e.g. O'Bryan et al. 2018, Cunningham et al. 2018), especially given that apex predator declines are recorded globally (Ripple et al. 2014).

Finally, this thesis also showed that invasive species may comprise a dominant part of many Australian scavenger communities (Chapter 2 and 3). While invasive predators may have detrimental effects on prey, if they also contribute substantially to carrion removal in certain environments, lethal management of their populations could have unintended detrimental effects. For example, removal of dominant scavengers such as feral pigs in the Alpine bioregion could lead to reduced carcass removal rates, especially in cooler seasons when insects are less

active (Chapters 2 and 3). Further, studies have also shown that invasive species may comprise the dominant scavengers of carcasses from other invasive species (Abernethy et al. 2016). As there are many large carcasses produced across Australia that are derived from invasive species (e.g. feral pigs and deer), the impact of losing this subset of the carrion community could be substantial. Removing invasive species from systems without considering the potential flow-on effects of this decision has been demonstrated to have perverse outcomes in other situations. For example, rabbit removal may lead to trophic cascades in predators such as wedge-tailed eagles (*Aquila audax*) or large monitor lizards (*Varanus* spp.) (Cooke 1999). For this reason, it is essential that more thought is put in before invasive species are removed from scavenger webs.

7.4 Next steps in carrion research: developing the necrobiome framework

The Necrobiome was originally defined as the community of organisms that associate with animal carrion (sensu Benbow et al. 2013). More recently, Benbow et al. (2019) expanded this concept into a framework that draws together all decomposer communities, including those that associate with different types of necromass (e.g. such as carrion, plant detritus, and animal faeces). This framework also illustrates some of the links among organisms associated with the various types of necromass and includes the interactions they share with surrounding ecosystems (Figure 1.1) over different spatial and temporal scales.

In this thesis, I used the necrobiome framework to develop my research questions and addressed key gaps by providing one of the first empirical large-scale studies investigating how carrion communities are influenced by environmental drivers acting across different scales. In doing so, I revealed important trends across different Australian bioregions, and highlighted the context dependency of carrion communities. However, there is still much to be done to develop our understanding of the general processes that cause the structure and function of necrobiome communities to change over space and time. Future research should focus on developing macroecological theories that are relevant to scavenging or processes linked to decomposition, ideally accounting for differences across spatial, temporal, and taxonomic scales (Figure 7.2). Macroecology is a growing and important subdiscipline of ecology (McGill 2019), but it is yet to be explicitly incorporated into the necrobiome framework. Here, I explore some of the gaps within spatial, temporal, and taxonomic scales, which form current barriers in understanding large-scale trends in the necrobiome. I then go on to discuss how these gaps

could be addressed, through implementation of a standardised approach to global carrion research.
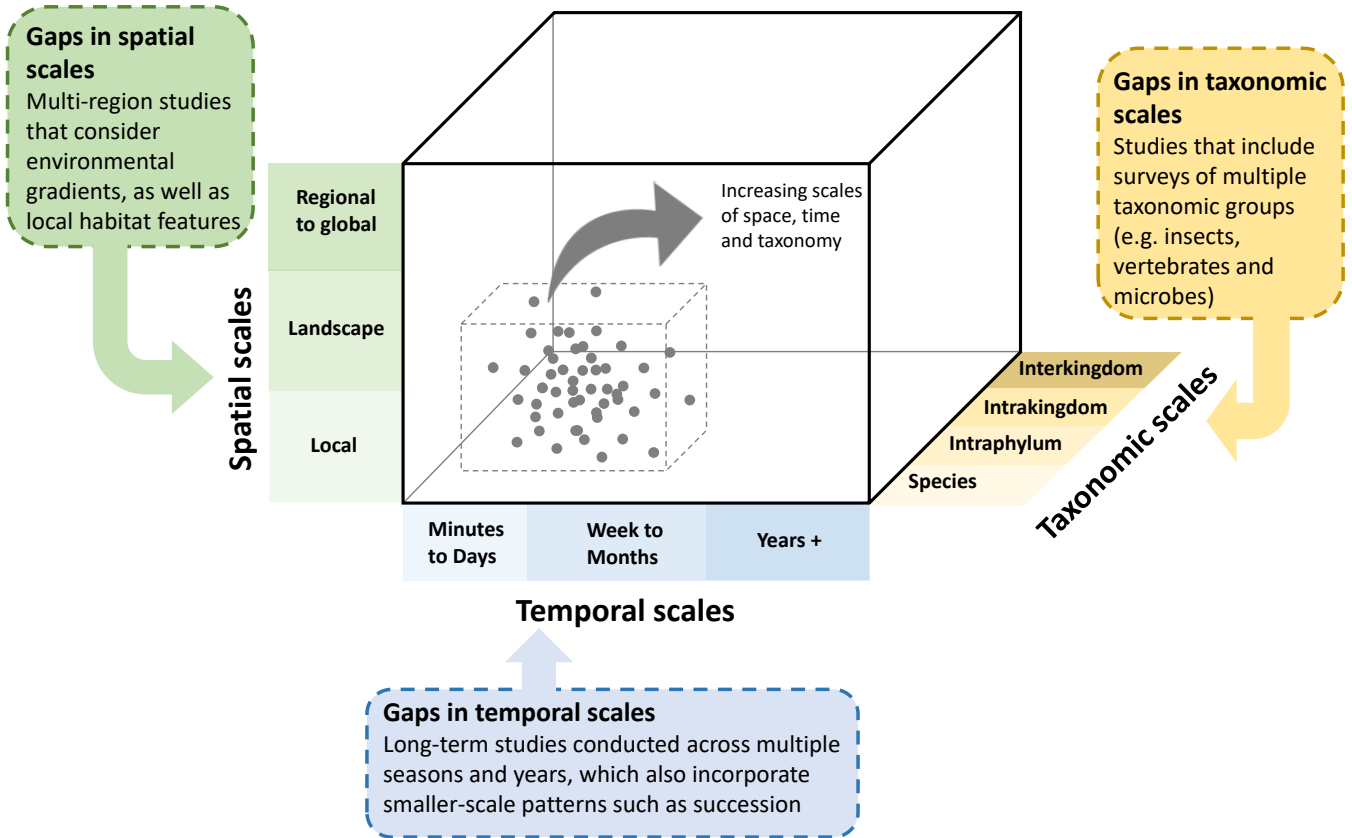
Figure 7.2 Conceptual model illustrating the different scales across space, time, and taxonomy that shape the necrobiome. Most empirical studies of the necrobiome (represented by the grey points) are currently bias towards smaller or limited spatial (e.g. local to landscape) and temporal (e.g. minutes to months) scales and have narrow taxonomic focus (e.g. focusing on species or intraphylum comparisons that include insects or vertebrates only). My thesis focused on larger spatial (landscape and region) and taxonomic (Intrakingdom; both insects and vertebrates) scales, and also considered temporal scales too (e.g. weeks to months). There is, however, still much to be done to develop our understanding of the general processes that cause the structure and function of necrobiome communities to change over space and time. The dashed boxes highlight some of the specific gaps or future research avenues across each of the three scales.

7.4.1 Spatial scales

In terms of spatial scales, scavenging can vary on smaller local scales, across different landscapes, and at larger regional or global scales (Figure 7.2). Most carrion research focuses on landscape scales, with some also considering smaller local-scale considerations too (e.g. Pardo-Barquín et al. 2019). This thesis, on the other hand, focused primarily on landscape and regional scales, as it incorporated different Australian bioregions and considered differences in two habitat types within each of those bioregions. Further work is needed, however, to increase the number of geographic regions that carcass studies are carried out in, so greater generalisation in carrion communities and their functions can be developed. In Australia, these studies should target biogeographic regions that have received less attention. For example, this thesis did not incorporate any tropical systems, although these environments comprise a large percentage of Australia's land mass, include large animal biomasses (Stobo-Wilson, 2020) and have received little to no attention in terms of scavenger research (Barton et al. 2013).

Larger-scale studies could also focus on examining different environmental gradients, to dissect changes in carrion community structure and functions across, for example, environments with varying altitude, aridity, and longitude. Within different geographic regions, it is further important that a range of different landscapes, or habitats, are studied, and that the local characteristics that define these different landscapes are considered too. In this thesis, I focused on two habitat types ("open" and "closed"), which I defined based on the presence or absence of tree cover. Within systems there is, however, far greater complexity that could be explored, including studying habitats with varying levels of complexity from low ground cover to mid-level shrub cover and higher-level canopy cover (e.g. such as grasslands, compared to heathlands, and closed and open forests; Goetz et al. 2014). Exploring the local features of the environment, such as vegetation complexity, types and even soil and litter condition, will further help to provide important context to aid in understanding of the habitat characteristics that shape carrion communities across different landscapes (Pardo-Barquín et al. 2019).

7.4.2 Temporal scales

Carcass use and scavenger communities may vary on smaller time scales from minute to minute and day to day, on medium time scales from weeks to months, or on larger time scales from year to year and beyond (Figure 7.2). In my work, I focused primarily on week to month changes, as I examined seasonal changes in insects and vertebrates on carcasses. While I did also include some smaller scale times, as I trapped insects over different time periods (Chapter

2) and monitored arrival patterns of vertebrates including dingoes (Chapter 4; Spencer and Newsome 2021), my analyses in this area could be expanded and deserve more focus in future work. Monitoring successional (day to day) and seasonal temporal changes are, however, relatively common in studies (although mine was the first to consider seasonal changes across different spatial scales) (e.g. Bajerlein et al. 2011, Benbow et al. 2013, Pereira et al. 2014). Carrion ecology research also needs to focus on the 'bigger picture' and develop studies comprising long-term surveys conducted over multiple seasons and years. While the importance of long-term studies in ecology has been long appreciated, allowing us to understand long-term drivers in species diversity and structure over time (Franklin 1989), we are yet to see their application in studies of carrion ecology. Conducting such studies that also include larger spatial scales will be key to understanding species declines and how climate change impacts scavenger communities and important ecological processes linked to decomposition e.g. carbon cycling (Schmitz et al. 2018).

7.4.3 Taxonomic scales

Carrion hosts a rich diversity of organisms that include a range of different species, and ecological kingdoms (Barton et al. 2013) (Figure 1.1). Despite this, most carrion research focuses only on a small component of this community. For example, many entomological studies consider only certain insects, such as specific fly and beetle species that are forensically significant (Lefebvre and Gaudry 2009). Further, there are very few studies that simultaneously investigate both the vertebrate and insect species that associate with carrion, especially in Australia (but see: Read and Wilson 2004). Nor are there studies that include multi-kingdom surveys that consider, for example, both insects and microbes, including the interactions they share (Jordan et al. 2016). This thesis provides a broad-spectrum survey of taxa, as it includes both vertebrates and insects in its survey methods, and further included some lesser studied insect groups such as ants and wasps. Still, future studies could profitably implement a broader range of sampling methods than those applied here. For instance, I used only pitfall traps to sample carrion insect communities. Pitfall traps provide a highly efficient means of sampling insects at carcasses, including both flying and ground-based species (Barton et al. 2017). However, additional traps (e.g. aerial netting and sticky traps) could have been implemented to capture a greater representation of flying insects, including fly species (order: Diptera) and wasp species (e.g. *Vespula germanica*) (Schoenly et al. 2007). Similarly, different camera trap methods could have been applied to specifically target smaller-sized mammals, which may be

missed because of their size (Glen et al. 2013), or reptiles, which are often underrepresented as their low body temperatures may not trigger cameras (Richardson et al. 2018).

Conducting surveys of microbial communities in addition to insect and vertebrate communities that associate with carrion should also be a key focus of future work. Such studies would help to determine more complex links and interactions between key components of carrion communities, including their roles in decomposition. Of course, to better understand decomposition processes, future work should also focus on conducting manipulative experiments to examine the functional role that different components of the carrion community play in terms of carrion decomposition or removal. Functional redundancy of different insect or vertebrate groups can be examined via the removal or addition of key species in controlled experimental environments (e.g. Heo et al. 2019), or by excluding different species or species groups such as apex scavengers, or from carcasses using barriers such as mesh wire (e.g. Barton and Evans 2017, Hill et al. 2018).

7.4.4 A broad-scale standardised approach is required

One of the greatest data barriers to building understanding of the necrobiome across different spatial, temporal, and taxonomic scales, is the lack of research that draws these three scales together. In this thesis, I successfully incorporated multiple spatial (bioregion and habitat), temporal (season), and taxonomic (insect and vertebrate) scales, although this kind of large-scale approach did present many difficulties. For example, setting up multiple survey methods to capture both insects and vertebrates can take time and I had several issues with vertebrates disturbing insect pitfall traps (e.g. by filling them with dirt while they scavenged, or by removing them from the ground). There were also significant challenges involved in navigating the three different bioregions from across Australia and transporting enough animal carcasses into the field to maintain adequate sampling sizes to assess differences in habitat and season. In the future, there may be alternative and simpler ways to undertake standardised studies across different bioregions, including using smaller carcasses such as rabbits or hares (Newsome et al. 2021).

There is a range of other, successful globally coordinated open source experiments that use standardised methods to quantify important global questions that could be learnt from (e.g. Nutrient Network and tea bag index; Stokstad 2011). Development of a global standardised scavenger network (e.g. DeadNet), should be designed with the intention to make the methods

as inclusive and accessible as possible, so that researchers focusing on different elements of the necrobiome can compare and contrast results more easily between studies.

While developing this standardised approach, we should also work on developing a more unified language or classification system to describe necrobiome community members. Currently, vertebrates are referred to as scavengers (or obligate scavengers and facultative scavengers), whereas insects are classified into specialised groups (e.g. necrophagous, necrophilous, sarcosaprophagous, detritivorous). Insects are almost never referred to as scavengers, despite many feeding on carrion in similar ways to vertebrates. While this may reflect actual differences in the complexity of functions and associations that insects and vertebrates share with carrion, it probably also has resulted from differences in preference expressed by two fields of research that are currently quite independent of each other.

7.5 Conclusions

There is something inherently repulsive about a rotting carcass or corpse. For some of us, it is the stuff of nightmares, an object we associate with disgust, sickness, and fear. This thesis has painted a very different picture – of carcasses as important resources that are teeming with life, and as cornerstones of a vast and complex ecosystem – the necrobiome. It has also highlighted the importance of the species that associate with carrion as integral members of the process of nutrient cycling, or the 'circle of life', and as organisms that interact with systems not only as scavengers, but as predators, and pollinators too. Finally, this thesis has further supported the great complexities of interactions that exist within and around different carrion communities, and the integral roles that different environmental drivers play, on different ecological scales, for these communities. This work has, however, left many areas open for further exploration, both in Australia but also more generally with the further development of the necrobiome framework and how we study and understand carrion communities on a global scale.

By developing knowledge of the necrobiome, we add to our general understanding of what is an incredibly complex but important component of every ecosystem across the planet. However, we also could be contributing to something potentially much more profound; a shift in how we view carrion and scavengers, and perhaps even death, in society. While we can gain solace in our religions, and the thought of an afterlife, I believe that we can also look towards the necrobiome for such peace, with the knowledge that our bodies and the elements that form our physical selves could go on to support and bring about new life through the fascinating process of decomposition.

7.6 Acknowledgements

7.7 References

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APPENDICES

APPENDIX A

THE C💬NVERSATION

Academic rigour, journalistic flair

Carcasses can feed a range of native animals, including goannas, wedge-tailed eagles and dingoes. AAP Image/Lukas Coch

Bushfires left millions of animals dead. We should use them, not just bury them

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Bushfires this season have left an estimated 1 billion dead animals in their wake, their carcasses dotting the blackened landscape.

Adding to the toll, farmers are being forced to euthanise injured and starving livestock and there are also calls to cull feral animals in fire-affected areas, including by aerial shooting.

The carcasses have already been flagged as a potential biosecurity threat, and the Australian Defence Force is tasked with collecting and burying the dead in mass graves.

Read more: Australia's bushfires could drive more than 700 animal species to extinction. Check the numbers for yourself

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There's logic in this. Carcasses can harbour nasty diseases such as botulism that threaten human, livestock and wildlife health. They also provide food for invasive pests like feral cats and red foxes.

But carcasses can play a positive role as landscapes recover from fire, providing rich nutrients for other native animal, microbial and plant species.

Carcasses provide important food sources to native animals, such as the lace goanna.

The Morrison Government has announced a A$50 million package to help wildlife and habitat recover from the fires, and yesterday met leading wildlife experts and environment groups to get advice on the recovery process.

We suggest this process should examine carcass disposal methods other than burial, such as composting – effectively "recycling" the dead. It should also involve monitoring the carcasses that remain to understand both their positive and negative roles in fire-ravaged areas.

The positives: carcasses feed the living

Carcasses feed a range of native animals, including goannas, wedge-tailed eagles and dingoes. Postfire, they can provide an alternative source of food for struggling native predators and pollinators.

And feeding hungry predators with carcasses could redirect them away from vulnerable prey.

Carcasses also feed insects such as flies, ants, beetles, and their larvae, and support important ecological processes such as pollination.

As they decompose, nutrients leach from carcasses into the surrounding environment and create "halos" of greenery in the landscape, where vegetation thrives around carcass sites. Their influence on soil and plant communities can last for years.

Vegetation growth 'halo' around a kangaroo carcass. When animals die their nutrients can influence the landscape for years.

The negatives: spreading disease and sustaining feral animals

Carcasses are home to bacteria that help break down animal tissues. But some carcasses also harbour harmful pathogens that bring disease.

For a disease outbreak to happen, the animal must generally have already been carrying dangerous infectious agents, like Anthrax or the Hendra virus, before they died. And many of these pathogens will not survive long on dead hosts.

Read more: Predators get the advantage when bushfires destroy vegetation

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Leaving carcasses out in the open can also feed introduced predators such as feral cats and red foxes, putting small native animals at risk. Some weeds thrive in the nutrient-rich soils around carcasses too.

Introduced insects like the European wasp, which appeared en masse following fires in Kosciuszko National Park, also take advantage of carcass resources. These wasps are highly aggressive and attack and kill other native insects.

How long does a carcass stick around?

We know very little about the ecological role of carcasses in fire-affected areas, and it's important that more research is carried out.

We know burnt animals can decompose faster than other carcasses and harbour different types of insect scavengers.

However the recent fires are likely to have wiped out entire scavenger communities, including larger scavengers like dingoes and eagles, that help to clean our landscapes of dead animals.

The effects of this are unknown, but could mean that carcasses stick around in the environment for prolonged periods, even months.

A feral cat scavenging on an animal carcass. Animal carcasses could increase the number of feral predators.

Finding the right solution to a grisly problem

As climate change accelerates the number of natural disasters and mass animal deaths, more thought and planning must be put into carcass management.

In Australia, carcasses are often dealt with by not dealing with them: they're left to rot. This happened for almost 100 feral horses that died last year at an empty water hole during a heatwave.

Animals culled in national parks and on farmlands are also often left to decay, untouched, as are the many dead animals that commonly line our country roads. But in landscapes where feral species are common, or where livestock or people are likely to encounter carcasses, leaving them alone isn't the best option.

Read more: A season in hell: bushfires push at least 20 threatened species closer to extinction

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Carcasses are more often buried following disease outbreaks or when livestock die. We saw this during the 2019 Queensland floods, where thousands of drowned cattle were buried in mass graves.

Burial is a relatively inexpensive, fast and effective method of dealing with the dead. But it must be done carefully to avoid polluting groundwater sources and causing nutrients like nitrogen to build up.

Burying carcasses can also be compared to sending rubbish to the tip. Breakdown will be slow, and no useful end product is created.

A more useful option

An alternative option is to "recycle" carcasses by composting them. Composting can accelerate the decomposition of animal tissues and is environmentally friendly, capturing nutrients.

Read more: Animal response to a bushfire is astounding. These are the tricks they use to survive

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Composting kills most pathogens, whereas burial just moves the problem underground. It also suppresses smelly odours and doesn't attract scavengers. The usable organic material resulting from the composting can also be applied to nutrient-poor soil.

Getting used to the 'yuck' factor of carcasses.

Composting can be time-consuming and hard to get right. It requires careful monitoring of temperature and moisture content to ensure all disease-causing pathogens are killed, and odours are suppressed.

There's also a "yuck" factor and the public would probably need convincing for the method to be widely adopted.

But whatever option we choose, it's clear there's more we can do with carcasses than simply burying them.

APPENDIX B

THE CONVERSATION

Academic rigour, journalistic flair

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Forget 'murder hornets', European wasps in Australia decapitate flies and bully dingoes

Published: June 1, 2020 5.50am AEST

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The impacts of invasive mammals such as feral horses and feral cats have featured prominently in the media over the years.

But the recent discovery of the infamous "murder hornet" (or giant Asian hornet *Vespa mandarinia*) in the US has shone a spotlight on a similar invasive insect in Australia, the European wasp (*Vespula germanica*).

Read more: National parks are for native wildlife, not feral horses: federal court

Our recent study showed this aggressive insect swarming decayed corpses, decapitating its prey and picking fights with dingoes.

Invasive plants and animals can have catastrophic impacts on wildlife. And along with habitat loss and overexploitation, they are the greatest threat faced by native Australian species.

European wasps feed on meat. Thomas Bresson/flickr

The rise of European wasps

European wasps are native to Europe, Northern Africa and parts of Asia. But hibernating queens stowed unintentionally in ships or trucks can colonise new areas, and this is how they arrived in Australia.

They were first discovered in Tasmania in 1959, and by the 1970s had reached mainland Australia. Today, European wasps are found in every state and territory, and are considered an

agricultural, urban and environmental pest. The species is firmly established in the eastern parts of the country, and constant vigilance is required to keep numbers down in other areas.

European wasps have no predators (other than humans) in Australia. And they tend to forage more efficiently than their native counterparts, such as the common paper wasp *Polistes humilis*.

Although they are typically most active in late summer and autumn, Australia's warmer climate means not all European wasp queens hibernate over winter as they do in Europe. This allows some wasp colonies to build "super nests" of up to 100,000 individuals.

European wasps are commonly encountered in urban areas and, unlike bees, can sting multiple times. They also release a pheromone when threatened that quickly attracts more wasps. So if you bother a nest, you may have to contend with the whole hive.

European wasps can be found swarming animal carcasses.

Wasps as ruthless scavengers

Our research looks into the role of European wasps as scavengers.

In Australia, animal carcasses aren't in short supply. Millions are produced each year due to culling, vehicle collision and drought. The recent bushfires also added to this.

Most carcasses are left to rot and provide perfect "free feed" stations for wasp colonies foraging for protein. For our study, we monitored 20 kangaroo carcasses at Kosciuszko National Park in New South Wales.

Wasps congregated in large numbers around each, and ruthlessly attacked blowflies that attempted to approach. We could sit next to a carcass and watch fly after fly tackled to the

ground by wasps. Many flies showed signs of mutilation. To our surprise, some were even missing their heads.

This unlucky blowfly was decapitated by a European wasp. Emma Spencer, author provided

In an effort to protect "their" carcass, the European wasps were decapitating the flies. This may have simply been defensive behaviour, but they could have also been taking bits of flies back to their nest for larvae to feed on.

We also observed the wasps bothering animals much larger than them, and our camera trap images showed dingoes snapping at wasps circling carcasses. Many of these animals retreated without feeding on the resource, presumably because the wasps were stinging them.

A dingo snaps at European wasps swarming a carcass site. Emma Spencer, author provided

We can't ignore the flow on effects

Our recent study is just the start of our investigations into European wasp impacts in Kosciuszko

National Park. But it has raised important points about the fate of carcasses dominated by wasps.

For one, it seems the wasps are preventing blowflies and dingoes from doing their job of "cleaning up" carcasses in the landscape. Also, flies are major pollinators, and decapitation isn't helpful for pollen transfer.

A European wasp attacks a blowfly.

Moreover, if European wasp numbers are supported by prevalent carcass resources (including those resulting from culling) this may suggest a need to cull pest species when the wasps are not active, such as during the coldest times of the year.

Are wasps and 'murder hornets' a danger to us?

Like the European wasp, the "murder hornet" also threatens insect pollinators. The hornets have raised alarms in the US because they decimate honeybee populations, and have a nasty sting.

Similarly in Australia, there has been a focus on the threat European wasps pose to humans. But as is the case in the US, this focus is largely misguided.

Read more: What are Asian giant hornets, and are they really that dangerous? 5 questions answered

While both insects have painful stings that can result in severe allergic reactions, fatalities are rare. And we would do well to redirect our concerns towards the impacts such species have on our ecosystems.