Scavenging Dynamics of the Australian Alps

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This is to certify that to the best of my knowledge; the content of this thesis is my own work.

This thesis has not been submitted for any degree or other purposes.

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Table of Contents

Acknowledgments

In the spirit of reconciliation, the Ngarigo people, the Traditional Custodians of the land on which this study took place, are acknowledged. Respects are paid to their Elders past and present and also extended to all Aboriginal and Torres Strait Islander peoples today.

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Abstract

Carrion (dead animal biomass) has received little attention as a high energy and nutrient rich ecosystem resource. Recently, the ability of carrion to attract diverse groups of vertebrate scavengers has been utilised as a focal point within ecosystems to assess scavenging dynamics. Fluctuations in carrion biomass and differences in vertebrate scavenging rates are often linked to the seasons. However, despite the strong consensus that scavenging dynamics are seasonal, many field-based studies still fail to sufficiently consider the seasons and/or or replicate studies across all seasons. To address these shortcomings and highlight the importance of seasonal effects in scavenging ecology, this thesis describes vertebrate scavenging dynamics in the highly seasonal Australian Alps. Here, 15 carcasses were experimentally deployed each season to monitor vertebrate scavenging dynamics for 60 days via a remote camera. The findings demonstrated highly seasonal scavenging dynamics but were unique given that seasonal scavenging trends were dominated by highly abundant low-ranking mesoscavengers. The brushtail possum (*Trichosurus vulpecula*) dominated winter-time scavenging, presumably to supplement a lack of other available food sources. Whilst raven species (*Corvus coronoides* and *Corvus mellori*) were highly prolific scavengers during spring, likely to meet the demands of breeding. This mesoscavenger trend was apparent despite the presence of an apex predator, the dingo (*Canis dingo*). However, the dingo was found to scavenge at low rates, and this raised several questions regarding density dependent predator theories; carrion abundance, and availability; and how these potentially limit the top-down scavenging effects of the dingo. In conclusion, the methods used here serve as a practical example of a robust and repeatable experimental design for monitoring and assessing scavenging dynamics and exemplifies the inclusion and importance of seasonal effects in scavenging ecology.

Chapter 1 – Introduction

Carrion in the landscape

The cycle of life and death is one of the few predictable processes on Earth. Within an ecological framework, this cycle provides a means to an end by recycling the energy, nutrients, and resources, accumulated by an organism over its lifetime, into the broader environment as it decomposes [1, 2]. Until recently, the sum of dead matter contributing to this cycle was treated as a single resource pool [3]. This resource pool is dominated by plant-based detritus given that its living counterparts total global biomass (450Gt) shadows that of any other biomass types: bacteria (70Gt); fungi (12Gt); and animal (2Gt) [1, 4]. Because this interface between life and death is dominated by the sheer scale in which plant biomass exists, the subsequent ecosystem processes (e.g., trophic structuring and ecological cascades) serviced by the decomposition of plant-based detritus are well understood [3]. Consequently, a significant bias exists in the literature whereby the ecosystem services provided by the decomposition of non-plant-based detritus are likely underestimated [1, 5, 6].

Carrion (dead animal biomass) has received little attention in the literature as an available resource within ecosystems. Compared to plant-based detritus carrion is a much more spatially and temporally patchy resource [3, 7]. In highly seasonal environments, for instance, fluctuations in carrion biomass can be extreme due to processes interlinked with the seasons such as thermal extremes, food availability, and breeding seasons [8]. For example, each year *en masse* Pacific salmon (*Oncorhynchus* spp.) migrate from the ocean to coastal feeding freshwater rivers and creeks to spawn. This salmon run only happens over a 2–3-month period after which all the salmon succumb to a rapid senescent death. Gende et al. (2004) found that in one Alaskan creek alone, the total run size for a season was 674 salmon. This run size equated to this single creek receiving 80.2 kg of N, 11.6 kg of P, and 1.2 x 10^7 kJ of energy in the form of carrion [9]. The fate of salmon carcasses (i.e., scavenged or *in situ* decomposition) also determines ecosystem specific flow-on effects [10, 11]. For example, nutrients and energy derived from salmon carcasses scavenged by bears often enter terrestrial systems and accumulate in vegetation after being carried ashore, partially consumed, and left to decay, or via bear urine and faeces [12, 13]. Conversely, nutrients and energy derived from carcasses that come to rest within the waterway, enter the aquatic system and can supplement lower trophic level species (e.g., algae) that sustain such aquatic ecosystems [14].

Anthropogenic impacts can also increase carrion loads in ecosystems. Roads pose a significant threat to a vast array of wildlife and as such have become one of the most common places where carrion can be observed [15, 16]. For example, in the United States alone it has been estimated that between 89-340 million birds die annually as roadkill [17] and that vehicle collision now accounts for more vertebrate mortality than hunting [18]. In Australia, it is estimated that marsupial roadkill exceeds 4 million individuals per year [19]. There is also evidence that mass animal mortality events are on the rise globally because of anthropogenic factors including climate change [20]. These events can similarly result in large carrion inputs into ecosystems. The historical tendency to overlook carrion as a resource, when considered in conjunction with the increasing rates with which anthropogenic impacts are altering the carrion pool, highlights the need to further understand the role of carrion within ecosystems.

Carrion as a resource

Despite carrion being much more spatially, temporally, and quantitatively variable than plant-based detritus, its rate of decomposition is in fact 10-100 times faster than that of plant-based detritus [1, 21]. This is because carrion is a much more energy and nutrient rich resource characterised by higher nitrogen, phosphorus, and water contents, and fewer deterrent compounds [7, 22]. Consequently, carrion is a valuable high-quality resource to which a unique group of species that scavenge have become specifically adapted to exploit. The ecosystem services provided by scavengers are often overlooked despite the critical role they play within all ecosystems, benefiting both the natural and human environment [23]. This is especially true given the recognition that predators receive for the ways in which their ecosystem services structure communities across multiple trophic levels [24, 25]. Scavengers have evolved to become a highly specialised group of species that in unison can efficiently break down and consume carrion [26]. This fast rate at which carrion is processed makes it difficult to observe the inner workings, intricacies, and dynamics of scavenging in a natural setting. However, scavenging has been demonstrated to (i) provide critical linkages in food webs; (ii) distribute nutrients within and among ecosystems; and (iii) inadvertently reap economic and human health benefits related to carcass disposal and sanitary measures [27].

Scavenger guilds and their members

The group of taxa responsible for scavenging includes both vertebrate and invertebrate species as well as bacteria/microbes, all of which are globally prevalent in both terrestrial and aquatic ecosystems. For the purposes of this thesis, discussion will be primarily focusing on the vertebrate scavengers. Broadly, vertebrate scavenger guilds are composed of obligate scavengers and facultative scavengers. The former relies entirely on carrion as a food resource, and it is this specificity that makes them so rare. As such, vultures are the only true terrestrial vertebrate obligate scavengers due to their ability to soar over large areas in search of carrion which is more or less spatially and temporally consistent within their landscapes [8, 28]. The social behaviours of vultures, the primary mechanism of which is local enhancement, also further facilitates their ability to locate carcasses [29, 30]. However, due to widespread human persecution, many vulture species are experiencing catastrophic population declines which in turn is altering scavenging dynamics globally [31].

Facultative scavengers

All other terrestrial vertebrate scavenging species are facultative scavengers. These species are not reliant on carrion as their primary food resource. Instead, they scavenge on carrion at different points in their life stage, in response to seasonal changes, in low resource times, or in the absence of competitively dominant scavengers [32, 33]. Of the facultative scavengers, predators (that scavenge) are some of the most common species recorded at carcasses. These predators are typically classified as either apex predators or mesopredators. The former are species characterised by their position at the top of the food chain and lack natural predators [34], whilst the latter are any "midranking predator in a food web, regardless of size or taxonomy" [35]. The presence or absence of either species group within ecosystems can cause trophic cascades that can result from their interspecific interactions or lack thereof [34]. One of the most well-known of these cascades is described by the mesopredator release hypothesis. This phenomenon explains how constraints to the population growth of mesopredators, which are controlled by competitively dominant apex predators, are released following a decline in apex predator population levels [25, 36, 37]. The consequences of such interactions can also have profound effects on scavenging dynamics when occurring surrounding carrion i.e., 'mesoscavenger release' [38, 39].

Apex predators can also influence scavenging dynamics by way of other top-down effects and this can come via two main pathways [40]. *Firstly*, the predatory activities of apex predators can dictate scavenging rates within an ecosystem via the provision of carrion from their partially consumed prey [41]. This dynamic has been demonstrated in Yellowstone National Park following the reintroduction of the grey wolf (*Canis lupus*). Prior to the reintroduction, carrion biomass pulsed in March-April when many elk (*Cervus canadensis*) succumb to the harsh conditions of winter. Consequently, much of the scavenging activity in Yellowstone National Park primarily occurred during this period. However, carrion biomass is now more seasonally available via the remains left from grey wolf kills, and thus, scavenging rates have followed a similar trend [42].

Secondly, apex predators can dictate scavenging dynamics via their own scavenging activities and interspecific interactions surrounding non-prey killed carrion [43]. Apex predators, like vultures, can rapidly consume carrion biomass including bones, and their presence at carcass sites, can therefore, accelerate decomposition rates [44]. Through fear effects (i.e., smaller species avoiding larger species), the scavenging activities of apex predators can also reduce scavenger species richness and the time spent scavenging by other scavenger species at carrion [39, 45, 46]. Furthermore, kleptoparasitic scavenging (i.e., scavenging of stolen prey) by apex predators can have compounding effects on the victim predator whose kill has been stolen. Not only will the victim predator expend energy for little to no return, but subsequently time spent hunting will increase per consumed kill which can have detrimental impacts on overall individual fitness [46]. Such apex predator effects can be so extreme that some mesopredators have developed flexible behavioural strategies when handling prey, as well as spatial and temporal measures, in order to avoid confrontations and coexists with apex predators within the landscape [47, 48].

A whole suite of other species completes the facultative scavenger group. This includes many omnivorous species that are not strictly predators and are highly opportunistic, these species include corvid spp., racoon and possum spp., wild pigs, and many species of reptile [49]. These (mostly) non-predatory species can be common scavengers in systems not dominated by competitively superior scavengers [50-52]. However, in the presence of such dominant scavengers, the scavenging rates of these non-predatory subordinate scavengers are often supressed, and this has consequently caused scavenging by such species to be underestimated and even unknown [32]. Additionally, carrion is not exclusively a food resource but also a more practical focal point within ecosystems for scavengers that may exploit other carcass resources.

For instance, many passerine species utilise carcasses as a source of hair or feathers for nesting material [53]. Furthermore, carcasses also attract a host of invertebrate scavenger species, upon which vertebrates, and indeed other invertebrates, can subsequently predate without explicitly utilising the carcass [53].

Invertebrate scavengers

Invertebrate scavenger species are also a crucial component of any scavenger guild. In many cases, invertebrate scavenging is much more complex than that of vertebrates, largely due to the complexity of chemical and visual cues utilised by invertebrates for carrion detection, colonization, and succession [54]. Terrestrial invertebrate scavenging is primarily limited to insects which in turn are dominated by *Diptera* (true flies) and *Coleoptera* (beetles) but also include *Hymenoptera* (ants, bees, and wasps), and *Acari* (mites) [54]. Scavenging by such species orders can be highly contrasting on multiple temporal scales [55]. This is especially apparent when considering the seasons, with carrion biomass loss attributed to insect scavenging generally highest during summer and lowest during winter [54]. In some ecosystems, this seasonal difference can be so extreme that during summer insect scavenging is the primary driver of carrion decomposition rates, not vertebrate scavenging, despite the vast amounts of carrion that vertebrates can consume at once [27, 56].

Seasonality in scavenging ecology

As previously noted, carrion is temporally patchy, and this is largely due to seasonality in the carrion pool which is linked to animal deaths and predation rates [3, 7, 8]. Consequently, scavenging is highly seasonal. The seasonal scavenging rates and activities of invertebrates can largely be attributed to warm (high scavenging rates) and cold (low scavenging rates) conditions [54]. However, the scavenging rates of vertebrates are more complex within this seasonal framework due to contrasting seasonality in the available carrion pool and the scavenging rates of the scavengers themselves [41]. For instance, it is generally accepted that vertebrate scavenging rates are highest during winter, especially in the higher and lower latitudes. This is due to a lack of alternative food sources and potentially more carcasses within the landscape as many individuals succumb to the harsh conditions of winter [33, 42, 57-59]. However, it is also likely that during winter carcasses are harder to detect as olfactory cues related to decomposition are lower due to reduced temperatures and decreased invertebrate/microbial scavenging activity [51]. Further still, scavenging rates, activities, and behaviours can also be linked to the life histories of vertebrate scavengers which are also often linked to seasonal considerations such as breeding [60].

Seasonal effects (e.g., seasonality in the carrion pool, invertebrate scavenging, and vertebrate scavenging) can have cascading impacts on scavenging dynamics that ultimately determine how long carrion persist within ecosystems [61]. However, despite the strong consensus that scavenging ecology is seasonal, many field-based studies still fail to sufficiently consider the seasons, or replicate studies across all seasons [62]. A common field approach in scavenging ecology is to sample and/or monitor only during two seasons of interest (e.g., hot and cold, or wet and dry, or breeding and non-breeding) [32, 38, 63, 64]. This method overlooks the importance of each of the seasons and simplifies the complexities of each, especially with regards to scavenging dynamics that may occur in response to breeding, migrations, and/or rapid vegetative change [32].

In response to this and other poor study designs, Schoenly et al. (2015) defined the successful design of any robust field study in carrion ecology as those that simultaneously accounted for temporal aspects, spatial aspects, and sample size, in conjunction with a suite of other minor considerations [62]. Temporal considerations are important to account for seasonal effects and variability over time [32, 62]. Spatial aspects can be equally as important when designing a field study so that enough natural and environmental variation is covered in order to sufficiently characterise a given ecosystem, as well as to consider spatial independence between monitored carcasses. Sample size is especially important in scavenging ecology to ensure there is enough independent units (i.e., carcasses) within a study to facilitate adequate seasonal replications and ultimately yield statistically and ecologically valid and meaningful results.

Scavenging in Australia

Australia is home to a plethora of unique ecosystems that support equally unique scavenger guilds. These diverse ecosystems exemplify the need to conduct ecological research in a systematic manner for each differing ecosystem and across ecologically relevant temporal (seasonal) and spatial scales [65]. This is particularly true given Australia's position in the southern hemisphere and the literary bias for ecological (including scavenging) research in northern hemisphere systems [66]. Further still, when considering the already highly variable spatial, temporal, and interspecific nature of scavenging ecology, the Australian context only exacerbates these complexities.

Despite this clear need for comprehensive studies, very little work has been done to extensively describe scavenging ecology in Australia and understand its current context. Indeed, research, thus far, has mostly focussed on imbedded topics within the scavenging field given the varied motivations of different researchers and research groups. One area that has received considerable attention is scavenging dynamics at the interface between the marine and terrestrial environments. This is logical given Australia's extensive coastlines and potential for harbouring considerable quantities of wave-swept carrion. Much of the work done here has focused on the community structure and assemblage of beach scavenger guilds including mammals, birds, and crustations, as well as how invasive species may impact the scavenging dynamics of such guilds [67-73].

The impacts of invasive species have warranted widespread attention not only on Australia's beaches and/or in the context of scavenging ecology, but also in many fields of ecology. In addition to the beach-based studies mentioned above, extensive work has also been done on invasive species including the cane toad (*Rhinella marina*), red fox (*Vulpes vulpes*), and feral cat (*Felis catus*). Cane toads have invaded much of northern eastern Australia and are rapidly expanding their range west and south [74, 75]. The invasive toads are highly toxic to native predators and/or scavengers that consume them. Consequently, this toxicity has significant potential to alter scavenging rates and scavenger guilds via a somewhat novel pathway that considers carcass species rather than scavenger species [76, 77]. Red fox and feral cat scavenging have also received some attention within Australian ecosystems for their abilities to alter interspecific interactions and scavenging dynamics surrounding carrion [64, 67, 68, 78].

Aside from the impacts imposed by invasive scavengers, native apex predators are the other highly influential scavenging taxa in Australia. Because of their status as a keystone species, the dingo (*Canis dingo*) and Tasmanian devil (*Sarcophilus harrisii*) are dominant scavengers on mainland Australia and Tasmania (an island state of Australia), respectively. Much of the scavenging work on these species, with some exceptions [39, 64, 79, 80], has largely been observational in nature, especially so for the dingo which, until recently, had been subject to very few studies describing their scavenging activity [79, 81-83]. The Tasmanian devil is recognised as a prolific scavenger, being one of the few terrestrial vertebrates globally (other than vultures) thought to rely largely on a diet of carrion [84]. As such, the scavenger guilds of Tasmania are highly unique, and their research has largely focussed on how the Tasmanian devil drives scavenging dynamics [39, 84, 85]. Due to the transmissible devil facial tumour disease (DFTD), and the associated catastrophic population declines, much of the work done on the Tasmanian devil has focused on understanding the diseases properties. Consequently, the scavenging rates and activities of Tasmanian devils remains relatively speculative [84, 86-88], and indeed, existing scavenging based research has largely considered how such population declines may change Tasmanian scavenger guilds and scavenging dynamics [39, 85].

Other areas covered with regards to scavenging in Australia include forensically important scavenging activities [89, 90], lead poisoning of scavengers [91-94], anthropogenic carrion subsidies [64, 78, 95, 96], and invertebrate scavenging dynamics [97-101]. With scavenging ecology being a new and emerging field, the number of studies done, thus far, in Australia is small. In addition, very few studies have been undertaken with adequate sample sizes and/or accounted for spatial and temporal aspects [62]. It is also difficult to make inferences from the findings of existing studies in the absence of the relevant natural history of scavenging in Australia broadly, and more specifically for each of its ecosystems [102].

Scavenging in the Australian Alps

Despite only encompassing 0.16% of Australia's total land mass, the Australian Alps is a unique and diverse ecosystem. This region has highly variable terrain ranging from steep mountain peaks to flat alpine plains and includes many of the highest peaks and ranges within Australia's Great Dividing Range, including Australia's highest peak – Mount Kosciuszko. As a consequence of the terrain, the landscape has evolved to become delineated into three altitudinally distinct ecological communities – montane (500m-1500m), subalpine (1500m-1850m), and alpine (1850m-2228m) [66]. Each of these communities are highly seasonal with the temperatures experienced throughout the course of a year differing by up to 50°C (-10°C – 40°C). During winter much of the landscape can be covered in snow, but by the following summer the same landscape can experience intense bushfires, such as those during the 2019-2020 Australian bushfire season [103]. With extreme weather events expected to become more frequent and severe, many of Australia's native alpine flora and fauna species are at risk to a rapidly changing climate in an already highly variable and vulnerable environment [104].

Despite being a highly volatile landscape, a vertebrate scavenger guild has become established within the Australia Alps. This native guild is primarily composed of dingoes (*Canis dingo*) and wedge-tailed eagles (*Aquila audax*) – apex predators; spotted-tail quolls (*Dasyurus maculatus*) – mesopredator; brushtail possums (*Trichosurus vulpecula*), raven spp. (*Corvus coronoides* and *Corvus mellori*), and pied currawongs (*Strepera graculina*) – facultative scavengers. Whilst no study to date has holistically described the scavenging dynamics of the Australian alpine guild, species specific scavenging has been described both within the Alps and elsewhere in Australia [64, 79, 99, 105]. Invasive species also play a significant role within the Australian alpine scavenger guild. Feral pigs (*Sus scrofa*), whose detrimental impacts are largely attributed to ground rooting [106], are also pervasive scavengers in Australia's alpine regions [99]. The invasive red fox and feral cat are likely two of the greatest threats to Australia's native mammals, marsupials, and birds [107]. Both these invasive species, however, do not exclusively hunt and are capable scavengers [64, 108]. In conjunction, the detrimental impacts of these three invasive scavengers, could have widescale effects on scavenging dynamics and the availability and persistence of carcasses within the Australian Alps, especially so regarding feral pigs which are capable of consuming an entire carcass in one scavenging bout. Many studies have demonstrated that dingoes can benefit the broader Australian environment by suppressing red fox and feral cat populations despite their invasive nature [109-111]. Therefore, a similar dynamic might be occurring in the Australia Alps, specifically surrounding carrion. This could provide novel evidence for the regulation of an invasive mesopredator population by a native apex predator within a scavenging context.

Aims and hypotheses

Carrion, in of itself, adds substance to the phrase 'life after death'. This is because even after the death of an animal its carcass can become a focal point within an ecosystem for a whole host of organisms. It is for these reasons that carrion can be used to specifically examine scavenging ecology. Within this thesis, the complex environmental dimensions (seasonality and altitude) of the Australian Alps were utilised to conduct a comprehensive and systematic analysis of this model ecosystems scavenging dynamics. To conform with the design principles set out by Schoenly et al. (2015), a long transect was utilised to adequately capture enough natural and altitudinal variability in the Australian Alps (spatial aspect). Along this transect, 15 spatially independent carcasses were monitored per season (60 total), to account for seasonal effects (temporal aspect), and this yielded statistically and ecologically relevant findings of scavenging dynamics. Therefore, this thesis provides one of the first comprehensive analyses of scavenging dynamics for an understudied Australian ecosystem and demonstrates a robust and repeatable study design valuable to understanding scavenging ecology globally.

The second chapter of the thesis will investigate how the seasons affect scavenging dynamics in the Australian Alps. Specifically, seasonal effects will be assessed to determine how they affect four vertebrate scavenging variables: scavenger species richness/composition, time to first arrival and scavenging at a carcass, scavenger activity (i.e., probability of a scavenger investigating vs scavenging a carcass), and time spent investigating and scavenging a carcass. Broadly, it is predicted that the seasonal effects will significantly impact most if not all of the scavenging variables, most notably during summer and winter when thermal extremes are at their peak. More detailed hypotheses are provided in *Chapter 2*.

The third chapter explores the top-down scavenging effects of an apex predator. Much of the literature describes the interspecific interactions of apex predators with mesopredators [25, 40, 45, 46, 48, 112, 113]. However, little is known about the interspecific interactions apex predators have with subordinate facultative scavengers considered potential prey species. In the Australian Alps, the dingo is the apex (scavenging) predator, and thus, may be exerting top-down scavenging effects on subordinate facultative scavengers such as the brushtail possum and raven spp., which were demonstrated to be the most common scavengers in *Chapter 2*. It is expected that brushtail possums, and to a lesser degree raven spp., may use a suite of spatial, temporal, and behavioural methods to avoid confrontations with dingoes surrounding carrion. More detailed hypotheses are provided in *Chapter 3*.

Implications

In addition to providing a comprehensive account for the scavenging dynamics of the Australian Alps, the findings of this thesis are relevant to environmental managers. The Australian Alps are home to a plethora of invasive animal species including feral horses/brumbies (*Equus ferus caballus*), various deer species, feral pigs (*Sus scrofa*), red foxes (*Vulpes vulpes*), feral cats (*Felis catus*), feral goats (*Capra hircus*), and feral rabbits (*Oryctolagus cuniculus*). As such, extensive management practices are routinely undertaken to control the populations of these species and their negative impacts on the fragile Australian alpine ecosystem. Often, many of these operations leave culled animal carcasses *in situ* to decay, and this provides a sudden influx of available energy and nutrient within the landscape. Therefore, the Australian Alps may at times harbour high rates of carrion biomass.

Scavengers provide vital ecosystem services valuable to both the natural and human environment, the latter of which is often overlooked. To take advantage of these services, the findings of this thesis may assist in determining when (i.e., which season) invasive species management practices should occur. Firstly, many of the key invasive species in the Australian Alps (feral pigs, red foxes, and feral cats) are scavengers. Therefore, management programs have the potential to supplement and support such invasive species populations by increasing carrion biomass, and thus, nullifying control efforts. Using my findings to determine the seasons in which native scavenging rates and invasive scavenging rates are highest and lowest respectively may reduce the chance of such a counterintuitive result. Secondly, in addition to the natural/environmental features of the Australian Alps there is also a complex human dimension. The Australian Alps is home to many popular recreational pursuits and as such has become a tourism hotspot within Australia [114]. Therefore, the faster processing and decomposition times of carcasses, as facilitated by the scavenger guild during their most efficient seasons, would be beneficial to the overall environmental aesthetics of the Australian Alps as perceived by humans.

This thesis will provide an ecological context for the natural history of scavenging dynamics in the Australian Alps. Using this ecosystem, one previously ignored, our findings will supplement the relatively new literary foundation of scavenging ecology. In addition to the ecological findings, it is also anticipated that this thesis will set a new standard for field-based scavenging research. The methods used here, specifically regarding the temporal scales and sample sizes used, if adopted by future studies at a minimum, can adequately describe localised scavenging dynamics within any given ecosystem, thus, facilitating the advancement and our understanding of scavenging ecology globally.

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Chapter 2 – Carcass use by mesoscavengers drives seasonal shifts in scavenging dynamics

Abstract

Carrion is a high energy and nutrient rich resource that attracts a diverse group of vertebrate scavengers and consequently can be utilised as a focal point within an ecosystem to assess scavenging dynamics. Despite the carrion pool being highly seasonal, many studies utilising carrion to investigate scavenging dynamics, have neglected to account for seasonal effects. Therefore, using the highly seasonal Australian alpine ecosystem, carrion deployed experimentally each season were utilised to assess vertebrate scavenging dynamics. Time to first detection of carcasses by vertebrate scavengers was longer during summer, likely a product of increased invertebrate scavenging rates and an abundance of other available food sources. Scavenging was more likely than investigation of carcasses during winter and spring. During winter, this trend was driven by an increase in brushtail possum scavenging which accounted for 78% of all scavenging events and was likely in response to a scarcity of other food sources. Conversely, during spring, scavenging was more likely as the scavenging rates of raven species increased four-fold to meet the demands of breeding (i.e., increased energetic requirements, nest construction, and chick rearing). The frequent but brief trips between nest and carcass by raven spp. during the breeding seasons was also likely the reason scavenging events were significantly shorter during spring. These results demonstrate highly seasonal scavenging dynamics in the Australian Alps and supports the importance of seasonal effects in scavenging ecology. However, the findings are unique given seasonal trends in scavenging dynamics were dominated by low-ranking mesoscavengers: the brushtail possum and raven species.

Introduction

Carrion is a valuable ecosystem resource which in contrast to plant-based detritus is high in energy and nutrient rich [1]. Although carrion is spatially and temporally patchy [2, 3], it is exploited by species that have evolved to scavenge. Historically, scavengers have been viewed as ‘bottom-feeders’, due to associations with rotting matter, disease, and death [4]. But scavenging is present in most taxa, including obligate and facultative large vertebrate scavengers capable of consuming a whole carcass in one feeding event, to invertebrate scavengers that can aggregate around carrion in the thousands [5]. Together, these species form scavenger guilds, which in addition to acting as ‘natures clean-up crew’ [6], are also important to supporting critical linkages, structure, and stability in food webs [2]; distributing nutrients within and among ecosystems; and providing economic and human health benefits related to carcass disposal and sanitary measures [7].

Carrion biomass within an ecosystem fluctuates in response to key modes of death such as predation, but also in response to environmental factors [5, 8]. Seasons are one of the strongest governing environmental forces and can dictate the life histories of many herbivorous and/or migratory species that form a major component of the carrion pool [5, 8-10]. This is because, in highly seasonal environments carrion biomass can become cyclically pulsed towards the ends of harsh and/or prolonged seasons when such species incur increased mortality rates [11]. This is evident in tropical and sub-tropical Africa following wet and dry season cycles [12-14]. For example, each year over 1 million wildebeest (*Connochaetes taurins*) migrate through the Serengeti Mara ecosystem [15], including through the Mara River, where mass wildebeest drownings occur during its crossing [16, 17]. This sudden annual influx of carrion provides many terrestrial and aquatic scavengers with an abundance of available energy and nutrients [18]. Similar trends are also common in the higher northern latitudes where many ungulate species face increased mortality rates towards the ends of harsh northern winters [19-21].

Season, along with daily temperatures, humidity, and moisture levels can also influence carrion persistence rates via the effects they have on regulating microbial and insect activity [22-24].

It is in response to such seasonal fluctuations in the availability of carrion, that scavengers have adapted and evolved to exploit such a pulsed food resource. Indeed, facultative scavengers have considerable flexibility in their diets regarding both the relative contribution of predated vs scavenged food and meat vs other food sources [25]. For example, the Białowież Forest (Poland) scavenger guild demonstrated increased scavenging rates during winter in response to greater energy expenditure (i.e., keeping warm, traversing snow), carcass availability, and lack of other food sources [26-28]. These dynamics can become even more complex when considering the contrasting seasonality in the life histories of each scavenger species within a guild. For instance, during peak chick rearing season, the energy requirements of herring gulls (*Larus argentatus*) and lesser black-backed gulls (*Larus fuscus*) are inherently greater, and consequently both species were less selective of fish species when scavenging fishery discards [29]. A plethora of other environmental, life history, and inter/intra specific factors can also affect species specific scavenging, and thus, add further complexities to scavenging dynamics [30].

Despite obvious seasonal trends in scavenging ecology, the experimental designs of many field-based scavenging studies often overlook the impact of seasonal effects [31]. Indeed, it is common to monitor scavenging dynamics surrounding carrion only during two seasons of interest (i.e., hot and cold, or wet and dry, or breeding and non-breeding) [23, 32-36]. Such an approach potentially oversimplifies the ways in which the various dimensions of scavenging ecology can change not only between each of the seasons, but over the course of a year, and even between years [36]. Moreover, some studies completely ignore seasonal effects by only monitoring scavenging dynamics during one season [37-41]. The successful design of any robust field study in carrion ecology should simultaneously accounts for temporal aspects (i.e., diel, seasonal, yearly), spatial aspects (i.e., representative of ecosystem, spatially independent), and sample size, in conjunction with a suite of other minor considerations [31].

In this study, the highly seasonal nature of the Australian Alps was exploited to monitor the use of carcasses by vertebrate scavengers. Carcass monitoring was replicated across all four seasons to account for seasonal effects. Such an approach, whilst accounting for environmental variability, provided an opportunity to determining how important the seasons are in influencing scavenger species richness/composition, and to test specific predictions related to (1) the time to first detection and scavenging at a carcass; (2) scavenger activity (i.e., probability of a scavenger investigating vs scavenging a carcass); and (3) the time spent investigating and scavenging a carcass. Accelerated decomposition of carrion during summer as a product of increased invertebrate and microbial activity is known to produce stronger carcass-linked odours [42]. Consequently, it was predicted that increased olfactory cues during summer would result in greater detectability of carrion by vertebrate scavengers, and thus, shorter time to first arrival and scavenging at carcasses. Conversely, despite carrion being less detectible during winter, it was predicted that the probability of vertebrate scavenging would increase, and time spent scavenging would be longest. This prediction was informed by the findings of previous scavenging studies that demonstrate vertebrate scavengers to rely on carrion more heavily during winter when other food resources are scarce [26-28]. The results are used to highlight the importance of replicating field-based scavenging studies across the seasons in order to fully understand the complex scavenging dynamics and interactions that take place surrounding carrion.

Methods

Study site

This study was conducted in Kosciuszko National Park, located in southern New South Wales, Australia. This region includes many of the highest peaks and ranges within Australia's Great Dividing Range, including Australia's highest peak – Mount Kosciuszko. The landscape is delineated into three altitudinally distinct ecological communities – montane (500m-1500m) subalpine (1500m-1850m), and alpine (1850m-2228m) [43]. This work was undertaken within the montane zone (between approximately 1000m – 1500m) which is characterised by forest stands dominated by snow gum (*Eucalyptus pauciflora*) in association with various other *Eucalyptus* species.

Ethics, licenses, and permits

The following described work received all required ethics, licenses, and permits approved by the relevant authorities (i.e., The University of Sydney; New South Wales Office of Environment and Heritage; and New South Wales National Parks and Wildlife Services). All kangaroo carcasses used for the purposes of this research were sourced fresh and locally from existing authorised and legally approved management culls that are conducted to control overabundant kangaroo populations.

Fieldwork

A 15 km transect was established through Kosciuszko National Park along which all carcass monitoring took place (Figure 1). This transect ran northeast – southwest from a border region of the national park inwards towards its interior and was selected due to its accessibility (i.e., road access) and because it is a relatively undisturbed area with little human activity. Monitoring periods were established to coincide with the four seasons: autumn – March 2020; winter – July 2020; spring – October 2020; summer – January 2021. During each season, 15 sites were established along the transect, separated by approximately 1 km from the nearest sites monitored within the same season and approximately 250m from the nearest sites monitored during other seasons (60 different sites in total; Figure 1). The separation of sites ensured a level of spatial independence and it prevented habituation of scavengers to a carrion source location [35, 44-46].

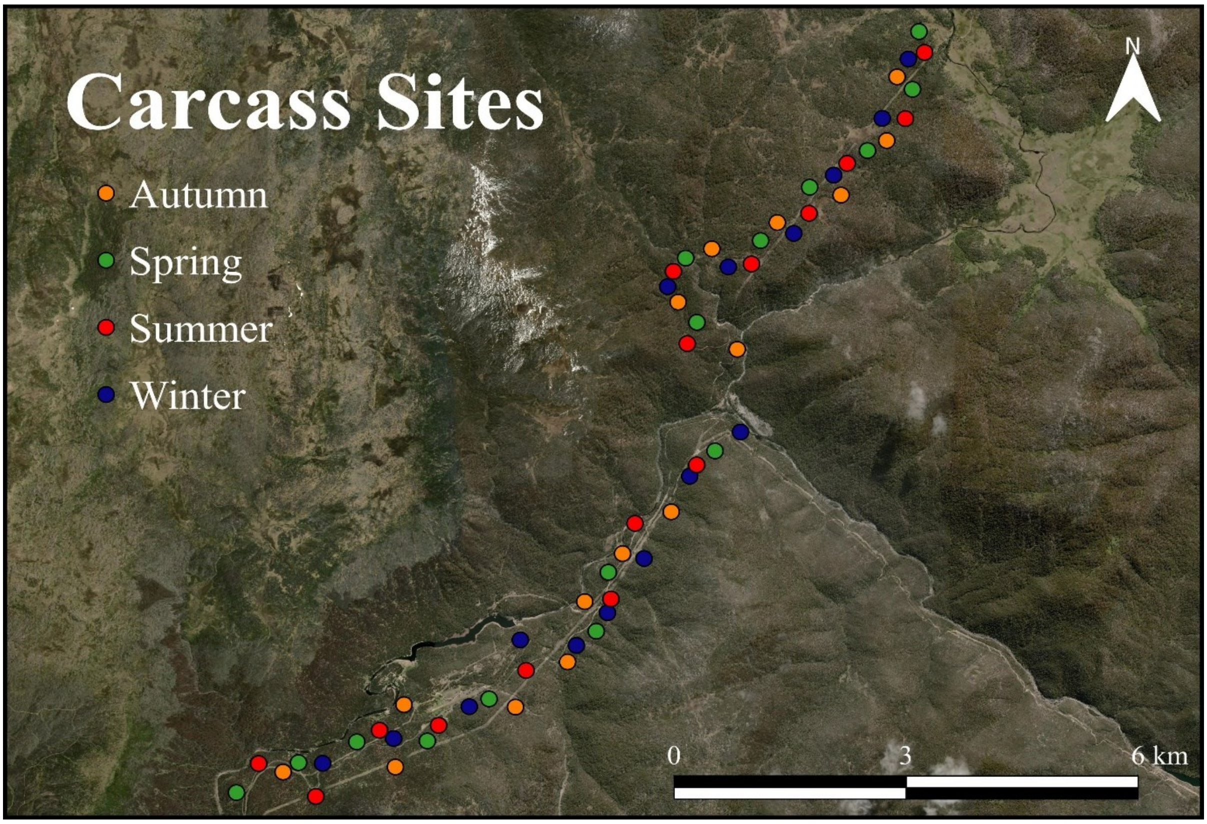

Figure 1. Location of the monitoring transect along which all 60 carcass sites were established within Kosciuszko National Park (red = summer, orange = autumn, blue = winter, green = spring).

Within each seasonal monitoring period, one fresh eastern grey kangaroo carcass was placed at each site (15 total). The carcasses ranged in weight from 10kg-70kg and on average were 28.3kg (± 1.498 – standard deviation). Each carcass was secured, using wire ties, to star pickets driven into the ground to ensure they remained in situ to be monitored for 60 days [44-46]. Vertebrate scavenger activity was monitored at each site using a Reconyx PC800 Hyperfire™

remote camera. Each camera was placed on a free-standing star picket three meters north of the carcass – the southern aspect of the cameras decreased exposure to direct sunlight which would otherwise reduce image quality. The cameras were calibrated to take photographs continuously (approximately one image per second) when triggered by thermal movement (i.e., rapid-fire, no wait period). These approaches and methods follow those previously used in field-based scavenging research [21, 34, 35, 44-48].

Analyses

Remote camera images were analysed for species presence and the number of individuals of a species present. In order to determine distinct visitations of species, an 'event' was characterised as a visitation by a species that occurred more than 10 minutes after the last visitation by that same species. Only species-specific events could be characterised because identification of individuals for most species was not possible. An event was characterised as a 'scavenging event' if the species present scavenged on the monitored carcass in at least one of the remote camera images consisting of that event, otherwise the event was characterised as an 'investigation event'. Data from species recorded to have scavenged at least once were included in the statistical analyses.

The R software environment (version 1.4.1717) was used for all statistical analyses. Moran's I statistic was utilised to test for spatial autocorrelation in each of the scavenging response variables between the carcass sites (R Package 'ape'; [49]). To determine any differences in species composition between the seasons, a permutational multivariate analysis of variance (PERMANOVA; R Package 'vegan'; [50]) was used in conjunction [51] with an analysis of similarities (ANOSIM; R Package 'vegan'; [50]). To determine which scavenger species were driving any differences in species diversity between the seasons a similarity percentages (SIMPER) analysis was used (R Package 'vegan'; [39]).

To adequately characterise the seasonal nature of scavenging, four response variables were used: scavenger species richness (Conway-Maxwell Poisson distribution), the time to first detection of and scavenging at a carcass (in hours; Gamma distribution), scavenger activity (i.e., probability of a scavenger investigating vs scavenging a carcass; binomial distribution), and investigation and scavenging event duration (in minutes; Gamma distribution). Each of the response variables were modelled against the explanatory variables of season, as well as altitude to account for any differences in elevation, however, given the small altitudinal gradient used (500m) no altitudinal effects were expected. These models were constructed twice, once using only investigation events and once using only scavenging events. Only one model was constructed for scavenger activity as it is a binomial response variable (either investigation; 0, or scavenging; 1) designed specifically to determine the probability of either an investigation event or scavenging event.

The relationships of each of these scavenging response variables with the explanatory variables of season and altitude were modelled using either generalised linear models (GLM; R Package 'lme4' [52]) or generalised linear mixed models (GLMM; R Package 'lme4' [52]), and in the case of poorly fit models, generalised additive models were utilised (GAM; R Package 'mgcv' [53]). To determine the most parsimonious model(s), Akaike information criterion (AIC) [54] was used (ΔAICc level of significance < 2), with model selection facilitated by the utilisation of the dredge function (R Package 'MuMIn' [55]). AIC considers the different combinations of explanatory variables (i.e., combinations of season and altitude) within a model and as such the scavenging response variables had four possible models: non-interaction season and altitude model ($x \sim y + z$), season model ($x \sim y$), altitude model ($x \sim z$), and null model ($x \sim 1$).

Significance testing (p level of significance < 0.05) was also undertaken using the base model (i.e., non-interaction season and altitude model – $x \sim y + z$) to determine which explanatory variables (seasons and/or altitude) and/or their levels (summer, autumn, winter, spring) were important in explaining each of the scavenging response variables. To yield additional information from these models, Tukey's honest significance tests were used to determine which seasons were significantly different from one another regarding the modelled scavenging response variable (R Package emmeans) [56]. This pair-wise test approach could not be used when modelling species richness because it followed a Conway-Maxwell-Poisson distribution which does not support post-hoc analyses. However, the previously described PERMANOVA, ANOSIM, and SIMPER analyses provided similar relevant insights.

Results

Of the 60 carcass sites monitored, remote camera data was gathered for 58; remote camera data for two sites (one during winter and one during summer) were lost due to theft and camera failure. The camera traps took 745,599 images of 34 different species including both scavenger and non-scavenger species. Of these species nine were considered scavenger species based on recorded scavenging of the monitored carcasses (Figure 2). These were the: spotted-tail quoll (*Dasyurus maculatus*), feral cat (*Felis catus*), dingo (*Canis dingo*), pied currawong (*Strepera graculina*), wedge-tailed eagle (*Aquila audax*), brushtail possum (*Trichosurus vulpecula*), raven spp. (*Corvus coronoides* and *Corvus mellori* – indistinguishable from one another in the remote camera images), red fox (*Vulpes vulpes*), and feral pig (*Sus scrofa*).

Figure 2. Remote camera images for each of the members of the Australian alpine scavenger guild, determined by recorded scavenging of carcasses in Kosciuszko National Park.

These scavenger species occurred at carcass sites to investigate or scavenge carcasses at varying rates across the seasons (Figure 3). In total 6857 distinct events were recorded of which 2680 were investigation events and 4177 scavenging events (Figure 4.a). Brushtail possums and raven spp. accounted for 88% of the total recorded events, whilst spotted-tail quolls accounted for the fewest events (Figure 4.b).

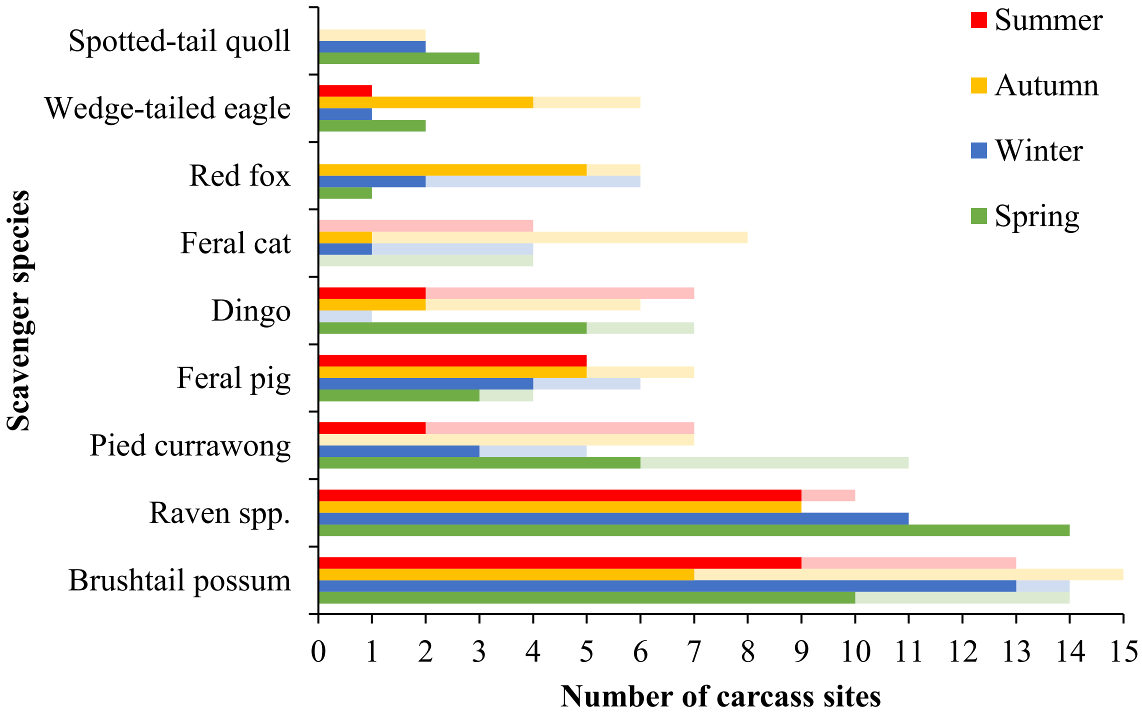

Figure 3. The total number of carcass sites visited by each scavenger species per season (red = summer, autumn = yellow, winter = blue, spring = green) where carcass sites that were recorded to have been scavenged (solid fill) are distinguished from those that were only investigated (shaded fill).

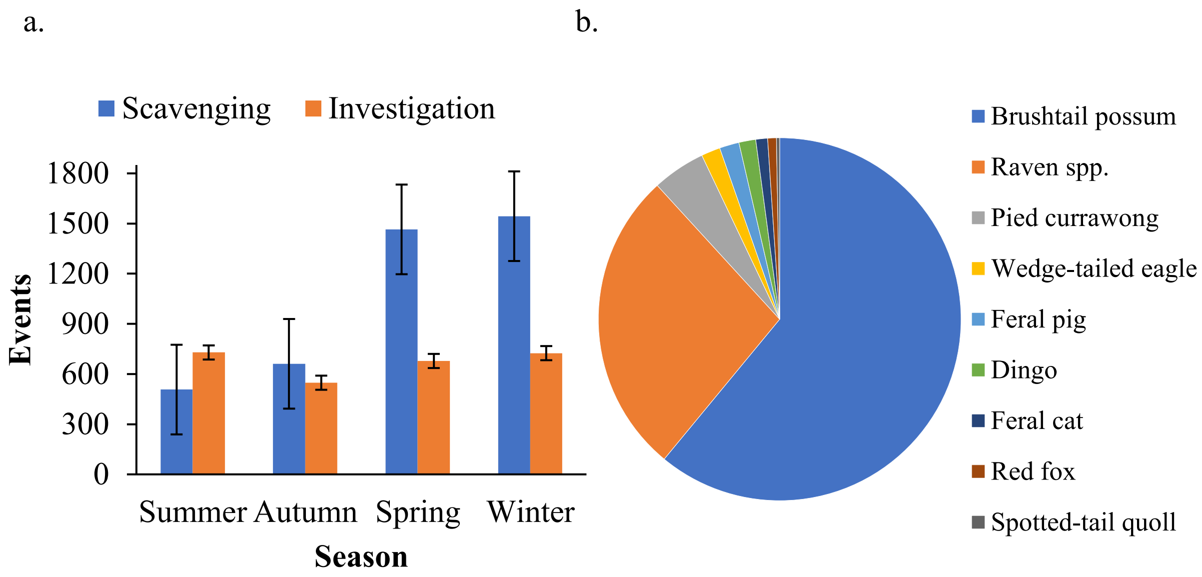

Figure 4. (a.) The total number of events (orange = investigation, blue = scavenging) per season and **(b.)** the percentage of total events attributed to each scavenger species where brushtail possums accounted for 61%, raven spp. 27%, pied currawongs 5%, and all other species < 2% each.

No spatial autocorrelation was detected in any of the scavenging response variables (Table S1). The PERMANOVAs demonstrated that there were differences in species composition between the seasons for both investigation events ($p = 0.001$) and scavenging events ($p = 0.004$) but that they were weak differences ($R^2 = 0.146$ and 0.152 respectively; Table S2). The Tukey's honest significance tests for the investigation events PERMANOVA demonstrated that species composition was significantly different between autumn and spring ($p = 0.030$) and between spring and winter ($p = 0.018$; Table S3). The Tukey's honest significance tests for the scavenging events PERMANOVA demonstrated that species composition was significantly different between autumn and winter ($p = 0.036$) and between spring and winter ($p = 0.012$; Table S3). Furthermore, in conjunction with the PERMANOVA, the investigation events ($R = 0.109$ with $p = 0.001$) and scavenging events ($R = 0.109$ with $p = 0.002$) ANOSIM analyses suggested that differences in species composition within the seasons and between the seasons was more or less the same (Table S4). The SIMPER analysis demonstrated that brushtail possum and raven spp. were the primary drivers of the observed differences in species composition between the seasons (Figure 5 & Table S5/S6).

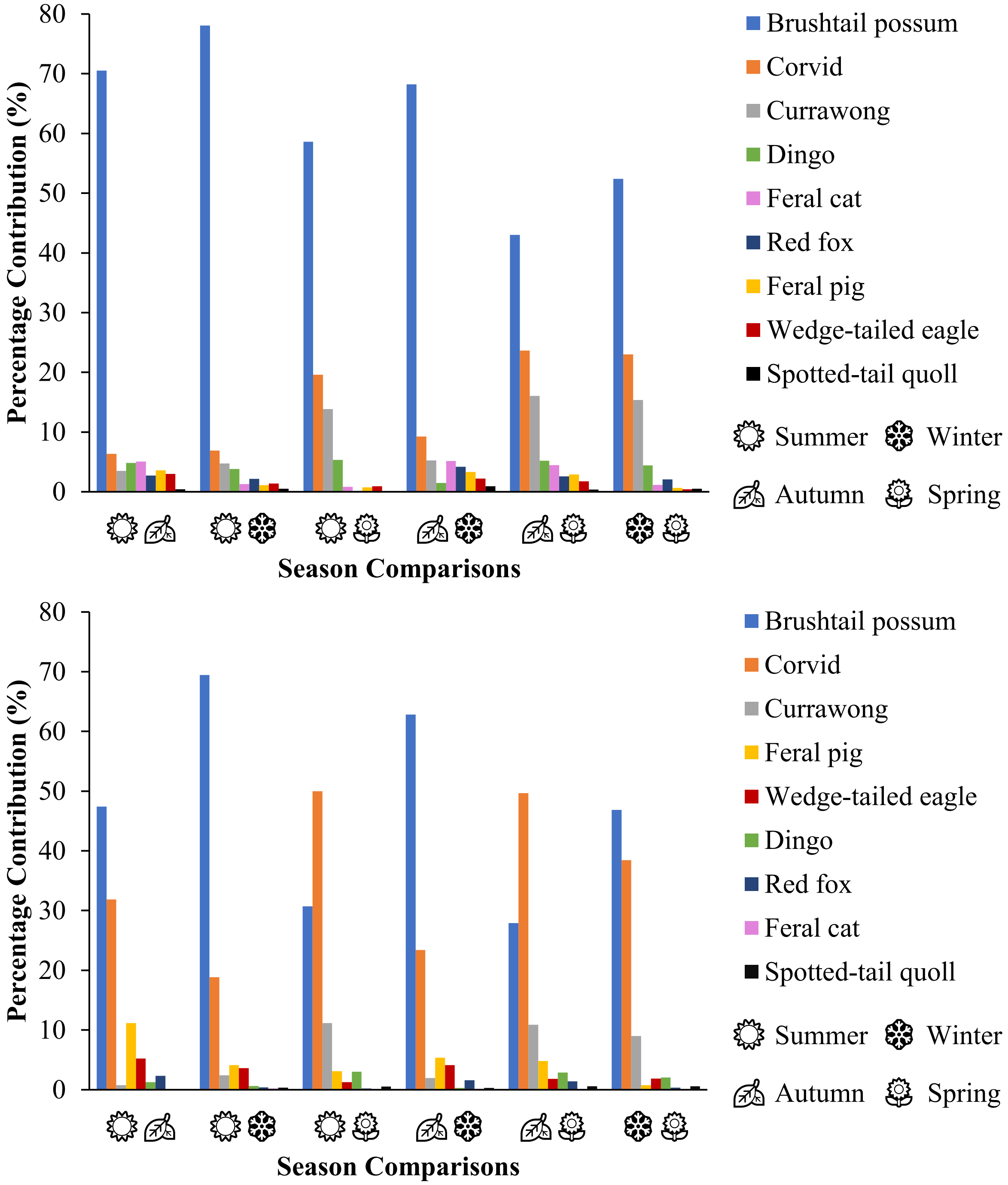

Figure 5. The percentage contribution of each scavenger species (contributed most to least, top to bottom of each respective legend) to the differences observed in species composition between each of the seasons for investigation events (top) and scavenging events (bottom). The

percentage contribution was adapted from the ‘cumulative sum’ results yielded from the SIMPER analyses (Table S5 and S6).

Scavenger species richness for investigation events

All four models were parsimoniously competitive (ΔAICc < 2) in explaining the variation in scavenger species richness for investigation events (Table S7). The base model demonstrated that summer (*p* = 0.040) and winter (*p* = 0.035) had a significant effect on scavenger species richness for investigation events (Table S8).

Scavenger species richness for scavenging events

Three models were parsimoniously competitive (ΔAICc <2) in explaining the variation in scavenger species richness for scavenging events (Table S7). The first was the null model (ΔAICc = 0.00), the second the seasons model (ΔAICc = 1.01), and the third the altitude model (ΔAICc = 1.26). The base model was not significant (Table S8).

Time to first detection of carcasses

Two models were parsimoniously competitive (ΔAICc <2) in explaining the variation in time to first detection of carcasses (Table S9). The first was the season model (ΔAICc = 0.00) and the second was the non-interaction season and altitude model (ΔAICc = 1.99). The base model demonstrated that summer had a significant effect on time to first detection of carcasses (*p* = 0.002; Figure 6; Table S10). Specifically, time to first detection of carcasses (in hours) was 4.289 and 6.527 times longer during summer than spring (*p* = 0.012) and winter (*p* = 0.0010) respectively (Table S11).

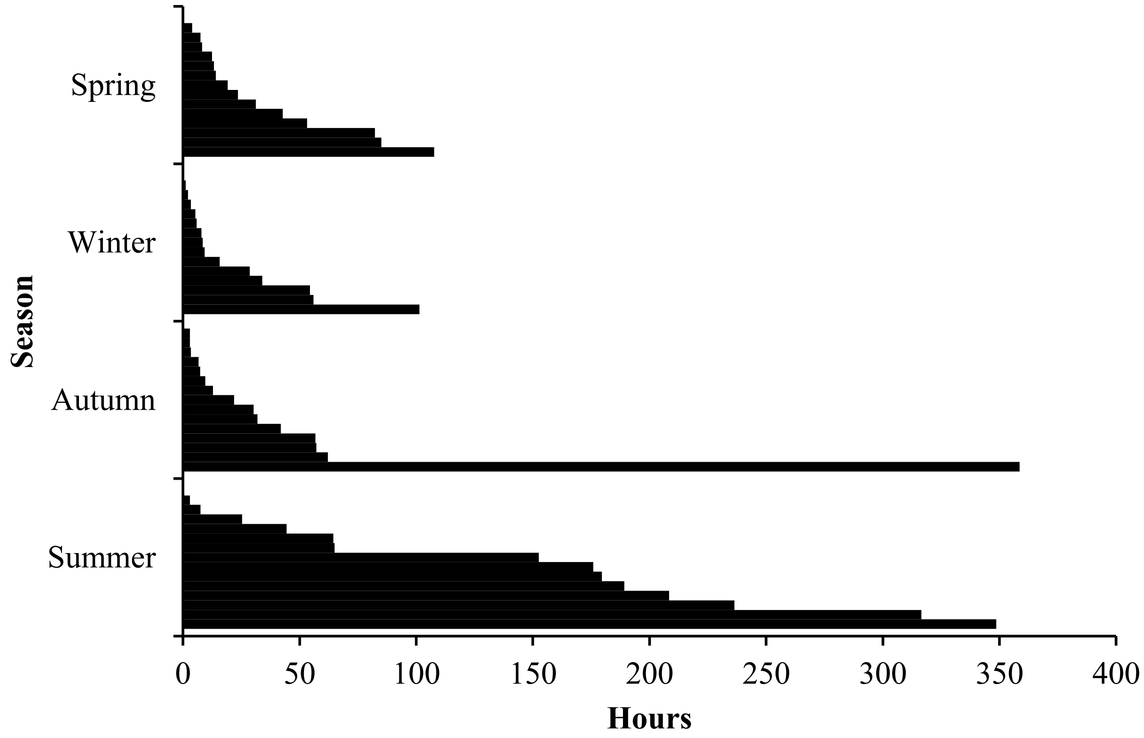

Figure 6. Hours to first detection of each carcass monitored during each of the seasons.

Time to first scavenging of carcasses

Three models were parsimoniously competitive (ΔAICc <2) in explaining the variation in time to first scavenging of carcasses (Table S9). The first was the season model (ΔAICc = 0.00), the second the null model (ΔAICc = 0.65), and the third the non-interaction season and altitude model (ΔAICc = 1.93). The base model demonstrated that winter had a significant effect on time to first scavenging of carcasses (*p* = 0.039; Table S10).

Scavenger activity

Two models were parsimoniously competitive (ΔAICc <2) in explaining the variation in scavenger activity (Table S12). The first was the season model (ΔAICc = 0.00) and the second was the non-interaction season and altitude model (ΔAICc = 1.61). The base model demonstrated that winter (*p* = 0.011) and spring (*p* = 0.003) had a significant effect on scavenger activity (Figure 4; Table S13). Specifically, scavenging was 2.173 and 3.108 times more likely than investigation during spring than autumn (*p* = 0.015) and summer (*p* = < 0.001) respectively, and 2.787 times more likely during winter than summer (*p* = < 0.001; Table S14).

Duration of investigation events

Two models were parsimoniously competitive (ΔAICc <2) in explaining the variation in the duration of investigation events (Table S15). The first was the null model (ΔAICc = 0.00) and the second was the season model (ΔAICc = 1.89). The base model was not significant (Table S16).

Duration of scavenging events

Two models were parsimoniously competitive (ΔAICc <2) in explaining the variation in the duration of scavenging events (Table S15). The first was the season model (ΔAICc = 0.00) and the second was the non-interaction season and altitude model (ΔAICc = 0.86). The base model demonstrated that spring had a significant effect on the duration of scavenging events (*p* = < 0.001; Figure 7; Table S16). Specifically, scavenging event duration (in minutes) was 1.895 and 1.493 times shorter during spring than autumn (*p* = < 0.001) and winter (*p* = 0.041) respectively (Table S17).

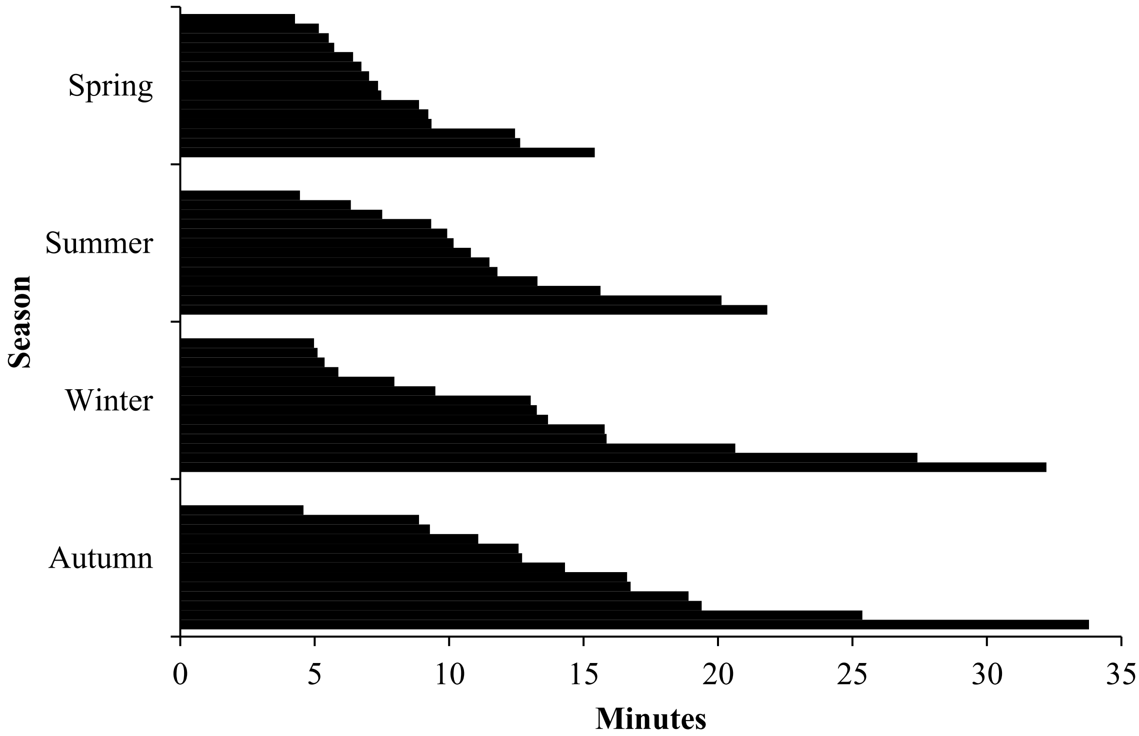

Figure 7. The average duration of scavenging events (minutes) at each carcass monitored during each of the seasons.

Discussion

This study determined how seasons affected vertebrate scavenging dynamics. It was expected that scavenging dynamics would be highly seasonal, and thus, highlight the importance of seasonal effects, a consideration often absent from the experimental designs of field-based research in scavenging ecology. The findings here demonstrate that scavenging dynamics were highly seasonal, and this trend was consistent (i.e., did not significantly change) across the altitudinal gradient where the carcasses were monitored. Shifts in scavenging dynamics were overwhelmingly dictated by the scavenging rates and activities of mesoscavengers, specifically brushtail possums and raven spp.. The scavenging rates observed by raven spp. were not unusual, with many studies both within Australia and globally describing raven spp. species as prolific scavengers [27, 44, 45, 57, 58]. However, the brushtail possum has received little recognition as a regular scavenger [59-61].

Australia has no true obligate vertebrate scavenger, but our study recorded carcass use by nine species of facultative scavenging vertebrates. Scavenging rates by these species should be highly seasonal, linked to factors such as carrion biomass, availability of other food sources, and/or the life histories of the scavenger species [12-14, 20, 25-28, 62-64]. This was supported by the results, but the trends uncovered were driven by the scavenging behaviours of the brushtail possum and raven spp who together accounted for 88% of all recorded events.

Scavenging dynamics surrounding carrion are not typically dictated by the species-specific scavenging rates of mesoscavengers, but that of larger dominant scavenger species [20, 65-67]. This is because larger species are generally more competitively dominant surrounding carrion [11, 25, 35], and are able to open up carcasses, and thus, provide access to smaller scavengers unable to do so [27, 68, 69]. In this study, however, larger scavengers such as dingoes, wedge-tailed eagles, and feral pigs only accounted for 5% of all recorded events, suggesting they were either not abundant during the study period or were not scavenging frequently. At carcass sites they did visit, there was evidence that they could rapidly consume the carcass biomass, including bones; in one case a dingo was observed consuming an entire kangaroo carcass within a 24-hour period. Whether the relative absence of larger scavengers at carcass sites in this study aided mesoscavenger access to the food resource is unknown but could reasonably be expected if this resulted in less competition for the food resource and/or reduced predation risk for the mesoscavengers. The relative absence of dingoes at carcass sites, along with similarly low rates of scavenging by red foxes and feral cats, is likely to have especially influenced the use of carcasses by brushtail possums, as they regularly feature in the diets of these three predators [70-79].

The time it takes scavengers to detect a carcass, and subsequently scavenge it, is intrinsically linked with carcass decomposition rates and persistence within the ecosystem [80]. In our study, carcasses took longer to be detected during summer, especially when compared to spring and winter. Carcass detection by scavengers is dependent on a number of factors including olfactory cues, visual cues, inter/intra specific cues, and search effort [36, 42, 81]. We therefore, expected that olfactory cues would be the primary mode of detection given that closed canopy forested ecosystems, such as the montane zone of Kosciuszko National Park, make visual detection and certain forms of inter/intra specific cues difficult [8, 24]. Consequently, it was predicted that during summer greater olfactory cues owing to increased temperatures, and increased invertebrate and microbial scavenging activity, would facilitate shorter time to first detection of carcasses than during the other seasons [3, 5, 24, 82, 83]. However, there was no evidence to support this hypothesis.

Instead, it is possible that the same mechanism expected to facilitate shorter time to first detection of carcasses, invertebrate and microbial scavenger activity, in fact, hindered detection of carcasses by the vertebrate scavengers. During summer (warmer months) carcasses are rapidly colonised (within minutes) *en masse* by invertebrates, and presumably microbes [83-88]. The intense scavenging activity that follows accelerates carcass decay through the different stages of decomposition, potentially at such a rate that vertebrate scavengers were given too little time to detect carcasses i.e., the invertebrate scavengers outcompeted vertebrate scavengers [83, 87, 88]. Indeed, previous observations of carcass persistence times in the study site indicated that eastern grey kangaroo carcasses take at least twice as long to reach the dry decay stage (only skin and bones remaining) in cool compared to warmer periods [46]. During the winter monitoring period of this study, some carcasses did not reach the dry decay stage, even after 60 days.

Many global studies have demonstrated that vertebrate scavenging rates are lowest during summer when other food sources are more abundant and vice versa during winter [26-28]. In our study, brushtail possums accounted for 81% of all recorded events during winter and they scavenged three times more often during winter than during summer. Generally, the diet of brushtail possums consists of leaves, flowers, fruit, (*Eucalyptus* and Acacia) and insects [89-91], most of which are only seasonally available during warmer months. Therefore, this marsupial may be exhibiting a dependence on carrion during winter that is similar to that of other scavengers in northern hemisphere ecosystems [26-28]. The dependence of the brushtail possum on carrion during winter likely influenced our analyses of the scavenger activity response variable which recorded scavenging to be 2.789 times significantly more likely than investigation of carcasses during winter when compared to summer. This may also explain why carcasses took six times longer to be detected during summer (144 hours – 6 days) than during winter (24 hours), contrary to our prediction that time to first arrival would be shortest in summer. Collectively, during autumn, winter, and spring, 93% of the first detections of a carcass were by either brushtail possums or raven spp. Conversely, during summer, only 57% of the first detections of a carcass were by either brushtail possums or raven spp. Therefore, it is possible that the brushtail possums and raven spp. may have a disproportionately greater bearing on the time it takes the collective scavenger guild to first detect a carcass.

The species-specific breeding seasons of scavengers can also have profound impacts on their respective scavenging behaviours [57, 64, 92, 93]. The Australian raven and little raven breed from late winter into spring [94-96]. Initially, nest construction is prioritised in this early breeding season, and the associated activities are characterised by frequent and short visitations between the nest and sources of nesting material [97]. In our study, numerous remote camera images captured during the spring monitoring period recorded raven spp. collecting hair and/or fur from the carcasses, presumably for nest construction (Figure S1). Following nest construction, chick rearing often requires breeding pairs to divide time between foraging, feeding chicks, and being vigilant and protective of the nest [98]. These considerations often mean that frequent but brief carcass visitations continue into the chick rearing season as the breeding pairs frequently fly back and forth between the nest and food sources [98]. Inherently, during this time both raven spp. incur greater energy costs associated with these activities, and thus, must supplement their diets with protein rich sources and/or greater quantities of food, such as carrion [57, 93]. Of all recorded raven spp. scavenging events during this study, 67% were during spring, and this suggests that raven spp. may heavily rely on carrion to supplement their diet, and that of their chicks, during the breeding season [57]. Further still, this flurry of raven spp. scavenging during spring (a 170% increase on average annual raven spp. scavenging events) accounted for 73% of all scavenging events for the collective scavenger guild. Therefore, given their dominance during spring, it is likely that the frequent but brief scavenging events, characteristic of the raven spp. breeding season, were also deterministic of the significantly shorter scavenging event duration recorded for the collective scavenger guild during spring.

The findings here regarding the raven spp. are also indirectly linked to the initial prediction for longer scavenging event duration during winter – models dictated that scavenging event duration during spring was 1.493 times significantly shorter than during winter. Whilst raven spp. scavenging behaviours during their breeding seasons (spring) likely determined this result and supported our prediction, it is juxtaposed to the initially used supporting evidence. That being, many previous studies, mostly undertaken in the northern hemisphere, having demonstrated scavenging rates to increase during winter in response to a lack of other available food sources [26-28]. This raises several questions that need be addressed regarding the degree to which the Australian alpine winter impacts food sources, species diets, and associated flow-on effects to scavenging dynamics vs other alpine areas in the world, and indeed non-alpine ecosystems that experience harsher winters.

Conclusion

Scavenging dynamics in this study were highly seasonal, but dictated by the scavenging activities and behaviours of mesoscavengers – the brushtail possum and raven spp.. The high rate of scavenging by these species drove the seasonal trends in scavenging dynamics, but the direction in which the seasonal effects impacted the scavenging response variables was not always as predicted. This exemplifies the unexpected influence that seasons can have on ecological processes linked to scavenging and highlights the need for seasonally replicated experimental approaches in field-based scavenging research; the primary motivation for undertaking this study.

The high rates of scavenging by the brushtail possum suggest that the species dietary status be reconsidered, and with regards to the raven spp. a potential avenue for future work could be to investigate the impact of carrion availability on breeding success. These findings, and indeed such recommended future research (discussed in further detail in *Chapter 4 – Conclusion and future directions*), have the potential to be of continental relevance given that the brushtail possum is the most widespread Australian marsupial and that both raven spp. are also relatively abundant across southern-east Australia [99].

In recent decades increased recognition of the ecosystem sustaining processes that scavengers provide have advanced our understanding of scavenging dynamics, a previously misunderstood and underappreciated area of ecology [7, 100]. In order to ensure that such scientific advances are maintained, seasonal effects need to be accounted for in the field of scavenging ecology. Not only are the findings of this study ecologically relevant to scavenging ecology within Australia, but also serve as a more practical example of a robust and repeatable method for monitoring and assessing scavenging dynamics surrounding carrion within any given ecosystem.

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Chapter 2 – Supplementary Material

Figure 1. A raven spp. (*Corvus coronoides* or *Corvus mellori*) breeding pair collecting hair/fur from a kangaroo carcass during the spring monitoring period, presumably for nest construction.

Table 1. Moran's I measure of spatial independence for the various scavenging response variables.

Observed	**Expected**	**SD**	***p***
Species Richness Investigation Events			
0.006	-0.018	0.033	0.473
Species Richness Scavenging Events			
-0.026	-0.018	0.034	0.808
Time to First Detection			
-0.021	-0.018	0.032	0.918
Time to First Scavenging			
0.005	-0.018	0.033	0.490
Total Investigation Time			
0.009	-0.018	0.033	0.417
Average Investigation Time			
-0.012	-0.018	0.034	0.870
Total Scavenging Time			
-0.064	-0.018	0.032	0.150
Average Scavenging Time			
-0.040	-0.018	0.033	0.503

Table 2. The permutational multivariate analysis of variance (PERMANOVA) for investigation events species composition (top) and scavenging events species composition (bottom). Significant p-values ($p < 0.05$) are denoted in **bold**.

	Df	**Sums of sqs**	**Mean sqs**	**F Model**	**R^2**	***p***
			Investigation Events			
Seasons	3	0.931	0.310	2.898	0.139	**0.002**
Residuals	54	5.779	0.107		0.861	
Total	57	6.710			1.000	
			Scavenging Events			
Seasons	3	1.488	0.496	2.991	0.152	**0.004**
Residuals	50	8.289	0.166		0.848	
Total	53	9.776			1.000	

Table 3. Tukey's honest significance tests between each of the seasons for the permutational multivariate analysis of variance (PERMANOVA) for investigation events species composition (top) and scavenging events species composition (bottom). Significant p-values ($p < 0.05$) are denoted in **bold**.

Contrast	**F Model**	**R^2**	***p***	***p* adjusted**
Investigation Events				
Autumn - Spring	4.554	0.140	0.005	**0.030**
Autumn - Summer	1.984	0.068	0.119	0.714
Autumn - Winter	1.658	0.058	0.169	1.000
Spring - Summer	1.147	0.041	0.358	1.000
Spring - Winter	4.995	0.156	0.003	**0.018**
Summer - Winter	3.436	0.117	0.015	0.090
Scavenging Events				
Autumn - Spring	3.252	0.115	0.009	0.054
Autumn - Summer	1.464	0.060	0.212	1.000
Autumn - Winter	3.857	0.138	0.006	**0.036**
Spring - Summer	2.974	0.103	0.030	0.180
Spring - Winter	5.500	0.169	0.002	**0.012**
Summer - Winter	1.797	0.067	0.152	0.912

Table 4. The analysis of similarities (ANOSIM) for investigation events species composition (top) and scavenging events species composition (bottom). Significant p-values ($p < 0.05$) are denoted in bold.

ANOSIM statistic R	**Significance**
Investigation Events	
0.109	**0.001**
Scavenging Events	
0.109	**0.002**

Table 5. The similarity percentages (SIMPER) analysis demonstrating the contribution of each species to explaining differences between the seasons in investigation event species composition.

	Average	**SD**	**Ratio**	**AVA**	**AVB**	**CUMSUM**
Summer vs Autumn						
Brushtail possum	0.433	0.244	1.772	47.214	27.067	0.705
Raven spp.	0.039	0.046	0.849	1.500	2.333	0.769
Feral cat	0.031	0.074	0.420	0.357	1.933	0.819
Dingo	0.030	0.046	0.644	1.571	0.667	0.868
Feral pig	0.022	0.043	0.511	0.214	1.200	0.904
Pied currawong	0.022	0.035	0.606	0.786	1.000	0.939
Wedge-tailed eagle	0.018	0.034	0.538	0.429	0.800	0.969
Red fox	0.017	0.033	0.504	0.000	1.400	0.996
Spotted-tail quoll	0.002	0.007	0.336	0.000	0.133	1.000
Summer vs Winter						
Brushtail possum	0.436	0.247	1.765	47.214	44.929	0.781
Raven spp.	0.039	0.054	0.721	1.500	2.857	0.850
Pied currawong	0.026	0.042	0.626	0.786	1.786	0.897
Dingo	0.021	0.033	0.651	1.571	0.071	0.936
Red fox	0.012	0.020	0.593	0.000	0.857	0.957
Wedge-tailed eagle	0.008	0.023	0.338	0.429	0.214	0.971
Feral cat	0.007	0.011	0.651	0.357	0.429	0.984
Feral pig	0.006	0.011	0.541	0.214	0.357	0.995
Spotted-tail quoll	0.003	0.010	0.305	0.000	0.286	1.000

Summer vs Spring						
Brushtail possum	0.375	0.223	1.683	47.214	23.600	0.586
Raven spp.	0.126	0.169	0.743	1.500	13.200	0.783
Pied currawong	0.089	0.146	0.607	0.786	6.200	0.921
Dingo	0.034	0.045	0.764	1.571	1.800	0.974
Wedge-tailed eagle	0.006	0.022	0.269	0.429	0.000	0.984
Feral cat	0.005	0.008	0.685	0.357	0.267	0.992
Feral pig	0.005	0.011	0.417	0.214	0.067	0.999
Red fox	0.001	0.003	0.248	0.000	0.067	1.000
Spotted-tail quoll	0.000	0.000	0.000	0.000	0.000	1.000
Autumn vs Winter						
Brushtail possum	0.347	0.223	1.559	27.067	44.929	0.682
Raven spp.	0.047	0.055	0.865	2.333	2.857	0.775
Pied currawong	0.027	0.041	0.646	1.000	1.786	0.827
Feral cat	0.026	0.058	0.454	1.933	0.429	0.879
Red fox	0.021	0.027	0.794	1.400	0.857	0.921
Feral pig	0.017	0.031	0.549	1.200	0.357	0.954
Wedge-tailed eagle	0.011	0.019	0.607	0.800	0.214	0.976
Dingo	0.007	0.014	0.528	0.667	0.071	0.991
Spotted-tail quoll	0.005	0.010	0.457	0.133	0.286	1.000
Autumn vs Spring						
Brushtail possum	0.250	0.174	1.442	27.067	23.600	0.430
Raven spp.	0.138	0.167	0.826	2.333	13.200	0.667
Pied currawong	0.094	0.146	0.641	1.000	6.200	0.827
Dingo	0.030	0.047	0.647	0.667	1.800	0.879

Feral cat	0.026	0.060	0.436	1.933	0.267	0.924
Feral pig	0.017	0.031	0.548	1.200	0.067	0.953
Red fox	0.015	0.028	0.552	1.400	0.067	0.979
Wedge-tailed eagle	0.010	0.018	0.568	0.800	0.000	0.997
Spotted-tail quoll	0.002	0.005	0.377	0.133	0.000	1.000
			Winter vs Spring			
Brushtail possum	0.272	0.192	1.419	44.929	23.600	0.524
Raven spp.	0.119	0.142	0.840	2.857	13.200	0.754
Pied currawong	0.080	0.115	0.689	1.786	6.200	0.908
Dingo	0.023	0.039	0.583	0.071	1.800	0.952
Red fox	0.011	0.016	0.668	0.857	0.067	0.973
Feral cat	0.006	0.009	0.689	0.429	0.267	0.984
Feral pig	0.004	0.005	0.659	0.357	0.067	0.991
Spotted-tail quoll	0.003	0.008	0.326	0.286	0.000	0.996
Wedge-tailed eagle	0.002	0.008	0.273	0.214	0.000	1.000

Table 6. The similarity percentages (SIMPER) analysis demonstrating the contribution of each species to explaining differences between the seasons in scavenging event species composition.

	Average	**SD**	**Ratio**	**AVA**	**AVB**	**CUMSUM**
Summer vs Autumn						
Brushtail possum	0.355	0.293	1.214	30.615	25.500	0.474
Raven spp.	0.238	0.211	1.129	5.154	20.083	0.793
Feral pig	0.084	0.137	0.610	1.846	4.000	0.904
Wedge-tailed eagle	0.039	0.086	0.454	0.769	1.750	0.956
Red fox	0.017	0.025	0.702	0.000	1.167	0.980
Dingo	0.010	0.025	0.388	0.385	0.333	0.992
Pied currawong	0.006	0.022	0.261	0.231	0.000	1.000
Feral cat	0.000	0.000	0.000	0.000	0.000	1.000
Spotted-tail quoll	0.000	0.000	0.000	0.000	0.000	1.000
Summer vs Winter						
Brushtail possum	0.496	0.290	1.711	30.615	86.357	0.694
Raven spp.	0.135	0.154	0.874	5.154	14.214	0.883
Feral pig	0.030	0.072	0.408	1.846	0.714	0.924
Wedge-tailed eagle	0.026	0.071	0.362	0.769	4.429	0.960
Pied currawong	0.017	0.050	0.345	0.231	4.000	0.985
Dingo	0.004	0.014	0.311	0.385	0.000	0.991
Red fox	0.003	0.009	0.293	0.000	0.214	0.995
Spotted-tail quoll	0.002	0.009	0.292	0.000	0.286	0.998
Feral cat	0.001	0.006	0.253	0.000	0.071	1.000
Summer vs Spring						

Raven spp.	0.410	0.310	1.322	5.154	71.000	0.500
Brushtail possum	0.252	0.254	0.993	30.615	14.600	0.807
Pied currawong	0.091	0.162	0.564	0.231	8.133	0.919
Feral pig	0.026	0.047	0.541	1.846	0.733	0.950
Dingo	0.025	0.041	0.608	0.385	2.267	0.980
Wedge-tailed eagle	0.010	0.037	0.283	0.769	0.133	0.993
Spotted-tail quoll	0.005	0.011	0.394	0.000	0.667	0.998
Red fox	0.002	0.006	0.254	0.000	0.133	1.000
Feral cat	0.000	0.000	0.000	0.000	0.000	1.000
Autumn vs Winter						
Brushtail possum	0.440	0.281	1.564	25.500	86.357	0.628
Raven spp.	0.164	0.158	1.041	20.083	14.214	0.862
Feral pig	0.038	0.071	0.530	4.000	0.714	0.916
Wedge-tailed eagle	0.029	0.060	0.483	1.750	4.429	0.957
Pied currawong	0.014	0.048	0.291	0.000	4.000	0.977
Red fox	0.011	0.017	0.652	1.167	0.214	0.992
Spotted-tail quoll	0.002	0.008	0.289	0.000	0.286	0.996
Dingo	0.002	0.005	0.367	0.333	0.000	0.998
Feral cat	0.001	0.005	0.240	0.000	0.071	1.000
Autumn vs Spring						
Raven sp.	0.365	0.276	1.325	20.083	71.000	0.497
Brushtail possum	0.205	0.219	0.939	25.500	14.600	0.776
Pied currawong	0.080	0.149	0.537	0.000	8.133	0.885
Feral pig	0.036	0.055	0.649	4.000	0.733	0.933
Dingo	0.021	0.037	0.565	0.333	2.267	0.962

Wedge-tailed eagle	0.014	0.023	0.598	1.750	0.133	0.980
Red Fox	0.010	0.015	0.691	1.167	0.133	0.994
Spotted-tail quoll	0.004	0.011	0.392	0.000	0.667	1.000
Feral cat	0.000	0.000	0.000	0.000	0.000	1.000
Winter vs Spring						
Brushtail possum	0.353	0.245	1.442	86.357	14.600	0.469
Raven spp.	0.290	0.248	1.166	14.214	71.000	0.853
Pied currawong	0.068	0.120	0.567	4.000	8.133	0.943
Dingo	0.015	0.030	0.510	0.000	2.267	0.963
Wedge-tailed eagle	0.014	0.049	0.290	4.429	0.133	0.982
Feral pig	0.006	0.009	0.614	0.714	0.733	0.990
Spotted-tail quoll	0.005	0.010	0.474	0.286	0.667	0.996
Red Fox	0.002	0.007	0.373	0.214	0.133	0.999
Feral cat	0.001	0.003	0.247	0.071	0.000	1.000

Table 7. The Akaike information criterion (AIC) ranking of each of the models for investigation events species richness (top) and scavenging events species richness (bottom). Parsimoniously competitive models (ΔAICc < 2.00) are denoted in *italics*.

No.	**Model**	**df**	**logLik**	**AICc**	**ΔAICc**	**weight**
Investigation Events Species Richness						
1	*Seasons*	*4*		*192.082*	*0.00*	*0.292*
2	*Null (intercept only)*	*1*		*192.131*	*0.05*	*0.285*
3	*Seasons + Altitude*	*5*		*193.360*	*1.28*	*0.154*
4	*Altitude*	*2*		*193.537*	*1.46*	*0.141*
Scavenging Events Species Richness						
1	*Null (intercept only)*	*1*		*194.288*	*0*	*0.400*
2	*Seasons*	*4*		*195.294*	*1.01*	*0.241*
3	*Altitude*	*2*		*195.546*	*1.26*	*0.213*
4	Seasons + Altitude	5		196.441	2.15	0.136

Table 8. The base generalised linear model (GLM) for investigation event species richness (top) and scavenging event species richness (bottom). Significant p-values ($p < 0.05$) are denoted in **bold**.

Variables	**Estimate**	**Std. error**	**t value**	***p***
		Investigation Events		
Intercept	1.852	0.531	3.487	**<0.001**
Spring	-0.236	0.122	-1.933	0.053
Summer	-0.258	0.125	-2.055	**0.040**
Winter	-0.264	0.125	-2.104	**0.035**
Altitude	<0.001	<0.001	-0.853	0.394
		Scavenging Events		
Intercept	1.498	0.779	1.922	0.055
Spring	0.293	0.179	1.640	0.101
Summer	-0.095	0.202	-0.470	0.638
Winter	0.174	0.186	0.934	0.350
Altitude	< - 0.001	<0.001	-0.920	0.358

Table 9. The Akaike information criterion (AIC) ranking of each of the models for time to first detection (top) and time to first scavenging (bottom). Parsimoniously competitive models (ΔAICc < 2.00) are denoted in *italics*.

No.	**Model**	**df**	**logLik**	**AICc**	**ΔAICc**	**weight**
Time to First Detection						
1	*Seasons*	*5*	*-282.223*	*575.6*	*0.00*	*0.730*
2	*Seasons + Altitude*	*7*	*-279.511*	*577.6*	*1.99*	*0.269*
3	Null (intercept only)	1	-292.747	589.7	14.11	0.001
4	Altitude	4	-291.294	592.5	16.92	0.000
Time to First Scavenging						
1	*Seasons*	*5*	*-330.042*	*671.3*	*0.00*	*0.438*
2	*Null (intercept only)*	*2*	*-333.864*	*672.0*	*0.65*	*0.317*
3	*Seasons + Altitude*	*9*	*-325.495*	*673.2*	*1.93*	*0.167*
4	Altitude	5	-331.655	674.8	3.46	0.078

Table 10. The base generalised linear model (GLM) for time to first detection (top) and time to first scavenging (bottom). Significant p-values ($p < 0.05$) are denoted in **bold**.

Variables	**Estimate**	**Std. error**	**t value**	***p***
		Time to First Detection		
Intercept	3.796	0.260	14.621	< **0.001**
Spring	-0.308	0.369	-0.835	0.404
Summer	1.148	0.373	3.077	**0.002**
Winter	-0.729	0.374	-1.948	0.051
Variable	**edf**	**Ref.df**	**Chi.sq**	***p***
Altitude	2.265	2.867	5.16	0.13
		Time to First Scavenging		
Intercept	5.255	0.281	18.674	< **0.001**
Spring	-0.650	0.387	-1.681	0.092
Summer	0.354	0.397	0.893	0.372
Winter	-0.808	0.392	-2.064	**0.039**
Variable	**edf**	**Ref.df**	**Chi.sq**	***p***
Altitude	3.294	4.115	9.227	**0.048**

Table 11. The Tukey's honest significance test of the base generalised linear model (GLM) for time to first detection (top) and time to first scavenging (bottom). Significant p-values ($p < 0.05$) are denoted in **bold**.

Contrast	**Estimate**	**SE**	**df**	**t ratio**	***p***
Time to First Detection					
Autumn - Spring	0.308	0.448	51.7	0.688	0.901
Autumn - Summer	-1.148	0.453	51.7	-2.535	0.066
Autumn - Winter	0.729	0.454	51.7	1.605	0.385
Spring - Summer	-1.456	0.453	51.7	-3.216	**0.012**
Spring - Winter	0.421	0.456	51.7	0.922	0.793
Summer - Winter	1.876	0.461	51.7	4.071	**< 0.001**
Time to First Scavenging					
Autumn - Spring	0.650	0.506	47.7	1.286	0.576
Autumn - Summer	-0.354	0.519	47.7	-0.683	0.903
Autumn - Winter	0.808	0.512	47.7	1.578	0.400
Spring - Summer	-1.004	0.499	47.7	-2.013	0.198
Spring - Winter	0.158	0.494	47.7	0.320	0.989
Summer - Winter	1.163	0.507	47.7	2.291	0.114

Table 12. The Akaike information criterion (AIC) ranking of each of the models for scavenging activity. Parsimoniously competitive models (ΔAICc < 2.00) are denoted in *italics*.

No.	Model	df	logLik	AICc	ΔAICc	weight
1	*Seasons*	*5*	*-4279.252*	*8568.5*	*0.00*	*0.690*
2	*Seasons + Altitude*	*6*	*-4279.054*	*8570.1*	*1.61*	*0.309*
3	Null (intercept only)	2	-4289.519	8583.0	14.53	0.000
4	Altitude	3	-4289.413	8584.8	16.32	0.000

Table 13. The base generalised linear model (GLM) for scavenging activity. Significant p-values ($p < 0.05$) are denoted in **bold**.

Variables	**Estimate**	**Std. error**	**z value**	***p***
Spring	0.776	0.260	2.981	**0.003**
Summer	-0.358	0.274	-1.307	0.191
Winter	0.667	0.264	2.529	**0.011**
Altitude	-0.059	0.093	-0.628	0.530

Table 14. The Tukey's honest significance tests of the base generalised linear model (GLM) for scavenging activity. Significant p-values ($p < 0.05$) are denoted in **bold**.

Contrast	**Estimate**	**SE**	**df**	**z ratio**	***p***
Autumn - Spring	-0.776	0.260	Inf	-2.981	**0.015**
Autumn - Summer	0.358	0.274	Inf	1.307	0.558
Autumn - Winter	-0.667	0.264	Inf	-2.529	0.056
Spring - Summer	1.134	0.265	Inf	4.278	**< 0.001**
Spring - Winter	0.109	0.255	Inf	0.429	0.974
Summer - Winter	-1.025	0.269	Inf	-3.813	**< 0.001**

Table 15. The Akaike information criterion (AIC) ranking of each of the models for investigation event duration (top) and scavenging event duration (bottom). Parsimoniously competitive models (ΔAICc < 2.00) are denoted in *italics*.

No.	**Model**	**df**	**logLik**	**AICc**	**ΔAICc**	**weight**
			Investigation Event Duration			
1	*Null (intercept only)*	*3*	*-2567.223*	*5140.5*	*0.00*	*0.526*
2	*Seasons*	*6*	*-2565.157*	*5142.3*	*1.89*	*0.204*
3	Altitude	4	-2567.223	5142.5	2.01	0.193
4	Seasons + Altitude	7	-2565.140	5144.3	3.87	0.076
			Scavenging Event Duration			
1	*Seasons*	*6*	*-13666.05*	*27344.1*	*0.00*	*0.592*
2	*Seasons + Altitude*	*7*	*-13665.47*	*27345.0*	*0.86*	*0.385*
3	Null (intercept only)	3	-13672.62	27351.3	7.14	0.017
4	Altitude	4	-13672.57	27353.2	9.04	0.006

Table 16. The base generalised linear model (GLM) for investigation event duration (top) and scavenging event duration (bottom). Significant p-values ($p < 0.05$) are denoted in **bold**.

Variables	**Estimate**	**Std. error**	**t value**	***p***
Investigation Event Duration				
Intercept	-0.045	0.151	-0.298	0.765
Spring	-0.027	0.207	-0.130	0.897
Summer	0.357	0.216	1.657	0.098
Winter	0.196	0.209	0.937	0.349
Altitude	0.014	0.075	0.182	0.856
Scavenging Event Duration				
Intercept	2.683	0.124	21.678	**< 0.001**
Spring	-0.639	0.163	-3.925	**< 0.001**
Summer	-0.257	0.179	-1.439	0.150
Winter	-0.238	0.165	-1.445	0.149
Altitude	0.063	0.059	1.077	0.282

Table 17. The Tukey's honest significance test of the base generalised linear model (GLM) for investigation event duration (top) and scavenging event duration (bottom). Significant p-values ($p < 0.05$) are denoted in **bold**.

Contrast	**Estimate**	**SE**	**df**	**z ratio**	***p***
Investigation Event Duration					
Autumn - Spring	0.027	0.207	Inf	0.130	1.000
Autumn - Summer	-0.357	0.216	Inf	-1.657	0.347
Autumn - Winter	-0.196	0.209	Inf	-0.937	0.785
Spring - Summer	-0.384	0.210	Inf	-1.825	0.261
Spring - Winter	-0.223	0.204	Inf	-1.093	0.694
Summer - Winter	0.161	0.213	Inf	0.755	0.874
Scavenging Event Duration					
Autumn - Spring	0.639	0.163	Inf	3.925	**< 0.001**
Autumn - Summer	0.257	0.179	Inf	1.439	0.475
Autumn - Winter	0.238	0.165	Inf	1.445	0.472
Spring - Summer	-0.382	0.167	Inf	-2.183	0.102
Spring - Winter	-0.401	0.152	Inf	-2.643	**0.041**
Summer - Winter	-0.019	0.169	Inf	-0.112	1.000

Chapter 3 – Absence of apex predator top-down effects on mesoscavengers

Abstract

Apex predators are renowned for their abilities to structure ecological communities and regulate ecosystems. Conventional approaches to ecological theories regarding apex predators often only consider their predatory capabilities. However, despite their name, most apex predators scavenge and whilst largely opportunistic, scavenging rates can be substantial in response to low prey availability. Consequently, within a scavenging context, predators can influence the scavenging behaviours of other species as well as scavenging dynamics more broadly. Further still, scavenger guilds are composed of a unique and diverse group of taxa, and thus, the top-down scavenging effects of apex predators have the potential to result in novel inter-specific interactions surrounding carrion. Despite the presence of and scavenging by an apex predator, the dingo (*Canis dingo*), scavenging dynamics within Australian Alps have been demonstrated to be dominated by three low ranking mesoscavengers, the brushtail possum (*Trichosurus vulpecula*) and two raven species (*Corvus coronoides* and *Corvus mellori*) – *Chapter 2*. Therefore, here, top-down scavenging effects exerted by the dingo were assessed regarding potential impacts on the scavenging activities of these mesoscavengers. Overall, dingoes were found to scavenge at low rates and no evidence was found to suggest dingoes influenced the scavenging behaviours of brushtail possums or raven spp. This raised several questions regarding the extent to which dingoes scavenge when anthropogenically suppressed, and in response to an overabundance of carrion. Each of these concepts are discussed herein, with a particular focus on density dependent predator theories, and how each scenario may determine the extent to which dingoes can exert top-down scavenging effects.

Introduction

Globally, apex predators are one of the most recognised and studied groups of taxa due to their status as keystone species i.e., species that drive community dynamics and structure food webs within ecosystems [1]. The predatory activities of such species can directly regulate prey populations and their recognition as potentially dangerous predators can indirectly influence movement and habitat use by other species [2]. Both of these mechanisms facilitate trophic cascades which can maintain biodiversity in both the animal and plant kingdoms [3, 4]. These types of cascades are present in terrestrial, aquatic, and marine ecosystems. Some well cited examples include the suppression of elk (*Cervus canadensis*) populations following the reintroduction of grey wolves (*Canis lupus*) to Yellowstone National Park [5, 6], and the maintenance of near shore community biodiversity in the Aleutian Islands (Alaska) by sea otters (*Enhydra lutris*) [7].

Predators are typically classified as either an apex predator or mesopredator. The former are species characterised by their position at the top of the food chain and lack of natural predators [8], whilst the later are “any midranking predator in a food web, regardless of its size or taxonomy” [9]. The presence or absence of either species group within ecosystems can cause trophic cascades that can result from their interspecific interactions or lack thereof [8]. The mesopredator release hypothesis explains how constraints to the population growth of mesopredators, which are controlled by competitively dominant apex predators, are released following a decline in apex predator population levels [10-12]. Theories such as this, and indeed others, demonstrate how the preservation of apex predators alone, because of their high trophic level, can have flow-on effects on ecosystem health, biodiversity, and the conservation of other subordinate species [13].

Most conventional approaches to ecological theories regarding apex predators, however, often only consider their role as predatory species [2]. Whilst this predatory role is undoubtably crucial to a plethora of essential ecosystem services globally, the other roles that apex predators play are often overlooked [14, 15]. Despite their name, apex predators are not purely predatory, most, if not all, scavenge on dead animal remains (carrion) at some point in their lifetime. This phenomenon is mostly opportunistic, however, scavenging rates can be substantial in response to low prey availability [16]. For example, in Scandinavia, wolverine (*Gulo gulo*) feeding strategies (i.e., predation vs scavenging) were demonstrated to be seasonally dependent on prey body condition and carrion supply which in combination promoted predation during summer and scavenging during winter [17]. This flexibility in diet is important to distinguish, especially so regarding predators, because there is a clear differentiation in the fitness outcomes of scavenging which results in only a fraction of the energy costs associated with predation [18, 19]. Although only recently considered, it is, therefore, evident that scavenging may provide an important energy pathway for predators. Not only does this have cause to force the revaluation of the diets and energy budgets of predators but also expands the plethora of ecosystem processes dictated by predators to include scavenging.

Apex predators have most often been credited with dictating scavenging dynamics within ecosystems via the provision of carrion from their partially consumed prey [18]. Whilst this is an important consideration, it overshadows the fact that predators can also dictate scavenging dynamics via their own scavenging activities surrounding non-prey killed carrion [18]. Apex predators, similarly to vultures (obligate scavengers), can rapidly consume carrion biomass, including bones, and their presence at carrion can, therefore, accelerate carcass decomposition [20]. Scavenging on non-prey killed carrion by dominant scavenging predators can also directly force other scavengers from carrion (competition) and/or influence how they access carrion (landscape of fear) [19, 21-26]. For instance, the black bear (*Ursus americanus*), was demonstrated to influence the structure and composition of its scavenger guild in northern California [25]. Specifically, the presence of black bears at carcasses limited scavenger species richness, significantly reduced sum scavenging time by other scavengers, and increased the nestedness of the scavenger guild [25]. These types of top-down effects are often extreme enough that many mesoscavengers utilise spatial and temporal measures, as well as flexible behavioural strategies, to avoid confrontations with competitively dominant apex scavengers and exploit carrion [25, 27].

Within a scavenger guild a unique selection of species are present [28]. There is potential for dominant scavenging predators to influence the scavenging behaviours and activities of any of these species, be it directly or indirectly. Consequently, a suite of novel interspecific interactions can occur that are not purely considered competitive interactions strictly between predators, as discussed above and more broadly in the literature. The 'mesoscavenger release hypothesis' was recently coined and is essentially a reframing of the 'mesopredator release hypothesis' within a scavenging context [21]. Here, the importance of recognising predators also as scavengers is emphasised because the dynamics of such a 'mesoscavenger release' are equally as complex as the conventional 'mesopredator release' and have the potential to impact a much wider breadth of taxa [22, 25, 26, 28, 29]. For instance, in Tasmania (an island state of Australia), recent disease related declines in the population of Tasmanian devils (*Sarcophilus harrisii*), Tasmania's native marsupial apex predator and scavenger, has had cascading effects on other scavengers and scavenging dynamics [26, 29]. As a result, in the areas where Tasmanian devil density is low, a native avian scavenger, the forest raven (*Corvus tasmanicus*), scavenged longer on carcasses, whilst an invasive mesopredator, the feral cat (*Felis catus*), scavenged at more carcasses. This mesoscavenger release highlighted how apex predators within a scavenging context can exert top-down effects on a novel selection of species only present within scavenger guilds.

The Tasmanian devil is, however, absent from mainland Australia. The dingo (*Canis dingo*), despite having a brief evolutionary and ecological history in Australia (~ 4000 years) [30], has established itself as mainland Australia's dominant apex predator. Many government agencies and agricultural communities considering the dingo a pest species. However, the dingo can have a strong regulatory role within many Australian ecosystems that spans multiple trophic levels and includes the beneficial control of overabundant prey (i.e., kangaroo – *Macropodidae*) [31, 32] and the maintenance of biodiversity via suppression of invasive mesopredators (i.e., red fox – *Vulpes vulpes* and feral cat – *Felius catus*) [30, 33-36]. The regulatory role of the dingo is not only localised to specific ecosystems either, but is also exerted at a continental scale [37]. Whilst there has been a strong focus on the predation effects of dingoes, a common trend in the global predator-based literature, the dingo is also an extremely effective scavenger [38-41]. Dingoes, like most predators, are facultative scavengers and will opportunistically scavenge on carrion when available [38], however, carrion can become a crucial part of their diet during food shortages [41].

Numerous studies have documented the scavenging activities of dingoes [38, 41-43], the most comprehensive of which experimentally monitored dingo scavenging across three Australian ecosystems (alpine, forest, and desert) [38]. This study by Spencer and Newsome (2021) found that dingo scavenging dynamics were highly variable and complex, but intrinsically linked to the seasons, and that in certain contexts dingoes could substantially contribute to carrion biomass loss. However, Spencer and Newsome (2021) did note a limitation of their study being that the top-down scavenging effects of dingoes were not assessed, and thus, emphasised that additional seasonal replications may yield more detailed information on the role of dingoes as dominant scavenging predators. Of relevance here is Forsyth et al.'s 2014 study that found dingoes to limit the spatial and temporal availability of carcasses to an invasive mesoscavenger, the red fox [40]. Also of relevance, but to a lesser degree, are the findings of Schlacher et al.

(2014) which demonstrated domestic dogs (*Canis lupus familiaris*), close relatives of the dingo, to outcompete native scavengers for carrion on urban beaches [44]. However, these are the only two such studies describing the top-down scavenging effects of dingoes, and indeed, a recent review of canid scavenging effects by Wirsing and Newsome (2020) found that the scavenging effects of most canid species remain little understood [39]. Furthermore, the top-down effects of dingoes in general (i.e., those not limited to scavenging) are often only considered regarding larger mesopredators and/or competitors [30, 33-37, 45]. This makes it difficult to transfer such findings to a scavenging context given the diverse selection of species present within scavenger guilds. Therefore, the fear effects that dingoes exert surrounding carrion and its impacts on more novel scavenger species (i.e., potential prey) is an area that warrants further attention.

The brushtail possum (*Trichosurus vulpecula*) and raven spp. (*Corvus coronoides* and *Corvus mellori*) are such facultative scavengers that could potentially have novel interspecific interactions with dingoes surrounding carrion. As outlined in *Chapter 2*, these species were the most abundant scavengers observed in the Australian Alps and dominated the scavenging dynamics of the guild. When scavenging, these species must consider the threats posed to them by dominant scavenging predators such as the dingo. A key question is, therefore, whether the high rates of scavenging by brushtail possums and raven spp. are regulated by the top-down scavenging effects of dingoes. To understand if such a scavenging dynamic was important within the Australian Alps, firstly, the baseline scavenging rates of the dingo at two temporal scales (daily and seasonal) was determined. By understanding the ways in which an apex predator utilises an opportunistic resource, the extent to which dingo scavenging effects impact the scavenging of other species can then be established. Specifically, the presence of dingoes at carcasses, whether it be to investigate or scavenge, was analysed to determine how it influences the probability and duration of scavenging by brushtail possums and raven spp.. Broadly, it was predicted that predator avoidance (i.e., the landscape of fear [46]) behaviours would determine the scavenging dynamics of brushtail possums and raven spp. surrounding carrion [24]. Specifically, it was expected that at carcasses visited by dingoes, brushtail possums would investigate carcasses more often than scavenging on the carcass itself. In addition, it was also predicted that at carcasses visited by dingoes, brushtail possum scavenging bouts would be of shorter duration. Similar results were expected for raven spp., however, to a lesser degree given their more effective predator avoidance abilities (flight), and thus, lower perceived risk to predation. This study provides insights into the role an apex predator has within a scavenger guild and uncovers the strength of intraspecific interactions between predator and novel prey occurring around carrion.

Methods

Due to both *Chapters 2* and *3* being formatted for submission to relevant scientific journals, there is unavoidable repetition of methods between the two chapters.

Study site

This study was conducted in Kosciuszko National Park, located in southern New South Wales, Australia. This region includes many of the highest peaks and ranges within Australia's Great Dividing Range, including Australia's highest peak – Mount Kosciuszko. The landscape is delineated into three altitudinally distinct ecological communities – montane (500m-1500m) subalpine (1500m-1850m), and alpine (1850m-2228m) [47]. This work was undertaken within the montane zone (between approximately 1000m – 1500m) which is characterised by forest stands dominated by snow gum (*Eucalyptus pauciflora*) in association with various other *Eucalyptus* species.

Ethics, licenses, and permits

The following described work received all required ethics, licenses, and permits approved by the relevant authorities (i.e., The University of Sydney; New South Wales Office of Environment and Heritage; and New South Wales National Parks and Wildlife Services). All kangaroo carcasses used for the purposes of this research were sourced fresh and locally from existing authorised and legally approved management culls that are conducted to control overabundant kangaroo populations.

Fieldwork

A 15 km transect was established through Kosciuszko National Park along which all carcass monitoring took place (Figure 1). This transect ran northeast – southwest from a border region of the national park inwards towards its interior and was selected due to its accessibility (i.e., road access) and because it is a relatively undisturbed area with little human activity. Monitoring periods were established to coincide with the four seasons: autumn – March 2020; winter – July 2020; spring – October 2020; summer – January 2021. During each season, 15 sites were established along the transect, separated by approximately 1 km from the nearest sites monitored within the same season and approximately 250m from the nearest sites monitored during other seasons (60 different sites in total; Figure 1). The separation of the sites as such ensured a level of spatial independence and it prevented habituation of scavengers to a carrion source location [38, 48-50].

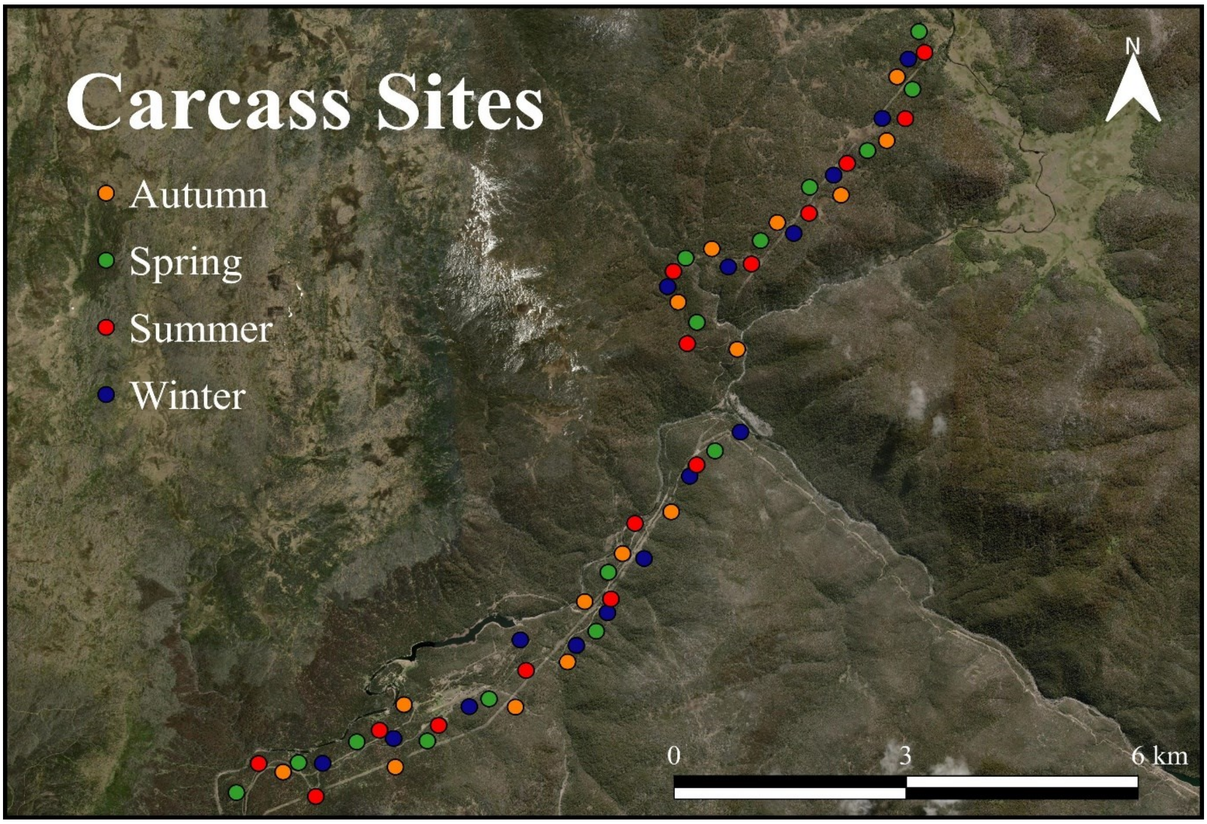

Figure 1. Location of the monitoring transect along which all 60 carcass sites were established within Kosciuszko National Park (red = summer, orange = autumn, blue = winter, green = spring).

Within each seasonal monitoring period, one fresh eastern grey kangaroo carcass was placed at each site (15 total). The carcasses ranged in weight from 10kg-70kg and on average were 28.3kg (± 1.498 – standard deviation). Each carcass was secured, using wire ties, to star pickets driven into the ground to ensure they remained in situ to be monitored for 60 days [38, 48, 49]. Vertebrate scavenger activity was monitored at each site using a Reconyx PC800 Hyperfire™ remote camera. Each camera was placed on a free-standing star picket three meters north of the carcass – the southern aspect of the cameras decreased exposure to direct sunlight which would otherwise reduce image quality. The cameras were calibrated to take photographs continuously (approximately one image per second) when triggered by thermal movement (i.e., rapid-fire, no wait period). These approaches and methods follow those previously used in field-based scavenging research [38, 48-54].

Analyses

Remote camera images were analysed for species presence and the number of individuals of a species present. In order to determine distinct visitations of species, an ‘event’ was characterised as a visitation by a species that occurred more than 10 minutes after the last visitation by that same species. Only species-specific events could be characterised because identification of individuals for most species was not possible. An event was characterised as a ‘scavenging event’ if the species present scavenged on the monitored carcass in at least one of the remote camera images consisting of that event, otherwise the event was characterised as an ‘investigation event’. Data from species recorded to have scavenged at least once were included in the statistical analyses.

The R software environment (version 1.4.1717) was used for all statistical analyses. Similarly to *Chapter* 2, scavenger activity (i.e., probability of a scavenger investigating vs scavenging a carcass; binomial distribution), and investigation and scavenging event duration (in minutes;

Gamma distribution) were again used as response variable. However, these variables were only modelled species specifically for each of the scavengers in question – the dingo, brushtail possum, and raven spp.. For the dingo, each of the response variables were modelled only against the explanatory variable of season. For the brushtail possum and raven spp., each of the response variables were modelled against the explanatory variables of season and dingo presence. Dingo presence was a binary explanatory variable that simply recorded whether any given monitored carcass was visited by a dingo (1) or not visited by a dingo (0). Altitude was excluded from these models given that it was demonstrated to be insignificant in Chapter 2. These models were constructed twice, once using only investigation events and once using only scavenging events. Only one model was constructed for scavenger activity as it is a binomial response variable (either investigation; 0, or scavenging; 1) designed specifically to determine the probability of either an investigation event or scavenging event.

The relationships of each of these scavenging response variables with the explanatory variables of season and dingo presence were modelled using either generalised linear models (GLM; R Package 'lme4' [55]) or generalised linear mixed models (GLMM; R Package 'lme4' [55]), and in the case of poorly fit models generalised additive models were utilised (GAM; R Package 'mgcv' [56]). To determine the most parsimonious model(s), Akaike information criterion (AIC) [57] was used (ΔAICc level of significance < 2), with model selection facilitated by the utilisation of the dredge function (R Package 'MuMIn' [58]). AIC considers the different combinations of explanatory variables (i.e., combinations of season and presence) within a model and as such the scavenging response variables had four possible models: non-interaction season and dingo presence model ($x \sim y + z$), season model ($x \sim y$), dingo presence model ($x \sim z$), and null model ($x \sim 1$).

Significance testing (*p* level of significance < 0.05) was also undertaken using the base model (i.e., non-interaction season and dingo presence model – $x \sim y + z$) to determine which explanatory variables (seasons and/or dingo presence) and/or their levels (summer, autumn, winter, spring) were important in explaining each of the scavenging response variables. To yield additional information from these models, Tukey's honest significance tests were used to determine which seasons were significantly different from one another regarding the modelled scavenging response variable (R Package emmeans) [59].

Results

Of the 60 carcass sites monitored, remote camera data was gathered for 58 – remote camera data for two sites (one during winter and one during summer) were lost due to theft and camera failure. In total, there were 247,985 images of raven spp., 225,052 images of brushtail possums, and 19,772 images of dingoes. These images recorded 4182 distinct events for brushtail possums, 1866 distinct events for raven spp., and 103 distinct events for dingoes (Figure 2 and 3).

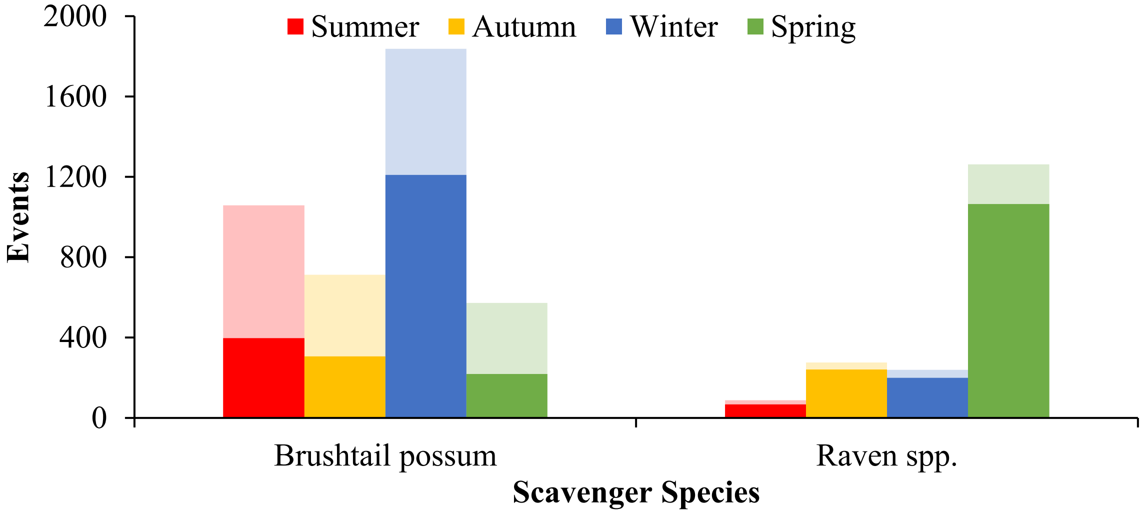

Figure 2. The total number of investigation events (shaded fill) and scavenging events (solid fill) each seasons for brushtail possums and raven spp..

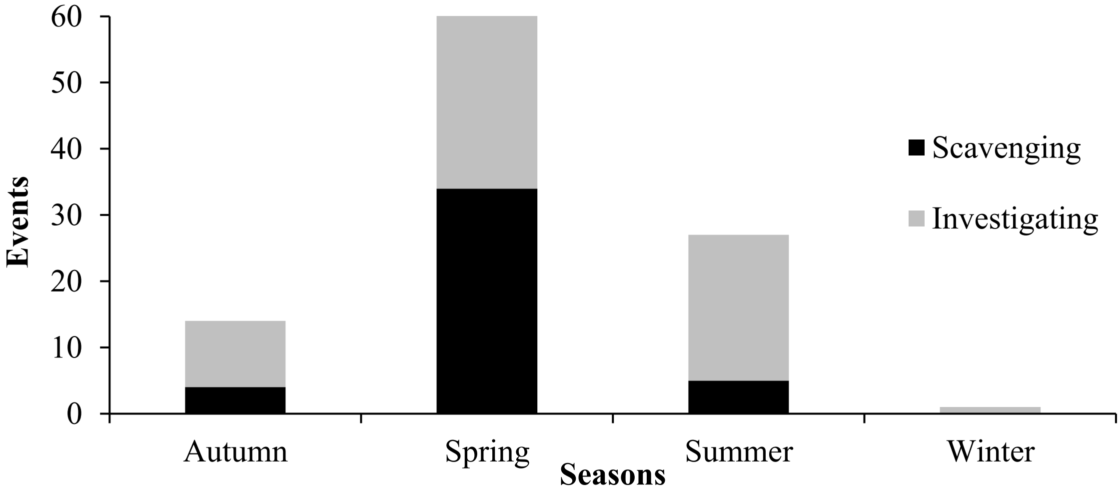

Figure 3. The total number of dingo investigation events (shaded fill) and scavenging events (solid fill) each season.

The diurnal patterns of scavenging revealed a peak in brushtail possum scavenging frequency and duration from the early evening until midnight. Whilst raven spp. scavenging frequency and duration peaked during the middle of the day and late afternoon (Figure 4). Dingoes seemingly showed no preference for the time of day in which they scavenged (Figure 5).

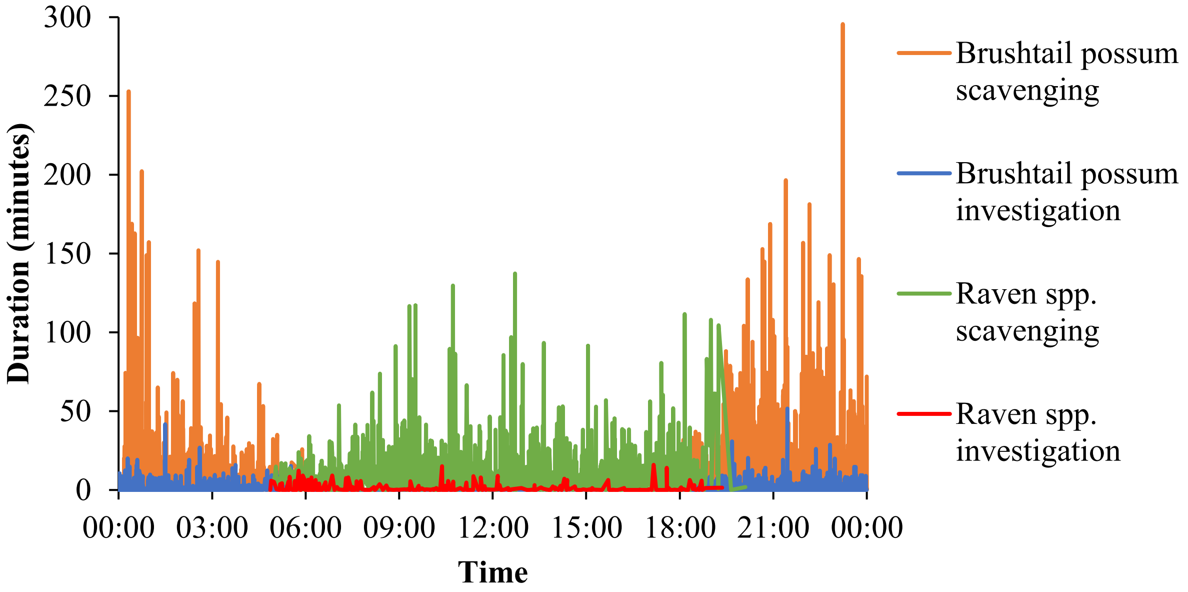

Figure 4. The duration (in minutes) and time (24 hour) of each investigation event and scavenging event for brushtail possums and raven spp..

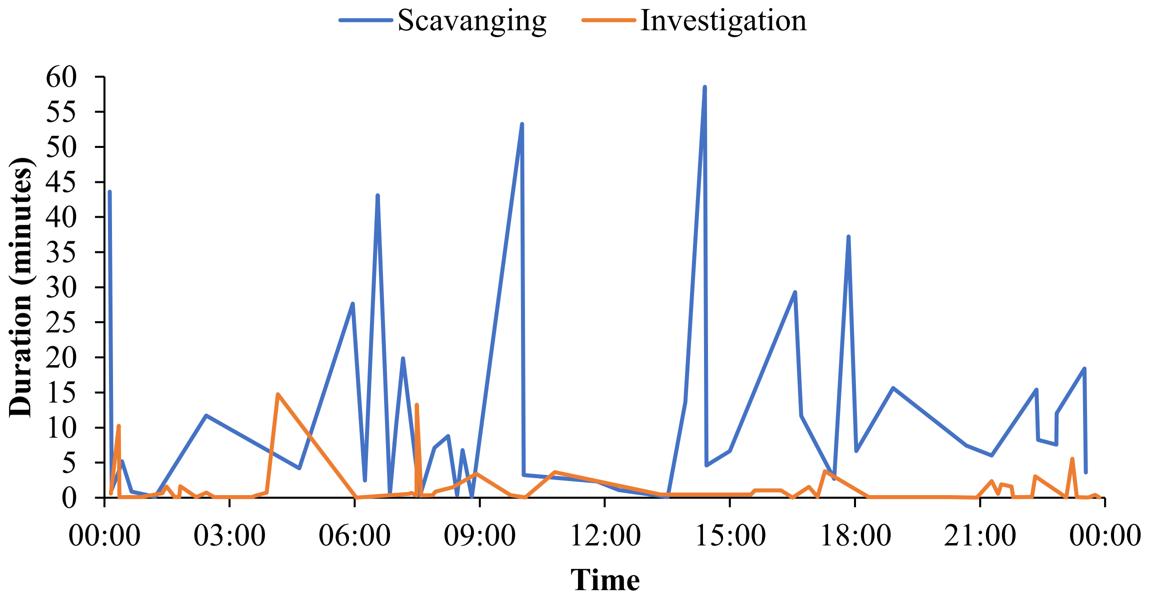

Figure 5. The duration (in minutes) and time (24 hour) of each investigation event (orange) and scavenging event (blue) for dingoes.

Dingo scavenging activity

Two models were parsimoniously competitive (ΔAICc <2) in explaining the variation in dingo scavenging activity (Table S1). The first model was the seasons model (ΔAICc = 0.00) and the second was the null model (ΔAICc = 0.09). The base model was not significant (Figure 4; Table S2 and S3).

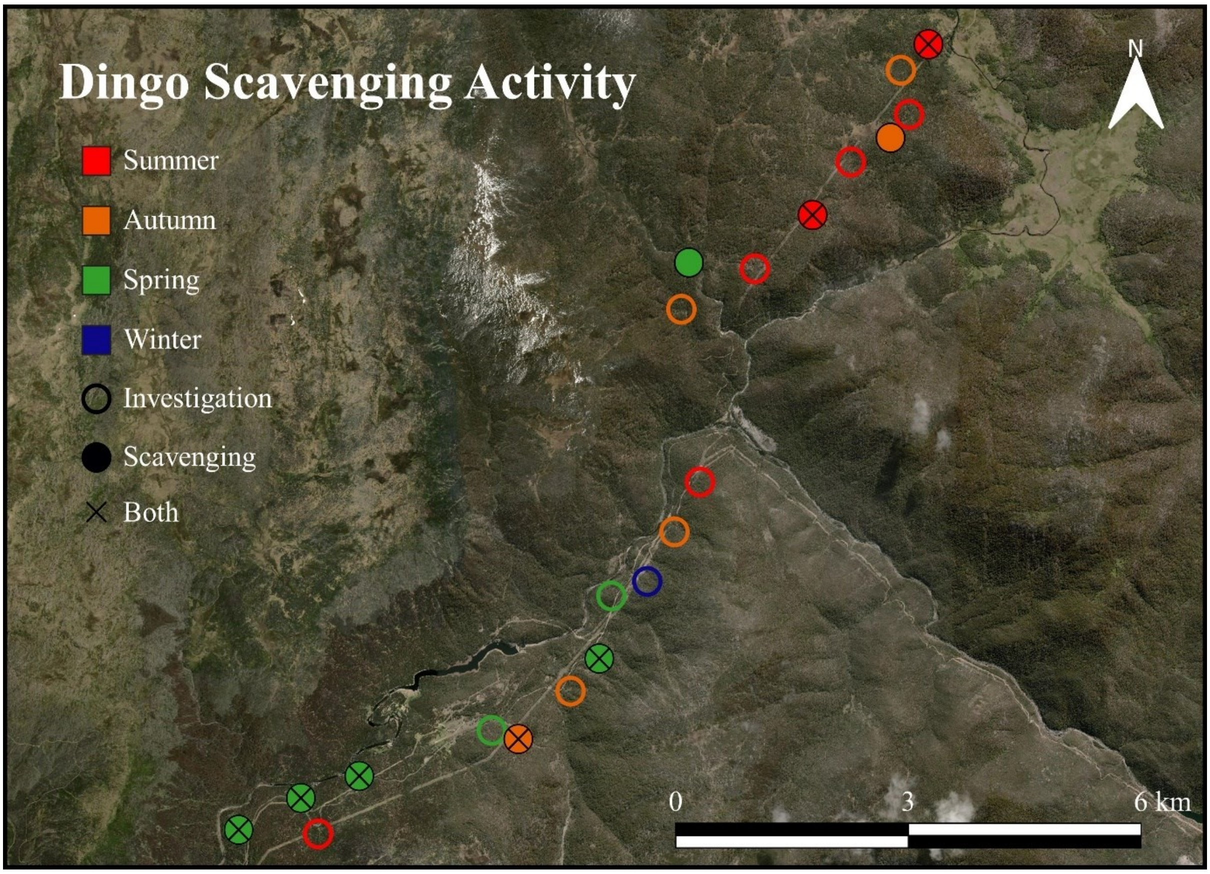

Figure 4. The carcass sites at which dingoes were recorded to investigate (ring), scavenge (circle), or both investigate and scavenge (X) the monitored carcass during each of the seasons.

Dingo investigation and scavenging duration

One model each was parsimoniously competitive (ΔAICc <2) in explaining the variation in dingo investigation duration and scavenging duration (Table S4). Both these models were the null models (ΔAICc = 0.00; Table S4). The base models were not significant (Table S5 and S6).

Brushtail possum scavenging activity

Two models were parsimoniously competitive (ΔAICc <2) in explaining the variation in brushtail possum scavenging activity (Table S7). The first was the season model (ΔAICc = 0.00) and the second the non-interaction season and dingo presence model (ΔAICc = 0.73). The base model demonstrated that winter had a significant effect on brushtail possum scavenging activity ($p = 0.001$; Table S8). Specifically, brushtail possums were 9.855, 6.117, and 7.029 times more likely to scavenge than investigate a carcass during winter than during autumn ($p = 0.003$), spring (p = 0.023), and summer (p = 0.016) respectively (Table S9).

Brushtail possum investigation and scavenging duration

Three models and two models were parsimoniously competitive (ΔAICc <2) in explaining the variation in brushtail possum investigation event duration and scavenging event duration respectively (Table S10). For both investigation and scavenging duration, the first was the null model (ΔAICc = 0.00), the second the dingo presence model (ΔAICc = 0.55 and 0.89), and for investigation event duration the third the non-interaction season and dingo presence model (ΔAICc = 1.56). The base models were not significant (Table S11 and S12).

Raven spp. scavenging activity

All four models were parsimoniously competitive (ΔAICc <2) in explaining the variation in the scavenging activity of raven spp. (Table S13). The first was the null model (ΔAICc = 0.00), the second the dingo presence model (ΔAICc =0.10), the third the season model (ΔAICc =1.15), and the fourth the non-interaction season and dingo presence model (ΔAICc = 1.27). The base model demonstrated that summer had a significant effect on raven spp. scavenging activity ($p = 0.043$; Table S14).

Raven spp. investigation and scavenging duration

Two models were parsimoniously competitive (ΔAICc <2) in explaining the variation in raven spp. investigation event duration (Table S16). The first was the null model (ΔAICc = 0.00) and the second the dingo presence model (ΔAICc = 1.92). The base model was not significant (Table S17 and S18).

Two models were parsimoniously competitive (ΔAICc <2) in explaining the variation in raven spp. scavenging event duration (Table S16). The first was the season model (ΔAICc 0.00) and the second the non-interaction seasons and dingo presence model (ΔAICc 2.00). The base model demonstrated that spring had a significant effect on raven spp. scavenging event duration (*p* = < 0.001; Table S17). Specifically, raven spp. scavenging event duration (in minutes) was 1.066 and 1.050 times shorter during spring than during autumn (*p* = < 0.001) and summer (*p* = 0.029) respectively (Table S18).

Discussion

Despite being the dominant apex predator and scavenger within the Australian Alps, here, the occurrence of dingoes at carcass sites was found to have no influence on the scavenging activities and behaviours of the brushtail possum or raven spp., contradicting initial hypotheses. Of the 58 carcasses monitored during this study only nine were scavenged on by dingoes (15%). This low rate of dingo scavenging, which peaked in spring and did not occur at all in winter, may allow other scavenger species to access carrion resources more easily (e.g., brushtail possums and raven spp. – *Chapter 2*), although further manipulative studies would be needed to demonstrate this link. Broadly, these findings also suggest the need to investigate links between dingo population sizes and densities, the occurrence of dingoes at carcass sites, and the severity of their top-down scavenging effects [21].

Apex predator density at any spatial or temporal scale within a landscape has been demonstrated to be an important determinant of the extent to which they can exert top-down effects [60-64]. In general, higher predator densities result in greater top-down effects [62, 63, 65]. By inference, the lack of top-down scavenging effects exerted by dingoes on brushtail possums and raven spp. in this study could simply be explained by sporadic dingo presence at carcasses (36%), and low dingo scavenging rates (15%), both of which are potentially indicative of low dingo densities. Whilst this is in fact a likely explanation for these results, it does oversimply density-dependent theories related to the top-down effects of predators.

There are many caveats to such theories. For instance, higher predator densities can result in increased inter/intra specific conflict between predators, and consequently, reduce top-down effects on prey species [62, 63]. Such complexities can also occur when considering a predator's density in conjunction with its home range, with both factors sharing an inverse relationship (i.e., as range increases density decreases) [66]. With regards to this study, anecdotal estimates suggest that there were at least three dingo packs recorded at carcass sites during the monitoring, and in fact, an active dingo den was observed within 50 meters of a carcass site at the western end of the transect. However, such observations remain circumstantial without further investigations into dingo population and pack dynamics, densities, home ranges, and the flow-on effects such factors have on other species within a scavenging context and more broadly.

Other studies have also described predator densities specifically regarding dingoes and its bearing on the magnitude of their top-down effects [45, 61, 67-69]. One highly relevant study investigated the scavenging dynamics of dingoes, invasive red foxes, and feral cats in an ecosystem similar to that of the Australian Alps [40]. The study, by Forsyth et al. (2014) [40], recorded dingo scavenging rates much higher than those recorded by this study (70% vs 15%). Despite this, Forsyth et al. (2014) found that dingoes contributed very little to carcass biomass loss and attributed this to low dingo densities, a legacy of intensive dingo control in the region.

Dingoes are also regularly baited and trapped, in and surrounding, Kosciuszko National Park [70, 71]. This likely knocks down dingo pack size and reduces overall species density in the area [72]. Therefore, similarly to Forsyth et al.’s (2014) proposal that anthropogenically controlled low dingo densities hinder the ability of dingoes to contribute to carcass biomass loss, the same concept may be applied to the dingo’s ability to exert top-down effects within scavenger guilds in the Australian Alps. It is apparent that there may be numerous density dependent predator theories that explain the results of this study. Whilst the aims, field design, and results of this study were not geared towards determining which of these theories best explains why dingoes had little effect on the scavenging of brushtail possums and raven spp., such theories are clearly at the foundations of these findings.

In addition to the dingo management regimes undertaken in the Australian Alps, there exists a plethora of invasive species that have also warranted extensive culling programmes to combat their detrimental impacts. The Australian Alps' susceptibility to vertebrate invasion has seen taxa including feral horses (*Equus ferus caballus*), deer (*Cervidae spp.*), feral goats (*Capra hircus*), feral pigs (*Sus scrofa*), and rabbits (*Oryctolagus cuniculus*) become established across the landscape since European colonisation. Often, many of the operations undertaken to suppress the populations of such invasive species leave culled animal carcasses *in situ* to decay. As a consequence of these management practises and operations, the Australian Alps may harbour abnormally high rates of carrion biomass.

The carcasses used in this study were those of Eastern grey kangaroos (*Macropus giganteus*), a native prey species, and thus, predicted to be highly attractive to dingoes. However, the carcasses of the larger culled ungulates (i.e., horses, deer, and pigs) may be more attractive to scavengers in Australia when compared to the smaller and leaner native prey species i.e., kangaroos. Therefore, with a likely abundance of available carrion biomass in the Australian Alps, dingoes may be more attracted to and/or selective for the carcasses of larger invasive species than to those of kangaroos. Once again, this study draws parallels to that of Forsyth et al. (2014), as the presence of unknown hunter shot carcasses in the landscape was also presented as an explanation for a lack of dingo scavenging effects [40]. The presence of other unrelated and unknown carcasses within the landscape is an ever-present variable within any experimental field-based scavenging study. However, it is of particular relevance here given the likely high carrion loads present within the Australian Alps.

Conclusion

It has already been established across much of mainland Australia that dingoes can influence the populations and movements of subordinate species as well as maintain biodiversity and regulate ecosystems [30-37, 45]. It was expected that such apex predator effects would translate into a scavenging context given similar findings for other apex predators globally, specifically canid predators [39]. This, however, was not the case with dingoes seemingly scavenging too little to be able to effectively exert any top-down scavenging effects on either the brushtail possum or raven spp..

These results raise several questions regarding the dingo's ability to scavenge and the frequency with which they do so. However, given past observations of relatively frequent dingo scavenging rates [38, 40], these findings are probably indicative of low dingo densities within the landscape. Additionally, given the high number of large bodied invasive species present within the Australian Alps and the culling programmes they warrant, during culling seasons there may be high carrion loads present within the landscape. Carrion saturation within ecosystems may impact the ability of dingoes to exert top-down scavenging effects and/or may have influenced the results of this study if dingoes are more attracted to the carcasses of invasive species than that of native taxa.

These conclusions provide considerable scope and future direction for subsequent studies investigating dingo scavenging rates and their consequential scavenging effects and whether they may be dependent on dingo densities or carrion loads. Such concepts and suggested approaches are discussed in the following chapter (*Chapter 4 – Conclusion and future directions*).

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Chapter 3 – Supplementary Material

Table 1. The Akaike information criterion (AIC) ranking of each of the models for dingo scavenging activity. Parsimoniously competitive models (ΔAICc < 2.00) are denoted in *italics*.

No.	**Model**	**df**	**logLik**	**AICc**	**ΔAICc**	**weight**
1	*Season*	*5*	*-63.883*	*136.4*	*0.00*	*0.511*
2	*Null (intercept only)*	*2*	*-66.178*	*136.5*	*0.09*	*0.489*

Table 2. The base generalised linear model (GLM) for dingo scavenging activity.

Variables	**Estimate**	**Std. error**	**t value**	***p***
Intercept	-1.109	0.812	-1.366	0.172
Spring	1.292	0.896	1.442	0.149
Summer	-0.713	0.996	-0.716	0.474
Winter	-18.463	1024.000	-0.018	0.986

Table 3. The Tukey's honest significance test of the base generalised linear model (GLM) for dingo scavenging activity.

Contrast	estimate	SE	df	z.ratio	p.value
Autumn - Spring	-1.292	0.896	Inf	-1.442	0.473
Autumn - Summer	0.713	0.996	Inf	0.716	0.891
Autumn - Winter	18.463	1024.000	Inf	0.018	1.000
Spring - Summer	2.005	0.885	Inf	2.265	0.106
Spring - Winter	19.755	1024.000	Inf	0.019	1.000
Summer - Winter	17.750	1024.001	Inf	0.017	1.000

Table 4. The Akaike information criterion (AIC) ranking of each of the models for dingo investigation event duration (top) and scavenging event duration (bottom). Parsimoniously competitive models (ΔAICc < 2.00) are denoted in *italics*.

No.	**Model**	**df**	**logLik**	**AICc**	**ΔAICc**	**weight**
			Investigation Event Duration			
1	*Null (intercept only)*	*3*	*-63.880*	*134.2*	*0.00*	*0.852*
2	Season	6	-62.051	137.7	3.5	0.148
			Scavenging Event Duration			
1	*Null (intercept only)*	*3*	*-144.141*	*294.9*	*0.00*	*0.922*
2	Season	5	-144.104	299.8	4.93	0.078

Table 5. The base generalised linear model (GLM) for dingo investigation event duration (top) and scavenging event duration (bottom). Significant p-values ($p < 0.05$) are denoted in **bold**.

Variables	**Estimate**	**Std. error**	**t value**	***p***
		Investigation Event Duration		
Intercept	0.156	0.450	1.146	0.252
Spring	-0.624	0.527	-1.184	0.236
Summer	0.102	0.543	0.188	0.851
Winter	-1.144	1.493	-0.767	0.443
		Scavenging Event Duration		
Intercept	2.340	0.833	2.808	**0.005**
Spring	-0.209	0.905	-0.231	0.818
Summer	-0.065	1.076	-0.061	0.952

Table 6. The Tukey's honest significance test of the base generalised linear model (GLM) for dingo investigation event duration (top) and scavenging event duration (bottom). There are no comparisons of dingo scavenging event duration (bottom) during winter because dingoes were not recorded to have scavenged during the winter monitoring period.

Contrast	**estimate**	**SE**	**df**	**z.ratio**	**p.value**
Investigation Event Duration					
Autumn - Spring	0.624	0.527	Inf	1.184	0.637
Autumn - Summer	-0.102	0.543	Inf	-0.188	0.998
Autumn - Winter	1.144	1.493	Inf	0.767	0.870
Spring - Summer	-0.726	0.409	Inf	-1.776	0.285
Spring - Winter	0.521	1.450	Inf	0.359	0.984
Summer - Winter	1.247	1.456	Inf	0.857	0.827
Scavenging Event Duration					
Autumn - Spring	0.209	0.905	Inf	0.231	0.971
Autumn - Summer	0.065	1.076	Inf	0.061	0.998
Spring - Summer	-0.144	0.768	Inf	-0.187	0.981

Table 7. The Akaike information criterion (AIC) ranking of each of the models for brushtail possum scavenging activity. Parsimoniously competitive models (ΔAICc < 2.00) are denoted in *italics*.

No.	**Model**	**df**	**logLik**	**AICc**	**ΔAICc**	**weight**
1	*Season*	*5*	*-2537.660*	*5085.3*	*0.00*	*0.574*
2	*Seasons + Dingo Presence*	*6*	*-2537.024*	*5086.1*	*0.73*	*0.398*
3	Null (intercept only)	2	-2544.019	5092.0	6.71	0.020
4	Dingo Presence	3	-2543.986	5094.0	8.64	0.008

Table 8. The base generalised linear model (GLM) for brushtail possum scavenging activity. Significant p-values ($p < 0.05$) are denoted in **bold**.

Variables	**Estimate**	**Std. error**	**t value**	***p***
Intercept	-2.224	0.548	-4.060	**< 0.001**
Spring	0.477	0.633	0.754	0.451
Summer	0.338	0.653	0.518	0.604
Winter	2.288	0.663	3.448	**0.001**
Dingo Presence	-0.559	0.499	-1.120	0.263

Table 9. The Tukey’s honest significance test of the base generalised linear model (GLM) for brushtail possum scavenging activity. Significant p-values ($p < 0.05$) are denoted in **bold**.

Contrast	estimate	SE	df	z.ratio	p.value
Autumn - Spring	-0.477	0.634	Inf	-0.753	0.876
Autumn - Summer	-0.338	0.654	Inf	-0.517	0.955
Autumn - Winter	-2.288	0.665	Inf	-3.442	**0.003**
Spring - Summer	0.139	0.638	Inf	0.218	0.996
Spring - Winter	-1.811	0.638	Inf	-2.839	**0.023**
Summer - Winter	-1.950	0.658	Inf	-2.965	**0.016**

Table 10. The Akaike information criterion (AIC) ranking of each of the models for brushtail possum investigation event duration (top) and scavenging event duration (bottom). Parsimoniously competitive models (ΔAICc < 2.00) are denoted in *italics*.

No.	Model	df	logLik	AICc	ΔAICc	weight
	Investigation Event Duration					
1	*Null (intercept only)*	*3*	*-1947.434*	*3900.9*	*0.00*	*0.404*
2	*Dingo Presence*	*4*	*-1946.703*	*3901.4*	*0.55*	*0.308*
3	*Season + Dingo Presence*	*7*	*-1944.191*	*3902.4*	*1.56*	*0.186*
4	Seasons	6	-1945.792	3903.6	2.75	0.102
	Scavenging Event Duration					
1	*Null (intercept only)*	*3*	*-6686.760*	*13379.5*	*0.00*	*0.555*
2	*Dingo Presence*	*4*	*-6686.199*	*13380.4*	*0.89*	*0.356*
3	Season	6	-6685.953	13383.9	4.41	0.061
4	Seasons + Dingo Presence	7	-6685.714	13385.5	5.95	0.028

Table 11. The base generalised linear model (GLM) for brushtail possum investigation event duration (top) and scavenging event duration (bottom). Significant p-values ($p < 0.05$) are denoted in **bold**.

Variables	**Estimate**	**Std. error**	**t value**	***p***
Investigation Event Duration				
Intercept	-0.557	0.246	-2.261	**0.024**
Spring	0.028	0.313	0.090	0.928
Summer	0.421	0.322	1.309	0.191
Winter	0.617	0.322	1.917	0.055
Dingo Presence	0.451	0.249	1.809	0.070
Scavenging Event Duration				
Intercept	1.996	0.383	5.209	**< 0.001**
Spring	-0.124	0.402	-0.309	0.757
Summer	0.196	0.414	0.474	0.635
Winter	0.156	0.418	0.374	0.709
Dingo Presence	-0.210	0.304	-0.690	0.490

Table 12. The Tukey's honest significance test of the base generalised linear model (GLM) for brushtail possum investigation event duration (top) and scavenging event duration (bottom).

Contrast	estimate	SE	df	z.ratio	p.value
Investigation Event Duration					
Autumn - Spring	-0.028	0.313	Inf	-0.090	1.000
Autumn - Summer	-0.421	0.322	Inf	-1.309	0.557
Autumn - Winter	-0.617	0.322	Inf	-1.917	0.221
Spring - Summer	-0.393	0.324	Inf	-1.213	0.618
Spring - Winter	-0.589	0.328	Inf	-1.796	0.275
Summer - Winter	-0.196	0.336	Inf	-0.584	0.937
Scavenging Event Duration					
Autumn - Spring	0.124	0.402	Inf	0.309	0.990
Autumn - Summer	-0.196	0.414	Inf	-0.474	0.965
Autumn - Winter	-0.156	0.418	Inf	-0.374	0.982
Spring - Summer	-0.320	0.371	Inf	-0.865	0.823
Spring - Winter	-0.280	0.339	Inf	-0.828	0.841
Summer - Winter	0.040	0.355	Inf	0.113	1.000

Table 13. The Akaike information criterion (AIC) ranking of each of the models for raven spp. scavenging activity. Parsimoniously competitive models (ΔAICc < 2.00) are denoted in *italics*.

No.	**Model**	**df**	**logLik**	**AICc**	**ΔAICc**	**weight**
1	*Null (intercept only)*	*2*	*-794.862*	*1593.7*	*0.00*	*0.328*
2	*Dingo Presence*	*3*	*-793.909*	*1593.8*	*0.10*	*0.312*
3	*Season*	*5*	*-792.423*	*1594.9*	*1.15*	*0.185*
4	*Seasons + Dingo Presence*	*6*	*-791.476*	*1595.0*	*1.27*	*0.174*

Table 14. The base generalised linear model (GLM) for raven spp. scavenging activity. Significant p-values ($p < 0.05$) are denoted in **bold**.

Variables	**Estimate**	**Std. error**	**t value**	***p***
Intercept	1.820	0.307	5.934	**< 0.001**
Spring	-0.099	0.337	-0.295	0.768
Summer	-0.865	0.428	-2.021	**0.043**
Winter	-0.100	0.407	-0.246	0.805
Dingo Presence	0.405	0.287	1.410	0.158

Table 15. The Tukey’s honest significance test of the base generalised linear model (GLM) for raven spp. scavenging activity.

Contrast	estimate	SE	df	z.ratio	p.value
Autumn - Spring	0.099	0.337	Inf	0.295	0.991
Autumn - Summer	0.865	0.428	Inf	2.021	0.180
Autumn - Winter	0.100	0.407	Inf	0.246	0.995
Spring - Summer	0.766	0.384	Inf	1.993	0.190
Spring - Winter	0.001	0.362	Inf	0.003	1.000
Summer - Winter	-0.765	0.444	Inf	-1.722	0.312

Table 16. The Akaike information criterion (AIC) ranking of each of the models for raven spp. investigation event duration (top) and scavenging event duration (bottom). Parsimoniously competitive models (ΔAICc < 2.00) are denoted in *italics*.

No.	**Model**	**df**	**logLik**	**AICc**	**ΔAICc**	**weight**
			Investigation Event Duration			
1	*Null (intercept only)*	*3*	*-267.151*	*540.4*	*0.00*	*0.534*
2	*Dingo Presence*	*4*	*-267.083*	*542.3*	*1.92*	*0.205*
3	Season	6	-265.077	542.4	2.06	0.190
4	Seasons + Dingo Presence	7	-265.010	544.4	4.03	0.071
			Scavenging Event Duration			
1	*Season*	*6*	*-5152.495*	*10317.0*	*0.00*	*0.726*
2	*Season + Dingo Presence*	*7*	*-5152.484*	*10319.0*	*2.00*	*0.267*
3	Null (intercept only)	3	-5160.473	10327.0	9.92	0.005
4	Dingo Presence	4	-5160.447	10328.9	11.88	0.002

Table 17. The base generalised linear model (GLM) for raven spp. investigation event duration (top) and scavenging event duration (bottom). Significant p-values ($p < 0.05$) are denoted in **bold**.

Variables	**Estimate**	**Std. error**	**t value**	***P***
Investigation Event Duration				
Intercept	0.456	0.354	1.287	0.198
Spring	-0.246	0.351	-0.702	0.483
Summer	0.156	0.456	0.341	0.733
Winter	-0.733	0.435	-1.683	0.092
Dingo Presence	-0.106	0.286	-0.370	0.711
Scavenging Event Duration				
Intercept	0.065	0.013	4.954	**< 0.001**
Spring	0.064	0.015	4.312	**< 0.001**
Summer	0.015	0.018	0.833	0.405
Winter	0.022	0.017	1.247	0.212
Dingo Presence	0.002	0.013	0.144	0.886

Table 18. The Tukey's honest significance test of the base generalised linear model (GLM) for raven spp. investigation event duration (top) and scavenging event duration (bottom). Significant p-values ($p < 0.05$) are denoted in **bold**.

Contrast	estimate	SE	df	z.ratio	p.value
Investigation Event Duration					
Autumn - Spring	0.246	0.351	Inf	0.702	0.897
Autumn - Summer	-0.155	0.456	Inf	-0.341	0.986
Autumn - Winter	0.733	0.435	Inf	1.683	0.333
Spring - Summer	-0.402	0.397	Inf	-1.011	0.743
Spring - Winter	0.487	0.371	Inf	1.312	0.555
Summer - Winter	0.888	0.467	Inf	1.901	0.228
Scavenging Event Duration					
Autumn - Spring	-0.064	0.015	Inf	-4.312	**< 0.001**
Autumn - Summer	-0.015	0.018	Inf	-0.833	0.839
Autumn - Winter	-0.022	0.017	Inf	-1.247	0.597
Spring - Summer	0.049	0.018	Inf	2.768	**0.029**
Spring - Winter	0.042	0.017	Inf	2.548	0.053
Summer - Winter	-0.006	0.019	Inf	-0.333	0.987

Chapter 4 – Conclusion and future directions

Conclusion

The Australian Alps is a unique system where the dynamics of the scavenging guild are dominated by mesoscavengers despite the presence of an apex predator. As expected, scavenging was seasonal but was ultimately dictated by the seasonality in the scavenging activities of the brushtail possum and raven spp. (mesoscavengers). The time to first detection of carcasses was significantly longer during summer and refuted the hypothesis that olfactory cues (signals greatest during warmer months [1]) increase carcass detectability by vertebrate scavengers during summer. A few theories may explain this, the least speculative of which regards the brushtail possums and raven spp. abilities to rapidly detect carcasses. During autumn, winter, and spring, 93% of the first detections of a carcass were by either brushtail possums or raven spp., but during summer they only accounted for 57%. This reduction in search effort by the brushtail possum and raven spp. during summer, when there is likely an abundance of other available food sources [2-4], may have alone increased the time to first detection of carcasses for the collective scavenger guild. Increased invertebrate scavenging rates during summer have been demonstrated to accelerate carcass decomposition, and in some cases even outcompete vertebrate scavengers' contribution to carrion biomass loss [5-7]. This may also explain why the time to first detection of carcasses was so long during summer as detection by vertebrates becomes increasingly difficult during the later stages of decomposition, and indeed less attractive [8, 9].

Collectively, the scavenger guild was significantly more likely to scavenge than investigate carcasses during both spring and winter. For spring, this was driven by the raven spp. breeding season, during which it was inferred that raven spp. became highly dependent on carcasses to meet increased energetic requirements, as well as for nest construction (i.e., hair/fur), and feeding chicks [10, 11]. The highly frequent but brief raven spp. scavenging events associated with the raven spp. breeding season i.e., frequent trips back and forth between the nest and resources [10], also potentially resulted in significantly shorter scavenging events during spring for the collective scavenger guild. With regards to winter, increased rates of scavenging vs investigation of carcasses were consistent with results observed globally, especially so in northern hemisphere systems, where rates of scavenging increase during winter in response to a lack of other available food sources [2-4]. However, here, this winter-time trend was completely dominated by an increase in the scavenging rates of brushtail possums which scavenged three times more often than during summer and accounted for 81% of all recorded events during winter. The rates of scavenging observed by possums during winter, and indeed during all seasons, provide evidence for considerable carnivory in the brushtail possum.

Despite the presence of the dingo, a dominant scavenging predator [12-15], within the Australia alpine scavenger guild, the scavenging rates, and behaviours of the brushtail possum and raven spp. were unaffected. Together the results of this study demonstrate a seasonal dynamic in the Australian Alps where scavenging is dominated by low ranking mesoscavengers in the notable absence of the dominant scavenging predator. With this in mind, a conceptual framework can be developed, which is of continental significance in Australia given that brushtail possums are the most widespread Australian marsupial and that both raven spp. are also relatively abundant throughout southern-east Australia. Here, autumn represents a relative ‘norm’, where scavenging is not completely dominated by the brushtail possum and raven spp.. Notably, the highest rates of scavenging were also recorded for many of the other scavenger’s species during autumn. Summer recorded the least amount of scavenging for the collective scavenger guild, especially so regarding brushtail possums and raven spp., and this was likely due to an abundance of other available food sources. Winter was completely dominated by a profound increase in the scavenging activities of brushtail possums as they supplemented their diet in the absence of other available food sources. Finally, the scavenging dynamics of spring were best explained by its overlap with the raven spp. breeding season which resulted in just over 1000 frequent but short raven spp. scavenging events. Additionally, dingo scavenging peaked during spring but had no effect on the scavenging of either raven spp. or brushtail possums (Figure 1).

Figure 1. Conceptual diagram indicating the proportion (i.e., size of wedge) of total scavenging events attributed to each season (yellow/top = summer, blue/right = winter, orange/bottom = autumn, and green/left = spring. Within each season wedge the scavenging dynamics of the three dominant mesoscavengers (brushtail possum and raven spp.), as well as other minor scavengers, are shown, where the relative size of the arrow is indicative of interaction strength.

Future directions

Foremost, this study exemplifies the importance of the seasons to ecological processes linked to scavenging. The direction in which seasonal effects impacted scavenging was not always as predicted. These unexpected influences highlight the need for seasonally replicated experimental approaches in field-based scavenging research. This was a primary motivation for undertaking this study as it was obvious that much of the literature describing scavenging ecology in the field inadequately accounted for seasonal effects, underestimating their potential to shape ecosystem scavenging dynamics.

In general, the methods used herein can be utilised to monitor scavenging dynamics surrounding carrion within any given ecosystem globally, and even be further developed to improve field-based designs and yield additional ecological information. Such improvements could include utilising an increased altitudinal gradient that may detect elevational differences in scavenging dynamics missed by this study given the small altitudinal gradient used (500m). This is especially important in scavenging studies elsewhere globally that experience much higher altitudes that those present in Australia. Increased sampling, including through the use of multiple transects, along with repicated studies over multiple years may also help to account for within site and annual variability [16].

A limiting factor of this study was the absence of measures for carrion biomass loss, and thus, species-specific contributions to biomass loss through scavenging were not estimated. Such findings would have been particularly interesting here given that the contributions of the brushtail possums and raven spp. to biomass loss may have been minimal when compared to larger scavengers (e.g., dingo, feral pig, wedge-tail eagle) capable of consuming greater quantities of carrion, despite scavenging less frequently. This means there is considerable scope to further our understanding of species-specific scavenging dynamics within the Australian

Alps by assessing the contributions of different scavengers to carrion persistence within the landscape.

Overall, the widescale carnivory of brushtail possums observed in this study is highly novel given that brushtail possums are commonly considered generalist herbivores/folivores [17-21]. Whilst brushtail possums have been known to on occasion predate insects, depredate birds' nests, and scavenge on carrion [22, 23], generally their diet is known to consist of leaves, flowers, and fruit (commonly *Eucalyptus* and *Acacia* species) [17, 21, 24]. In light of the findings here and their commonly cited dietary classifications, it is recommended that further dietary studies of the brushtail possum are undertaken which may potentially results in the reclassification of their dietary status. An experimental study that utilises scat analyses, a commonly used method in the literature [17, 24], could be particularly insightful here. Such an approach could compare the diets of brushtail possums (determined by scat analyses) that have access to carrion (experimentally placed carcasses) vs those that do not, and this may determine the extent to which carrion can supplement or even substitute other common food sources.

Seemingly, the raven spp. within the Australian Alps were somewhat dependent on carrion as both a source of energy and nesting material during the breeding season. Very little work has been done to determine how carrion biomass within an ecosystem (year to year) may affect the breeding success of facultative scavengers [7]. This is an area that demands future attention given the results of this study and also those elsewhere regarding raven spp. [10]. A similar approach to that discussed above regarding brushtail possums (i.e., access vs exclusion to carrion) could also be utilised here for comparisons of raven spp. breeding success across multiple breeding seasons.

Of global relevance is the seemingly low rates of dingo scavenging in the Australian Alps and the consequential lack of top-down scavenging effects exerted by an apex predator surrounding carrion. This raises several questions regarding how dominant scavenging predators affect scavenging dynamics under different scenarios. For this reason, specifically, there is a need for simultaneous comparisons of scavenging effects exerted by dominant scavenging predators in ecosystems where the predators are not subject to control vs ecosystems where predators are anthropogenically controlled or are already extirpated. Such comparisons would be highly valuable globally given the unique and varying circumstances under which apex predators exists. These findings would also assist in determining whether the lack of scavenging and scavenging effects by the dingo in the Australian Alps, is unique, or part of a more global trend, where the abilities of apex predators to control and regulate food web dynamics within ecosystems are being negatively impacted by anthropogenic activities [25-30].

The density dependent predator theories that were likely important to the lack of top-down scavenging effects exerted by dingoes in this study, provide a strong foundation for such comparative predator studies recommended above [31, 32]. Indeed, such studies have already been undertaken in Tasmania where a reduction in the density of Tasmanian devils resulted in a mesoscavenger release of forest ravens and feral cats [33, 34]. These studies exemplify such an approach that can link density dependent predator theories with scavenging and serve as relevant benchmark studies. However, further refinements (i.e., additional seasonal replications) are required and this could be specifically undertaken within the Australian Alps given the routine dingo control that take place within and surrounding Kosciuszko National Park [35, 36]. Such programmes have been demonstrated to negatively impact dingo density and pack size [37]. Therefore, by monitoring dingo density (i.e., camera trap grid) as a function of anthropogenic control, in tandem with scavenging dynamics surrounding carrion, the flow-on effects of dingo densities on dingo scavenging rates and top-down scavenging effects may be uncovered. In addition, more informative measures of dingo top-down scavenging effects other than that used in this study (i.e., presence or absence of dingoes at carcass sites) should be utilised in future studies to characterise more realistic effects on mesoscavengers. This could include the number of visitation to a carcass by dingoes, the time spent scavenging at a carcass, and/or time since last dingo visitation to a carcass.

These types of approaches could be further supplemented by a robust quantification of the relative contribution of scavenging vs predation in the diet of the dingo. The most recent continental review of the dingo diet suggested that 66% consisted of mammals, 22% birds, and 11% reptiles [38]. However, the dataset used did not provide the capacity to quantify what percentage of that was scavenged vs predated, and indeed, Doherty et al. (2019) highlighted this as an area of further study. A greater understanding of the dingo's diet would be a good first step towards determining how important an energy pathway scavenging is to dingoes, and thus, how important a species they are within their scavenging guilds and the likely extent to which they can exert top-down scavenging effects [39].

Lastly, the Australian Alps likely harbours high loads of carrion biomass due to the widespread presence of larger bodied invasive species. The extensive management programs they warrant can also pulse carrion biomass loads within the ecosystem during culling seasons. This raises two points: *firstly*, that estimates of carrion biomass within the Australian Alps, and other ecosystems more broadly, is a field that warrants further attention to determine how over availability or scarcity of carrion affects scavenging dynamics. *Secondly*, it highlights a relatively novel concept that has seldom been explored and experimentally quantified, the proportion to which scavengers utilise the carcasses of native species vs invasive species [40, 41]. Research in both these areas could yield particularly insightful findings that could explain how scavengers react to a variety of unpredictable, abundant, and/or scarce carrion sources, and thus, further develop concepts in the scavenging ecology field.

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