CSIRO
PUBLISHING

RESEARCH PAPER
https://doi.org/10.1071/WR22100

WILDLIFE RESEARCH

Carcass use by mesoscavengers drives seasonal shifts in Australian alpine scavenging dynamics

James Vandersteen[A,*], Christopher Fust[A], Mathew S. Crowther[A], Matt Smith[B], Benjamin Viola[C], Philip Barton[D] and Thomas M. Newsome[A,*]

For full list of author affiliations and declarations see end of paper

***Correspondence to:**
James Vandersteen
School of Life and Environmental Sciences,
The University of Sydney, Sydney,
NSW 2006, Australia
Email: james.vandersteen@outlook.com;
Thomas M. Newsome
School of Life and Environmental Sciences,
The University of Sydney, Sydney,
NSW 2006, Australia
Email: thomas.newsome@sydney.edu.au

Handling Editor:
Catarina Campos Ferreira

Received: 12 June 2022
Accepted: 18 January 2023
Published: 9 February 2023

Cite this:
Vandersteen J *et al.* (2023)
Wildlife Research
doi:10.1071/WR22100

ABSTRACT

Context. Carrion is a high-energy and nutrient-rich resource that attracts a diverse group of vertebrate scavengers. However, despite the carrion pool being highly seasonal in its availability, there is little understanding of how scavengers utilise carcasses across all four seasons. **Aim.** To assess how season influences carcass-detection times by vertebrate scavengers and their rates of scavenging. **Methods.** We used remote cameras to monitor vertebrate scavenging at 15 eastern grey kangaroo (*Macropus giganteus*) carcasses in four consecutive seasons (summer, autumn, winter, and spring; total 58 carcasses) in the Australian Alps. **Key results.** In total, 745 599 remote-camera images were captured, within which 34 vertebrate species were identified, nine of which were recorded to actively scavenge. Time to first detection of carcasses by vertebrate scavengers was 5.3 and 9.6 times longer during summer (average 144 h) than during spring (average 34 h) and winter (average 24 h) respectively. Rates of vertebrate scavenging were highest in winter and spring, with brushtail possums (*Trichosurus vulpecula*) accounting for 78% of all scavenging events during winter, and ravens (*Corvus* spp.) accounting for 73% during spring. High rates of carcass use by these mesoscavengers may reflect a scarcity of other food sources, the demands of their breeding season, or a relative absence of scavenging by larger dominant species such as dingoes (*Canis dingo*) and wedge-tailed eagles (*Aquila audax*). **Conclusions.** These findings demonstrate the highly seasonal nature of vertebrate scavenging dynamics in an alpine ecosystem, and that mesoscavengers, not apex scavengers, can dominate the use of carcasses. **Implications.** Accounting for the effects of season is integral to understanding the way animals utilise carcasses in alpine and other strongly seasonal environments; and for developing further our knowledge of ecosystem processes linked to decomposition.

Keywords: alps, apex scavenger, breeding, brushtail possum, carrion, food source, mesoscavenger, raven, scavenger guild.

Introduction

Carrion is a valuable ecosystem resource, which in contrast to plant-based detritus, is high in energy and nutrient rich (Barton *et al.* 2013). Although carrion is spatially and temporally patchy (Carter *et al.* 2007; Wilson and Wolkovich 2011), it is exploited by species that have evolved to scavenge. Historically, scavengers have been viewed as 'bottom-feeders', owing to associations with rotting matter, disease, and death (DeVault *et al.* 2003). However, scavenging is present in many taxa, from obligate and facultative large vertebrate scavengers capable of consuming a whole carcass in one feeding event (Mateo-Tomás *et al.* 2017), to invertebrate scavengers that can aggregate around carrion in the thousands (Forbes and Carter 2015). Together, these species form scavenger guilds which, in addition to acting as 'natures clean-up crew' (Grilli *et al.* 2019), also support critical linkages, structure, and stability in food webs (Wilson and Wolkovich 2011); distribute nutrients within and among ecosystems; and provide economic and human health benefits related to carcass disposal and sanitary measures (Beasley *et al.* 2019).

Carrion biomass within an ecosystem fluctuates in response to key modes of death such as predation, but also in response to environmental factors (Forbes and Carter 2015; Moleón *et al.* 2019). Seasons are one of the strongest governing environmental factors, and can dictate the life histories of many herbivorous and/or migratory species that form a major component of the carrion pool (Skellam 1967; Boyce 1979; Forbes and Carter 2015; Moleón *et al.* 2019). 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 (Moleón *et al.* 2014). This is evident in tropical and subtropical Africa following wet- and dry-season cycles (Knight 1995; Dudley *et al.* 2003; Jones *et al.* 2015). For example, each year over 1 million wildebeest (*Connochaetes taurins*) migrate through the Serengeti Mara ecosystem (Hopcraft *et al.* 2015), including through the Mara River, where mass wildebeest drownings occur during its crossing (Subalusky *et al.* 2017, 2020). This sudden annual influx of carrion provides many terrestrial and aquatic scavengers with an abundance of available energy and nutrients (Handler *et al.* 2021). 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 (Clutton-Brock *et al.* 1997; Wilmers *et al.* 2003; Flint *et al.* 2010), or in arid Australia where drought can cause food shortages resulting in rapid declines in kangaroo populations (~40%; Caughley *et al.* 1985; Robertson 1986).

In response to seasonal fluctuations in the availability of carrion, scavengers have adapted and evolved to exploit food resources when they are in abundance. Facultative scavengers have considerable flexibility in their diets regarding both the relative contribution of predated and scavenged food, but also of meat, compared with other food sources (Pereira *et al.* 2014). For example, the Białowieża Forest (Poland) scavenger guild 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 (Jedrzejewska and Jedrzejewski 1998; Selva *et al.* 2003, 2005). These dynamics can become even more complex when considering the contrasting seasonality in the life histories of each scavenger species. 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. Consequently, both species are less selective of fish species when scavenging fishery discards (Sotillo *et al.* 2014). 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 (Rahmstorf and Coumou 2011).

Despite the obvious potential for seasonal trends in scavenging dynamics, the experimental designs of field-based scavenging studies often overlook the impact of all four seasons (Schoenly *et al.* 2015). 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; Read and Wilson 2004; López-López *et al.* 2013; Forsyth *et al.* 2014; Turner *et al.* 2017; Pardo-Barquín *et al.* 2019; Sebastián-González *et al.* 2019; Inagaki *et al.* 2020; Rød-Eriksen *et al.* 2020; Enari and Enari 2021). However, such an approach potentially oversimplifies the ways in which the various dimensions of scavenging can change not only between each of the seasons, but over the course of a year, and even among years (López-López *et al.* 2013). For instance, season, along with daily temperatures, humidity, and moisture levels can influence carrion persistence rates via the effects they have on regulating microbial and insect activity (Matuszewski *et al.* 2010; Turner *et al.* 2017; Barton and Bump 2019). Moreover, some studies completely ignore seasonal effects by monitoring scavenging dynamics only during one season (Peisley *et al.* 2017; Bingham *et al.* 2018; Cunningham *et al.* 2018; Rees *et al.* 2020; Fielding *et al.* 2022). Therefore, we acknowledge that although the successful design of any robust field study in scavenging ecology is underpinned by temporal aspects (i.e. diel, seasonal, yearly), spatial aspects (i.e. representative of ecosystem, spatially independent), and sample size (Schoenly *et al.* 2015), in conjunction with a suite of other considerations (i.e. carcass size and weight; Moleón *et al.* 2015; Sebastián-González *et al.* 2019), seasonal aspects arguably have the most potential to consistently affect scavenging dynamics.

Here, we exploited the highly seasonal nature of the Australian Alps to monitor the use of carcasses by vertebrate scavengers. We undertook carcass monitoring across four seasons to test hypotheses related to (1) scavenger species richness/composition; (2) the time to first detection and scavenging at a carcass; (3) scavenger activity (i.e. probability of a scavenger investigating versus scavenging a carcass); and (4) 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 (Cammack *et al.* 2015). Consequently, we 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 hypothesis was based on vertebrate scavengers potentially being more heavily reliant on carrion during winter when other food resources are scarce (Jedrzejewska and Jedrzejewski 1998; Selva *et al.* 2003, 2005). Last, we predicted that our findings would highlight the importance of undertaking field-based scavenging studies across all four seasons, so as to fully understand the complexities of scavenging dynamics and the interactions that take place surrounding carrion.

Materials and methods

Study site

This study was conducted in Kosciuszko National Park, in southern New South Wales, Australia. This region includes many of Australia's highest peaks and ranges, including the highest peak, Mount Kosciuszko (2228 m asl). The landscape is delineated into three altitudinally distinct ecological communities, namely, montane (500–1500 m), subalpine (1500–1850 m), and alpine (1850–2228 m) (Bear *et al.* 2006). Each of these communities are highly seasonal, with the temperatures experienced throughout the course of a year differing by up to 50°C (−10 to 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 (Ward *et al.* 2020). This work was undertaken within the montane zone (between approximately 1000–1500 m) which is characterised by forest stands dominated by snow gums (*Eucalyptus pauciflora*) and various other *Eucalyptus* species.

Ethics and permits

Ethics approvals (Project number: 2019/1640, The University of Sydney) and scientific permits (Licence number: Sl102334, New South Wales Office of Environment and Heritage) were obtained to undertake the fieldwork. Carcasses of eastern grey kangaroos (*Macropus giganteus*) were sourced fresh and locally from legally approved shooting operations that are conducted to control or harvest overabundant kangaroo populations.

Fieldwork

A 15 km transect was established through Kosciuszko National Park, along which all carcass monitoring took place (Fig. 1). This transect ran from north-east to south-west and was selected because of its accessibility (i.e. road access), because it is an undisturbed area with little human activity, and because consistent vegetative structure allowed carcass-monitoring sites with similar canopy cover (~75%) to be established along the transect.

Monitoring periods coincided with the four seasons: March–May 2020 (autumn, average min/max: 1°C/13°C); July–September 2020 (winter, average min/max: −3°C/8°C); September–November 2020 (spring, average min/max: 2°C/15°C); January–March 2021 (summer, average min/max: 6°C/21°C). 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 250 m from the nearest sites monitored during other seasons (60 different sites in total; Fig. 1). The separation of sites ensured a level of spatial independence, and it prevented habituation of scavengers to a carrion source location (Inagaki *et al.* 2020; Spencer and Newsome 2021; Spencer *et al.* 2021; Newsome and Spencer 2022).

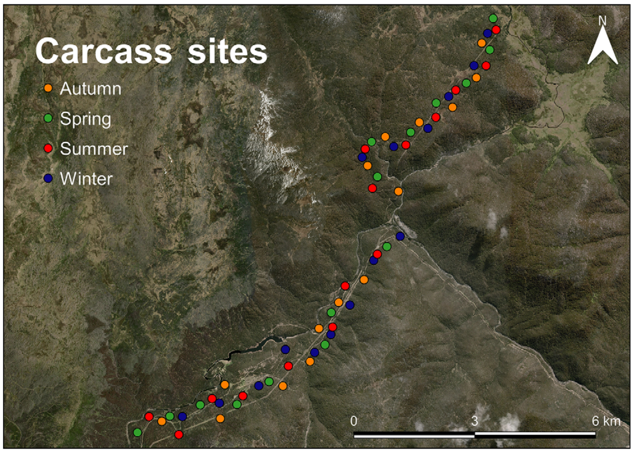

Fig. 1. Location of the monitoring transect, along which all 60 carcass sites were established within Kosciuszko National Park.

Within each season, one fresh eastern grey kangaroo carcass was placed at each carcass-monitoring site (15 in total). The carcasses ranged in weight from 12 kg to 70 kg and, on average, were 28.3 kg (±1.498 standard deviation; Supplementary material Table S1). Each carcass was secured, using wire ties, to star pickets driven into the ground to ensure that they remained *in situ* (methods used were as per Spencer and Newsome 2021; Spencer *et al.* 2021; Newsome and Spencer 2022).

Vertebrate scavenger activity was monitored at each site for 60 days by using a Reconyx PC800 Hyperfire™ remote camera. Each camera was placed on a free-standing star picket 3 m 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 (Kostecke *et al.* 2001; King *et al.* 2006; Flint *et al.* 2010; Inagaki *et al.* 2020; Rød-Eriksen *et al.* 2020; Spencer and Newsome 2021; Spencer *et al.* 2021; Newsome and Spencer 2022).

Analyses

Remote-camera images were analysed for species presence and the number of individuals of a species present. An 'event' was characterised as a visitation by a species that occurred more than 10 min after the last visitation by that same species (methods as per Spencer and Newsome 2021; Bragato *et al.* 2022; Newsome and Spencer 2022). 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 statistical environment (R Core Team, ver. 4.2.1; Vienna, Austria; https://www.R-project.org/) was used for all statistical analyses. To determine whether species composition differed among the seasons, we used a permutational multivariate analysis of variance (PERMANOVA) within the R Package 'vegan' (Oksanen *et al.* 2022). The PERMANOVA was used in conjunction with an analysis of similarities (ANOSIM; also within R Package 'vegan'; Oksanen *et al.* 2022) to also test whether the magnitude of difference among seasons was greater than that within seasons (Somerfield *et al.* 2021). To determine which scavenger species were driving any differences in species composition between the seasons, a similarity percentages (SIMPER) analysis was used, also within the R Package 'vegan' (Oksanen *et al.* 2022).

To characterise the seasonal nature of scavenging, the following four response variables were considered: scavenger species richness (Conway–Maxwell Poisson distribution); 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 was modelled against the explanatory variables of season, altitude, and carcass weight.

Models were constructed using either generalised linear models (GLM) within the R Package 'lme4' (Bates *et al.* 2015), or using generalised linear mixed models (GLMM) within the R Package 'glmmTMB' (Brooks *et al.* 2017). We utilised GLMs when modelling response variables that consisted of only one measurement at each independent carcass-monitoring site, namely, scavenger species richness and time to first detection/scavenging. GLMMs were used for response variables that yielded repeat measurements at each independent carcass-monitoring site (i.e. scavenger activity and event duration) to account for the random effect of site. Model assumptions were checked using residual diagnostics within the R Package 'DHARMa' (Hartig and Hartig 2017). This also included testing model residuals for spatial autocorrelation. If detected, a spatial autocorrelation covariate was created using the R Package 'spdep' (Bivand *et al.* 2013) and subsequently included as an explanatory variable in the model (Dormann *et al.* 2007). These models were constructed twice, once using only investigation events and once using only scavenging events. Only one model was constructed for scavenger activity because 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.

To determine the most parsimonious model(s), corrected Akaike information criterion ($\mathrm{AIC_c}$; Sakamoto *et al.* 1986) was used to consider the different combinations of explanatory variables (i.e. combinations of season, altitude, and carcass weight; with a $\Delta\mathrm{AIC_c}$ level of significance <2). Model selection was facilitated by the dredge function within the R Package 'MuMIn' (Bartoń 2022).

Significance testing (level of significance $P < 0.05$) was undertaken using the base model (i.e. where the scavenging response variable was modelled against all three explanatory variables, namely, season, altitude, and carcass weight). This determined which explanatory variables (season, altitude, and/or carcass weight) and/or their levels (with autumn used as the reference level) were important in explaining the scavenging response variable. Finally, a Tukey's honest significance test within the R Package 'emmeans' was used to determine which seasons were significantly different from one another regarding the modelled scavenging response variable (Lenth 2016). 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.

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 remote cameras took 745 599 images of 34 different species including both scavengers and non-scavengers. Of these taxa, nine were considered scavenger species on the basis of recorded scavenging of the monitored carcasses (Fig. 2). These were 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. (Australian raven (*Corvus coronoides*) and little raven (*Corvus mellori*), which were indistinguishable from one another in the remote camera images, and so were grouped together as 'raven(s)), red fox (*Vulpes vulpes*), and feral pig (*Sus scrofa*; Fig. 3).

In total, 6857 distinct events were recorded, of which, 2680 were investigation events and 4177 scavenging events (Fig. 4*a*). Brushtail possums and ravens accounted for 88% of the total recorded events, whereas spotted-tail quolls accounted for the fewest events (Fig. 4*b*).

There were weak differences in species composition among seasons for both investigation events (pseudo-F = 2.898, d.f. = 57, residual d.f. = 54, P = 0.002, nperm = 999) and scavenging events (pseudo-F = 2.991, d.f. = 53, residual

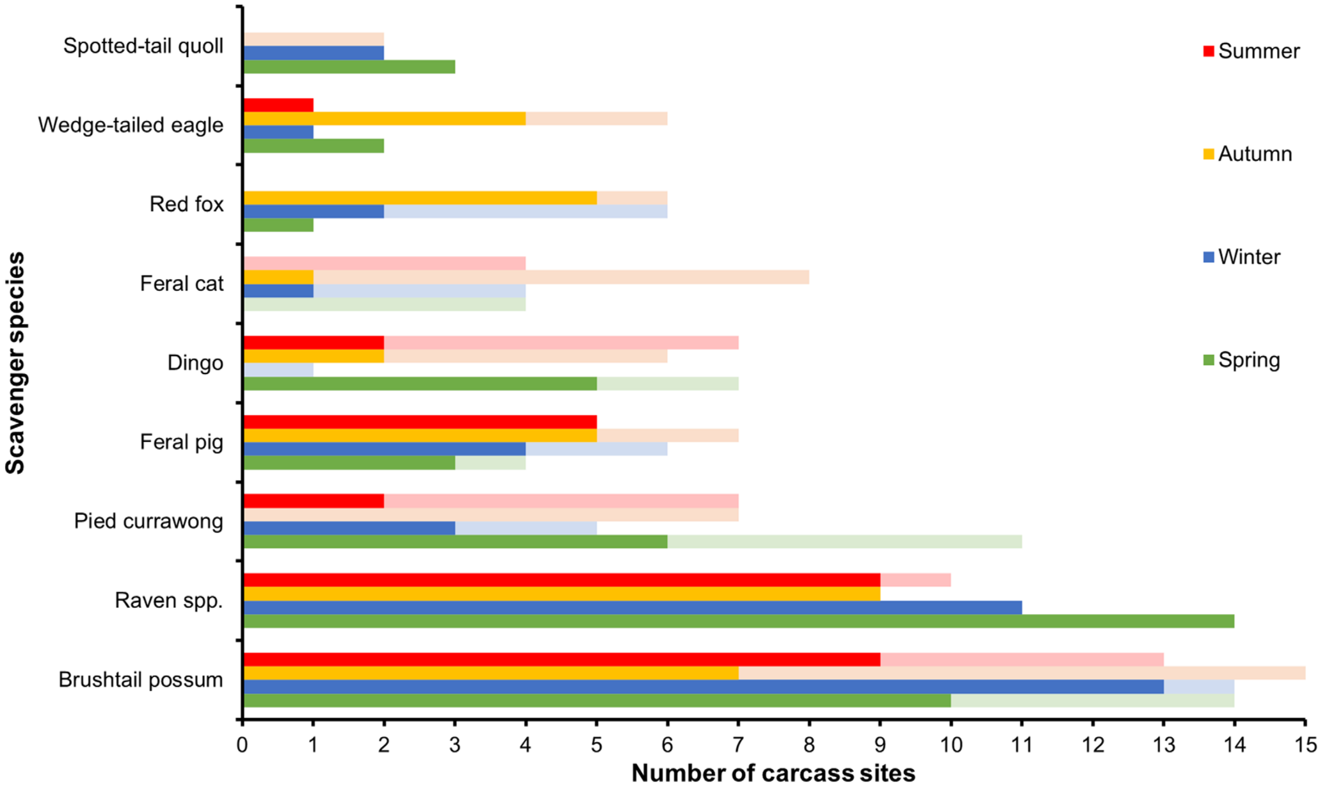

Fig. 2. The total number of carcass sites visited by each scavenger species per season. Carcass-monitoring sites where scavenging was recorded (solid fill) are distinguished from those that were only investigated (shaded fill).

d.f. = 50, $P = 0.004$, nperm = 999; Table S2). Species composition for investigation events was significantly different between autumn and spring ($P = 0.030$) and between spring and winter ($P = 0.018$; Table S3). Whereas for scavenging events, species composition was significantly different between autumn and winter ($P = 0.036$) and between spring and winter ($P = 0.012$; Table S3). Additionally, there was very little difference when comparing within-season species composition with between-season species composition for both investigation events ($R = 0.109$, $P = 0.001$, nperm = 999) and scavenging events ($R = 0.109$, $P = 0.002$, nperm = 999). Brushtail possums and ravens were found to be the primary drivers of the observed differences in species composition among the seasons (Fig. 5, Tables S4, S5).

Scavenger species richness

Seven models demonstrated equivalent levels of support ($\Delta\text{AIC}_c < 2$) for explaining the variation in scavenger species richness during investigation events (Table S6). Scavenger species richness was affected by season, with summer ($P = 0.023$) and spring ($P = 0.038$) being significantly different from autumn, the reference level (Table S7). Four models demonstrated equivalent levels of support ($\Delta\text{AIC}_c < 2$) for explaining the variation in scavenger species richness during scavenging events (Table S6), but the base model was not significant (Table S7).

Time to first detection and scavenging of carcasses

Spatial autocorrelation was detected in the model residuals for time to first detection; therefore, a spatial autocorrelation covariate (SACC) was included. Three models demonstrated equivalent levels of support ($\Delta\text{AIC}_c < 2$) for explaining the variation in time to first detection of carcasses (Table S8). The time to first detection of carcasses was affected by season (Table S9). Specifically, time to first detection of carcasses (in hours) was 5.344 and 9.622 times longer during summer than during spring ($P = 0.012$) and winter ($P = 0.001$) respectively (Fig. 6; Table S10).

Three models demonstrated equivalent levels of support ($\Delta\text{AIC}_c < 2$) for explaining the variation in time to first scavenging of carcasses (Table S8), but the base model was not significant (Table S9).

Scavenger activity

Three models demonstrated equivalent levels of support ($\Delta\text{AIC}_c < 2$) for explaining the variation in scavenger activity (Table S11). Scavenger activity was affected by

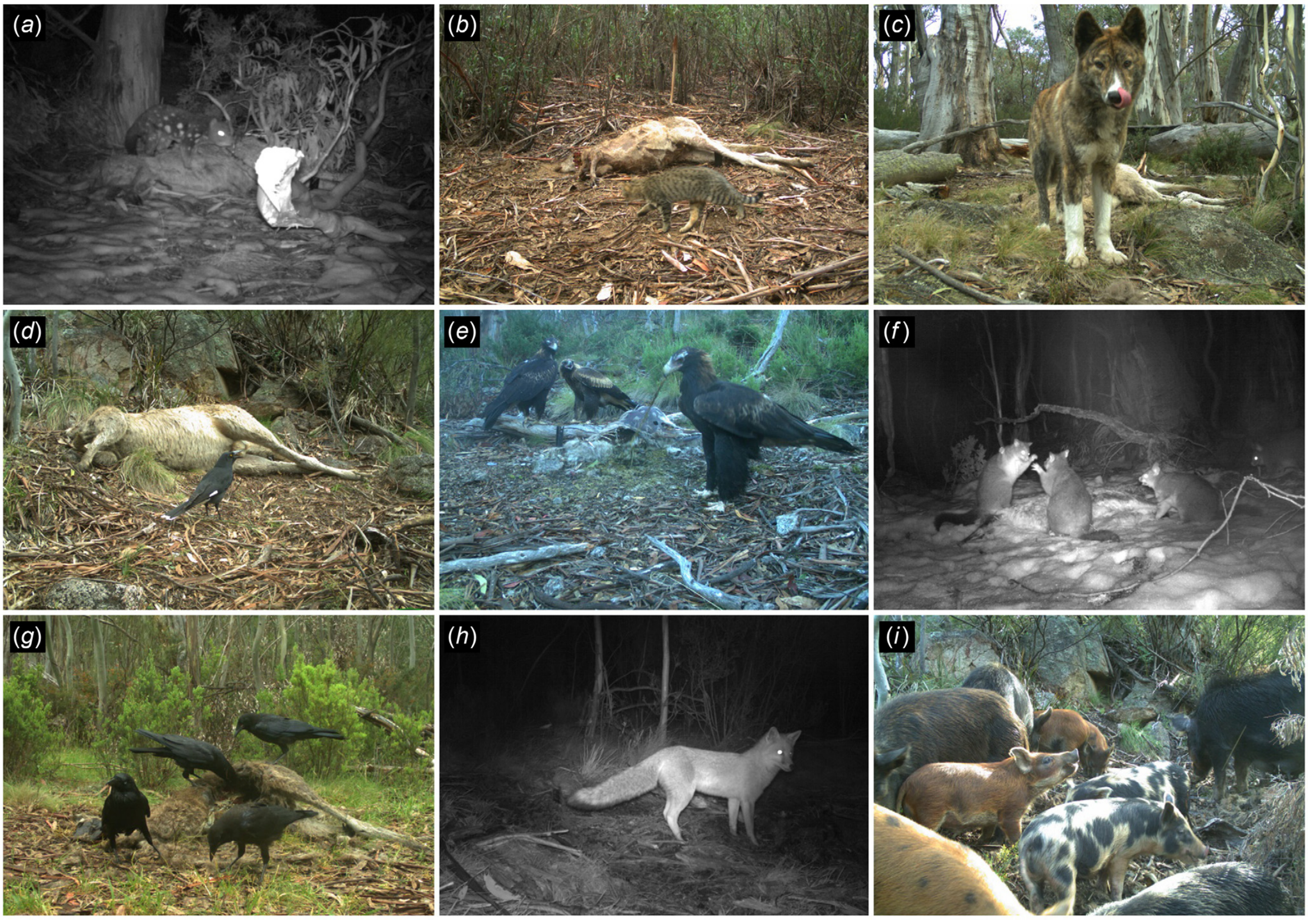

Fig. 3. Remote camera images for each of the members of the Australian alpine scavenger guild, determined by recorded scavenging of carcasses in Kosciuszko National Park. (*a*) Spotted-tail quoll (*Dasyurus maculatus*), (*b*) feral cat (*Felis catus*), (*c*) dingo (*Canis dingo*), (*d*) pied currawong (*Strepera graculina*), (e) wedge-tailed eagle (*Aquila audax*), (*f*) brushtail possum (*Trichosurus vulpecula*), (*g*) raven spp. (Australian raven (*Corvus coronoides*) and little raven (*Corvus mellori*), indistinguishable from one another in the remote camera images), (*h*) red fox (*Vulpes vulpes*), and (*i*) feral pig (*Sus scrofa*).

season (Table S12). Specifically, scavenging was 2.186 and 3.086 times more likely than investigation during spring than during autumn ($P = 0.014$) and summer ($P \leq 0.001$) respectively, and 2.683 times more likely during winter than during summer ($P = 0.002$; Table S13).

Duration of investigation and scavenging events

Four models demonstrated equivalent levels of support ($\Delta AIC_c < 2$) for explaining the variation in the duration of investigation events (Table S14). The duration of investigation events was affected by carcass weight, whereby larger carcasses were investigated for shorter durations ($P = 0.031$; Fig. S1, Table S15). Four models demonstrated equivalent levels of support ($\Delta AIC_c < 2$) for explaining the variation in the duration of scavenging events (Table S14). The duration of scavenging events was affected by season (Table S15). Specifically, the duration of scavenging events (in minutes) was 1.916 and 1.556 times shorter during spring than during autumn ($P = 0.001$) and winter ($P = 0.027$) respectively (Fig. 7; Table S16).

Discussion

In this study, we investigated how seasons affect vertebrate scavenging dynamics in an alpine environment. Our findings demonstrated that scavenging dynamics were highly seasonal, and this trend was consistent (i.e. did not significantly change) across an altitudinal gradient for carcasses of all weights. Australia has no strictly 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 fluctuations in carrion biomass within the landscape, availability of other food sources, and/or the life histories of the scavenger species (Knight 1995; Jedrzejewska and Jedrzejewski 1998; Dudley *et al.* 2003;

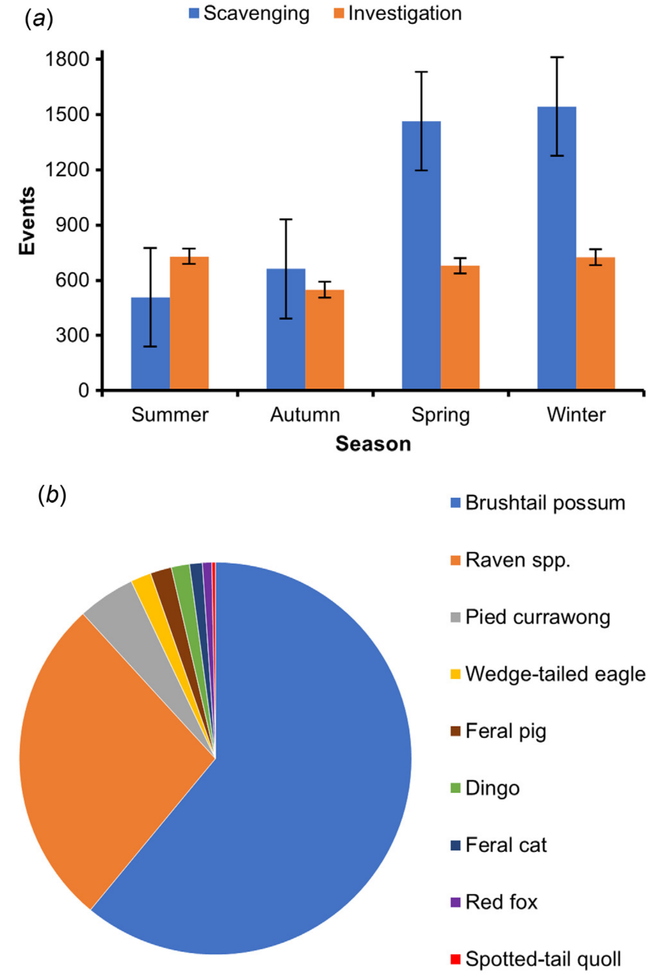

Fig. 4. (*a*) The total number of events per season and (*b*) the percentage of total events attributed to each scavenger species where brushtail possums accounted for 61%, raven spp. 27%, pied currawongs 5%, and all other species <2% each.

Selva *et al.* 2003, 2005; Wilmers *et al.* 2003; Wilmers and Getz 2004; Selva and Fortuna 2007; White 2011; Pereira *et al.* 2014; Jones *et al.* 2015). Such observations were made in this study, but the trends uncovered were overwhelmingly dictated by the scavenging rates and activities of mesoscavengers, specifically brushtail possums and ravens. Together, these species accounted for 88% of all recorded events. The scavenging rates observed by ravens were not unusual, with many studies both within Australia and globally describing raven species as prolific scavengers (Selva *et al.* 2003; O'Brien *et al.* 2010*a*; Mateo-Tomás *et al.* 2015; Spencer *et al.* 2021; Bragato *et al.* 2022; Newsome and Spencer 2022). However, the brushtail possum has received little recognition as a regular scavenger (but see Brown *et al.* 1993; Heinsohn and Barker 2006; O'Brien *et al.* 2010*b*).

Scavenging dynamics surrounding carrion are not typically dictated by the species-specific scavenging rates of mesoscavengers, but that of larger apex scavenger species (Wilmers *et al.* 2003; Wilmers and Post 2006; Krofel *et al.* 2012; Allen *et al.* 2014). This is because larger species are generally more competitively dominant surrounding carrion (Moleón *et al.* 2014; Pereira *et al.* 2014; Inagaki *et al.* 2020), and are able to open up carcasses, and, thus, provide access to smaller scavengers unable to do so (Selva *et al.* 2003, 2019; Moleón *et al.* 2015). However, in this study, larger scavengers such as dingoes, wedge-tailed eagles, and feral pigs accounted for only 5% of all recorded events, suggesting that they were either not abundant during the study period or were not scavenging frequently. Notably, in one case, a dingo was observed to have consumed an entire kangaroo carcass within a 24-h period. 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 who regularly feature in the diets of these three predators (Jones and Coman 1981; Newsome *et al.* 1983; Dickman 1996; Vernes *et al.* 2001; Kinnear *et al.* 2002; Brook and Kutt 2011; Pascoe *et al.* 2012; McComb *et al.* 2018; Fleming *et al.* 2021; Moseby *et al.* 2021). Further still, recent findings in Australia have demonstrated that ravens, in the absence of top scavengers, scavenged across all four seasons and not only during the cooler months when other resources were low (Fielding *et al.* 2021). Therefore, whether the relative absence of larger scavengers at carcass sites in this study aided mesoscavenger access to the food source is unknown; however, it could be reasonably expected if this resulted in reduced predation risk for the mesoscavengers and/or less competition for the food source.

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 (Santos *et al.* 2016). Carcass detection by scavengers is dependent on a number of factors including olfactory cues, visual cues, inter/intra specific cues, and search effort (López-López *et al.* 2013; Cortés-Avizanda *et al.* 2014; Cammack *et al.* 2015). 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 (Barton and Bump 2019; Moleón *et al.* 2019). 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 (Mann *et al.* 1990; Carter *et al.* 2007; Forbes and Carter 2015; Barton and Evans 2017; Barton and Bump 2019). However, there was no evidence to support this hypothesis and, instead, carcasses took longer to be detected during summer, especially when compared with spring and winter.

It is possible that the same mechanism as that expected to facilitate shorter time to first detection of carcasses, invertebrate and microbial scavenger activity, in fact,

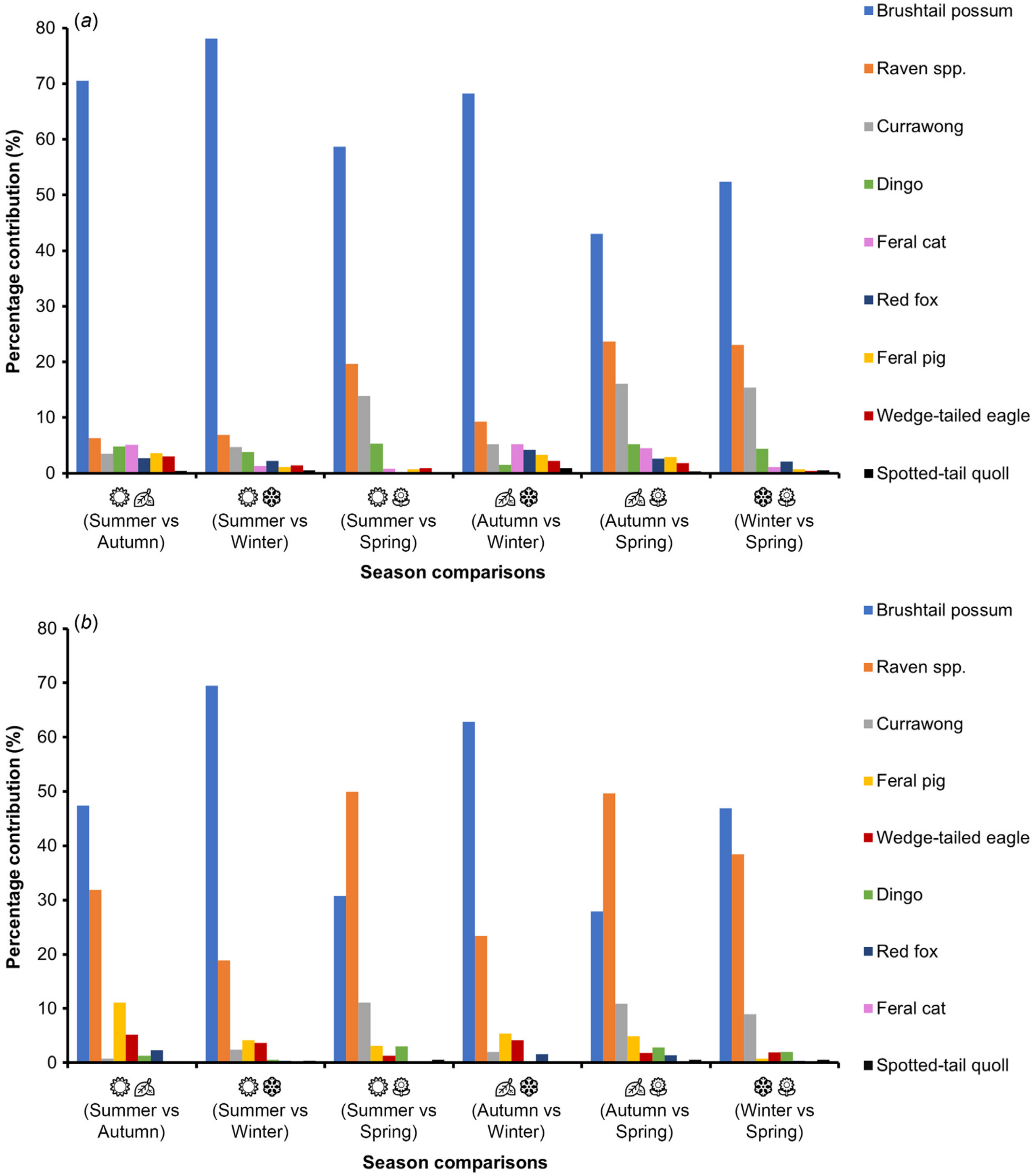

Fig. 5. The percentage contribution of each scavenger species (contributed most to least, top to bottom of each respective legend) to the observed differences in species composition between each of the seasons (summer, sun; autumn, leaf; winter, snowflake; spring, flower) for (*a*) investigation events and (*b*) scavenging events. The percentage contribution was adapted from the SIMPER analyses cumulative sum results (CUMSUM; Tables S4, S5).

hindered detection of carcasses by the vertebrate scavengers. During summer (warmer months), carcasses are rapidly colonised (within minutes) *en masse* by invertebrates and a plethora of microorganisms (Ray *et al.* 2014; Crippen *et al.* 2015; Merritt and De Jong 2015; Barton and Evans 2017; Anderson *et al.* 2019; Evans *et al.* 2020). 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

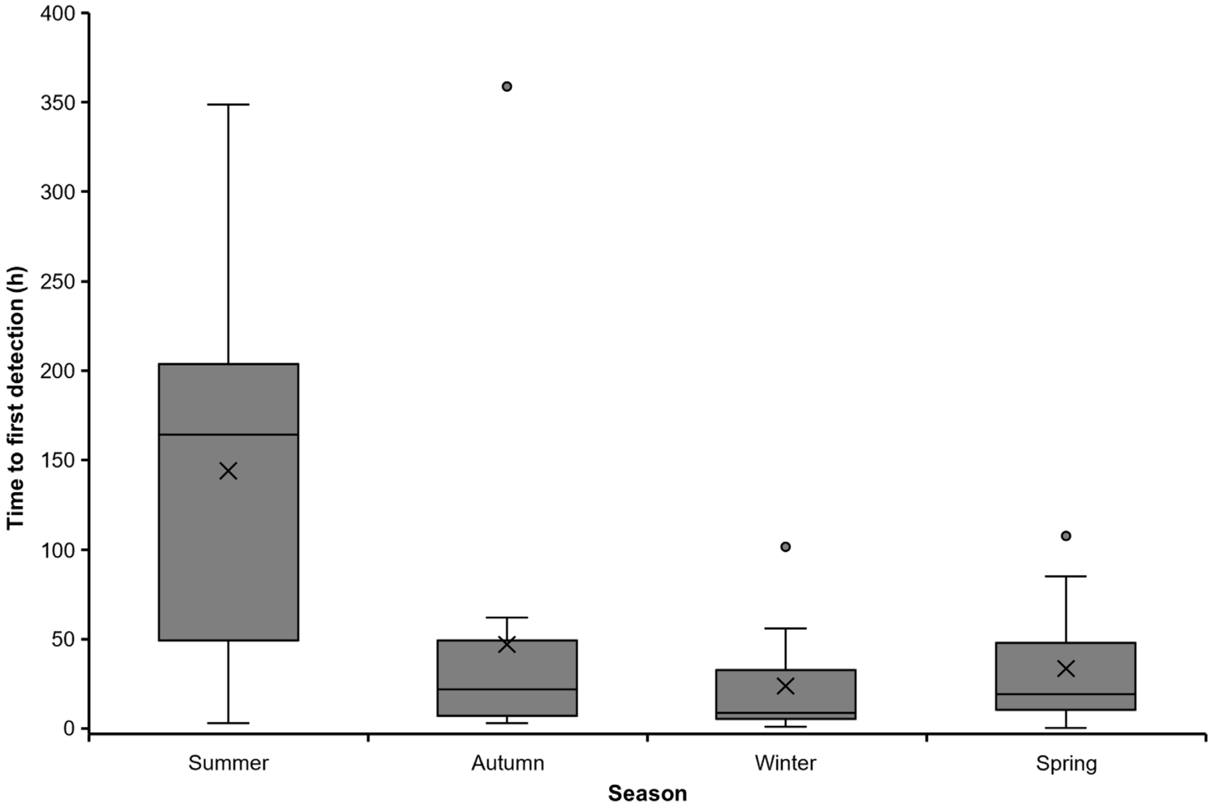

Fig. 6. The time to first detection (hours) of monitored carcasses by vertebrate scavengers during each of the seasons (mean is indicated by a cross).

outcompeted vertebrate scavengers (Ray *et al.* 2014; Barton and Evans 2017; Evans *et al.* 2020). Indeed, previous observations of carcass persistence rates within the study site have indicated that eastern grey kangaroo carcasses take at least twice as long to reach complete consumption/decomposition (only skin and bones remaining) in cool compared with warmer periods (Spencer and Newsome 2021). During the winter monitoring period, we observed that some carcasses had not reached complete consumption/decomposition, 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 (Jedrzejewska and Jedrzejewski 1998; Selva *et al.* 2003, 2005). In our study, brushtail possums accounted for 81% of all recorded events during winter when they scavenged three times more often than during summer. Generally, the diet of brushtail possums consists of leaves, flowers, fruit (*Eucalyptus* and *Acacia*) and insects (Evans 1992; How and Hillcox 2000; Wiggins *et al.* 2003), most of which are only seasonally available during warmer months. Therefore, this marsupial may be exhibiting a greater dependence on carrion during winter that is similar to that of other scavengers in the northern hemisphere (Jedrzejewska and Jedrzejewski 1998; Selva *et al.* 2003, 2005). This greater dependence on carrion by the brushtail possum during winter is likely to have influenced our analyses of the 'scavenger activity' response variable, which recorded scavenging to be 2.683 times more likely than investigation of carcasses during winter than in summer. This may also explain why carcasses took six times longer to be detected during summer (144 h; 6 days) than during winter (24 h), a finding that was 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 ravens. Conversely, during summer, only 57% of the first detections of a carcass were by either brushtail possums or ravens. Therefore, it is possible that the brushtail possums and ravens 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 (Camphuysen 1995; O'Brien *et al.* 2010*a*; White 2011; Coppola *et al.* 2020). The Australian raven and little raven breed from late winter into spring (Moon 2005; Whisson *et al.* 2015; Ekanayake *et al.* 2018). Initially, nest construction is prioritised in this early breeding season, and the associated activities are characterised by frequent and

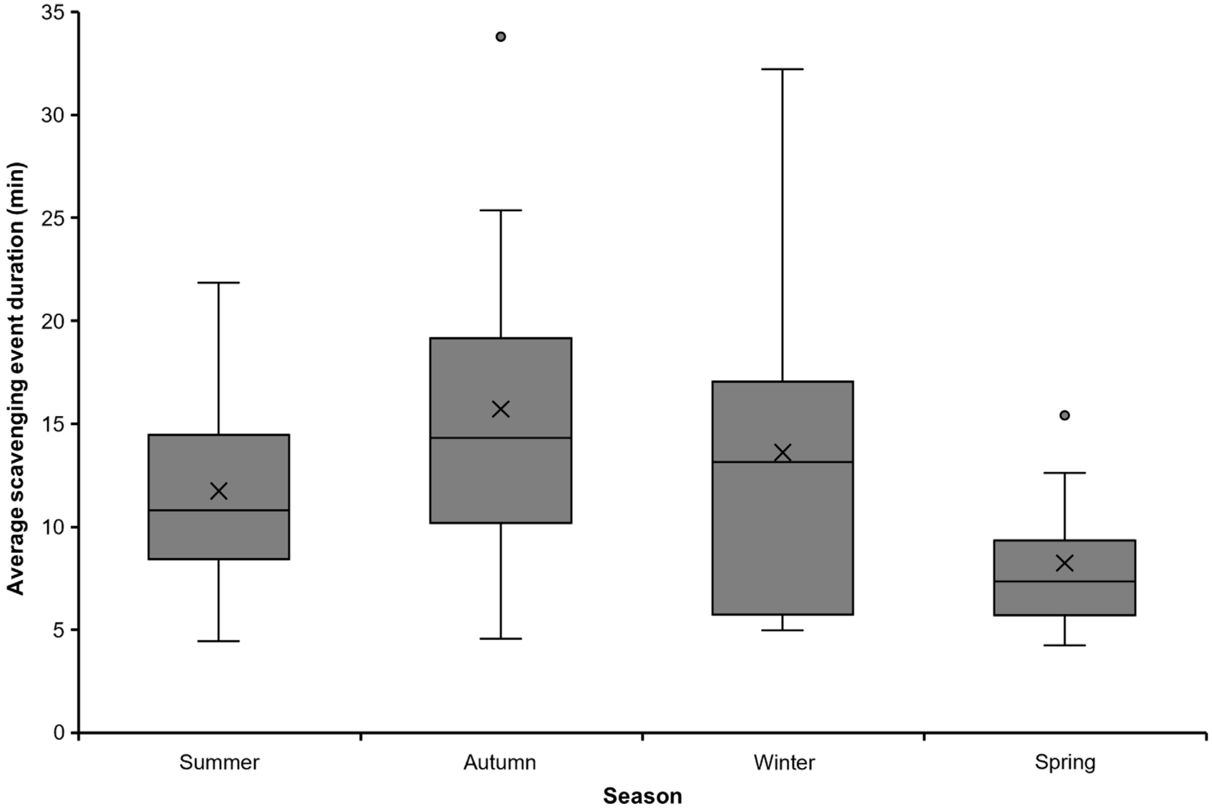

Fig. 7. The average duration of scavenging events (minutes) by vertebrate scavengers for each carcass monitored during each of the seasons (mean is indicated by a cross).

short visitations between the nest and sources of nesting material (Moreno-Opo and Margalida 2013). In our study, during the spring monitoring period, numerous remote-camera images captured ravens collecting fur from the kangaroo carcasses, presumably for nest construction (Fig. 8).

Fig. 8. A raven sp. (*Corvus coronoides* or *Corvus mellori*) breeding pair collecting fur from an eastern grey kangaroo (*Macropus giganteus*) carcass during the spring monitoring period, presumably for nest construction.

Following nest construction, chick rearing often requires breeding pairs to divide time between foraging, feeding chicks, and being vigilant and protective of the nest (O'Brien *et al.* 2010*a*). Inherently, during this time, ravens 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 (Camphuysen 1995; O'Brien *et al.* 2010*a*). Of all recorded raven scavenging events during this study, 67% were during spring, and this suggests that ravens may heavily rely on carrion to supplement their diet, and/or that of their chicks, during the breeding season (O'Brien *et al.* 2010*a*). Further still, this flurry of raven scavenging during spring (a 170% increase on the average of annual raven 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 breeding season (i.e. breeding pairs frequently flying back and forth between the nest and nesting materials and/or food sources), were also deterministic of the shorter scavenging event duration recorded for the collective scavenger guild during spring.

The findings here regarding ravens are also indirectly linked to our initial prediction for longer scavenging-event duration during winter; our models indicated that scavenging-event duration during winter was 1.556 times longer than during spring. Although raven scavenging behaviours during their breeding seasons (spring) are likely to have determined this result and supported our prediction, it is juxtaposed to the evidence we initially used to form our hypotheses. That being, previous studies in the northern hemisphere demonstrating scavenging rates to increase during winter in response to a lack of other available food sources (Jedrzejewska and Jedrzejewski 1998; Selva *et al.* 2003, 2005). This raises several questions that need be addressed regarding the degree to which the Australian alpine winter affects food sources, species diets, and associated flow-on effects to scavenging dynamics versus other alpine areas in the world, and indeed non-alpine ecosystems that experience harsh winters.

Conclusions and future directions

Scavenging dynamics in this study were highly seasonal but were dictated by the scavenging activities and behaviours of mesoscavengers, namely, the brushtail possum and ravens. The high rate of scavenging by these species drove the seasonal trends in scavenging dynamics, but the direction in which the seasonal effects affected the scavenging response variables was not always as we 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.

Although carcass weight was demonstrated to have a significant effect on the duration of investigation events, it is possible that this result was skewed by four carcass-weight outliers (55 kg, 55 kg, 57 kg, and 70 kg, compared with an average of 28.3 kg; Table S1). A cursory look at these four carcasses demonstrated relatively short investigation-event durations when compared with all other carcasses, resulting in an instance where potential statistical outliers represent an 'extreme' in the response variable (Supplementary material Fig. S1). The removal of said 'outliers' from the dataset was considered, but residual analyses did not demonstrate any significant outliers in the model, and, therefore, doing so could have potentially introduced bias. For exploratory purposes and transparency, we re-ran the model removing only the furthest outlier (carcass site 42; carcass weight 70 kg; Table S1) and this returned a model in which carcass weight was not significant (Table S17). It remains unknown if this trend was indeed a real ecological finding, or outlier skew as predicted. We, therefore, recommend that further research is needed to explore the relationship between carcass weight and event duration.

More generally, the methods used herein can be utilised to monitor scavenging dynamics surrounding carrion, and even be further developed to improve field-based designs and yield additional ecological information. Such improvements could include utilising a remote-camera grid in tandem with the carcass monitoring to determine the activity and diversity of scavenger species in the given study region. This direct comparison of scavenger species at carcasses and more generally in the landscape would allow for more informed conclusions surrounding scavenging dynamics, such as, for example, whether species-specific scavenging rates are a product of scavenging behaviour or species density in the study region. Additionally, comprehensive altitudinal gradients that may detect elevational differences in scavenging dynamics could lead to particularly novel findings, insights missed by this study given the small altitudinal gradient used (500 m). This is especially important in scavenging studies that experience much higher altitudes than those present in Australia. Because of geographic limitations, in this study, we were restricted to only 15 carcass-monitoring sites per season. An improved sampling design that includes more within-season replications, multiple transects, and replicated studies over multiple years may help detect more subtle seasonal differences missed by this study, as well as account for within-site (i.e. more representative of the ecosystem) and annual variability (Schoenly *et al.* 2015).

Our observations of frequent scavenging by the brushtail possum are highly novel, given that they mainly feed on leaves, flowers, and fruit (*Eucalyptus* and *Acacia*) and are commonly considered generalist herbivores/folivores (Evans 1992; Owen and Norton 1995; How and Hillcox 2000; Cochrane *et al.* 2003; Wiggins *et al.* 2003; Sweetapple *et al.* 2004). The results of this study, at the most, suggest that the high rates of brushtail possum scavenging were facilitated by reduced predations risk from, and competition with, larger dominant scavengers. Notably, brushtail possums have been previously observed to, on occasion, eat insects, raid birds' nests, and scavenge on carrion (Brown *et al.* 1993; Nugent *et al.* 2000). Therefore, it is also possible that other factors characteristic of the alpine environment, (i.e. less alternative food sources, harsher winters) in which this study was undertaken, resulted in our unique findings regarding brushtail possum scavenging. With this in mind, we recommend that more in-depth dietary studies are undertaken that specifically compare the diets of brushtail possums in the Australian Alps with those of brushtail possums in other Australian ecosystems. This will help quantify the amount of carrion brushtail possums consume compared with other food sources and provide further insights into the ecosystem factors that determine such dietary shifts.

We also observed that ravens were somewhat dependent on carrion both as a source of energy, and nesting material during the breeding season. Very little work has been conducted to determine how carrion biomass within an ecosystem (year to year) may affect the breeding success of facultative scavengers (Beasley *et al.* 2019). This is an area that warrants future attention, given the results of this study and also those elsewhere regarding ravens (O'Brien *et al.* 2010*a*).

Lastly, quantifying carrion biomass in the broader landscape would help determine whether it is a limited resource, or in abundance (Barton *et al.* 2019). Understanding scavenging dynamics in relation to the availability of carrion would help explain how scavengers react to changes in food supplies and, thus, further develop our knowledge of the role of carrion in supporting biodiversity and ecosystem function.

Supplementary material

Supplementary material is available online.

References

Allen ML, Elbroch LM, Wilmers CC, Wittmer HU (2014) Trophic facilitation or limitation? Comparative effects of pumas and black bears on the scavenger community. *PLoS ONE* **9**, e102257. doi:10.1371/journal.pone.0102257

Anderson GS, Barton PS, Archer M, Wallace JR (2019) Invertebrate scavenging communities. In 'Carrion ecology and management'. (Eds PP Olea, P Mateo-Tomás, JA Sánchez-Zapata) pp. 45–69. (Springer: Cham, Switzerland)

Bartoń K (2022) MuMIn: Multi-Model Inference. R package version 1.47.1. Available at https://CRAN.R-project.org/package=MuMIn

Barton PS, Bump JK (2019) Carrion decomposition. In 'Carrion ecology and management'. (Eds PP Olea, P Mateo-Tomás, JA Sánchez-Zapata) pp. 101–124. (Springer: Cham, Switzerland)

Barton PS, Evans MJ (2017) Insect biodiversity meets ecosystem function: differential effects of habitat and insects on carrion decomposition. *Ecological Entomology* **42**, 364–374. doi:10.1111/een.12395

Barton PS, Cunningham SA, Lindenmayer DB, Manning AD (2013) The role of carrion in maintaining biodiversity and ecological processes in terrestrial ecosystems. *Oecologia* **171**, 761–772. doi:10.1007/s00442-012-2460-3

Barton PS, Evans MJ, Foster CN, Pechal JL, Bump JK, Quaggiotto M-M, Benbow ME (2019) Towards quantifying carrion biomass in ecosystems. *Trends in Ecology & Evolution* **34**, 950–961. doi:10.1016/j.tree.2019.06.001

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* **67**, 1–48. doi:10.18637/jss.v067.i01

Bear R, Hill W, Pickering CM (2006) Distribution and diversity of exotic plant species in montane to alpine areas of Kosciuszko National Park. *Cunninghamia* **9**, 559–570.

Beasley JC, Olson ZH, Selva N, DeVault TL (2019) Ecological functions of vertebrate scavenging. In 'Carrion ecology and management'. (Eds PP Olea, P Mateo-Tomás, JA Sánchez-Zapata) pp. 125–157. (Springer: Cham, Switzerland)

Bingham EL, Gilby BL, Olds AD, Weston MA, Connolly RM, Henderson CJ, Maslo B, Peterson CF, Voss CM, Schlacher TA (2018) Functional plasticity in vertebrate scavenger assemblages in the presence of introduced competitors. *Oecologia* **188**, 583–593. doi:10.1007/s00442-018-4217-0

Bivand RS, Pebesma E, Gomez-Rubio V (2013) 'Applied spatial data analysis with R, second edition' (Springer: NY, USA)

Boyce MS (1979) Seasonality and patterns of natural selection for life histories. *The American Naturalist* **114**, 569–583. doi:10.1086/283503

Bragato PJ, Spencer EE, Dickman CR, Crowther MS, Tulloch A, Newsome TM (2022) Effects of habitat, season and flood on corvid scavenging dynamics in Central Australia. *Austral Ecology* **47**, 939–953. doi:10.1111/aec.13177

Brook LA, Kutt AS (2011) The diet of the dingo (*Canis lupus dingo*) in north-eastern Australia with comments on its conservation implications. *The Rangeland Journal* **33**, 79–85. doi:10.1071/RJ10052

Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Mächler M, Bolker BM (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal* **9**, 378–400. doi:10.32614/RJ-2017-066

Brown K, Innes J, Shorten R (1993) Evidence that possums prey on and scavenge birds' eggs, birds and mammals. *Notornis* **40**, 169–177.

Cammack JA, Pimsler ML, Crippen TL, Tomberlin JK (2015) Chemical ecology of vertebrate carrion. In 'Carrion ecology, evolution, and their applications'. (Eds ME Benbow, JK Tomberlin, AM Tarone) pp. 187–212. (CRC Press: Boca Raton, FL, USA)

Camphuysen CJ (1995) Herring gull *Larus argentatus* and lesser black-backed gull *L. Fuscus* feeding at fishing vessels in the breeding season: competitive scavenging versus efficient flying. *ARDEA-WAGENINGEN* **83**, 365–380.

Carter DO, Yellowlees D, Tibbett M (2007) Cadaver decomposition in terrestrial ecosystems. *Naturwissenschaften* **94**, 12–24. doi:10.1007/s00114-006-0159-1

Caughley G, Grigg GC, Smith L (1985) The effect of drought on kangaroo populations. *The Journal of Wildlife Management* **49**, 679–685. doi:10.2307/3801694

Clutton-Brock TH, Illius AW, Wilson K, Grenfell BT, MacColl ADC, Albon SD (1997) Stability and instability in ungulate populations: an empirical analysis. *The American Naturalist* **149**, 195–219. doi:10.1086/285987

Cochrane CH, Norton DA, Miller CJ, Allen RB (2003) Brushtail possum (*Trichosurus vulpecula*) diet in a north westland mixed-beech (*Nothofagus*) forest. *New Zealand Journal of Ecology* **27**, 61–65.

Coppola F, Guerrieri D, Simoncini A, Varuzza P, Vecchio G, Felicioli A (2020) Evidence of scavenging behaviour in crested porcupine. *Scientific Reports* **10**, 1–6. doi:10.1038/s41598-020-69252-z

Cortés-Avizanda A, Jovani R, Donázar JA, Grimm V (2014) Bird sky networks: how do avian scavengers use social information to find carrion? *Ecology* **95**, 1799–1808. doi:10.1890/13-0574.1

Crippen TL, Benbow ME, Pechal JL (2015) Microbial interactions during carrion decomposition. In 'Carrion ecology, evolution, and their applications'. (Eds ME Benbow, JK Tomberlin, AM Tarone) pp. 31–64. (CRC Press: Boca Raton, FL, USA)

Cunningham CX, Johnson CN, Barmuta LA, Hollings T, Woehler EJ, Jones ME (2018) Top carnivore decline has cascading effects on scavengers and carrion persistence. *Proceedings of the Royal Society B: Biological Sciences* **285**, 20181582. doi:10.1098/rspb.2018.1582

DeVault TL, Rhodes J, Olin E, Shivik JA (2003) Scavenging by vertebrates: behavioral, ecological, and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems. *Oikos* **102**, 225–234. doi:10.1034/j.1600-0706.2003.12378.x

Dickman CR (1996) 'Overview of the impacts of feral cats on Australian native fauna' (Australian Nature Conservation Agency: Canberra, ACT, Australia)

Dormann CF, McPherson JM, Araújo MB, Bivand R, Bolliger J, Carl G, Davies RG, Hirzel A, Jetz W, Daniel Kissling W, Kühn I, Ohlemüller R, Peres-Neto PR, Reineking B, Schröder B, Schurr FM, Wilson R (2007) Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography* **30**, 609–628. doi:10.1111/j.2007.0906-7590.05171.x

Dudley JP, Criag GC, Gibson DSC, Haynes G, Klimowicz J (2003) Drought mortality of bush elephants in Hwange National Park, Zimbabwe. *African Journal of Ecology* **39**, 187–194. doi:10.1046/j.0141-6707.2000.00297.x

Ekanayake KB, Whisson DA, Schlacher TA, Weston MA (2018) Urban corvids on the move: habitat use and movement ecology of the little raven *Corvus mellori* at a peri-urban wetland. *Corella* **42**, 29–37.

Enari H, Enari HS (2021) Not avian but mammalian scavengers efficiently consume carcasses under heavy snowfall conditions: a case from northern Japan. *Mammalian Biology* **101**, 419–428. doi:10.1007/s42991-020-00097-9

Evans MC (1992) Diet of the Brushtail Possum *Trichosurus vulpecula* (Marsupialia: Phalangeridae) in central Australia. *Australian Mammalogy* **15**, 25–30. doi:10.1071/AM92003

Evans MJ, Wallman JF, Barton PS (2020) Traits reveal ecological strategies driving carrion insect community assembly. *Ecological Entomology* **45**, 966–977. doi:10.1111/een.12869

Fielding MW, Buettel JC, Brook BW, Stojanovic D, Yates LA (2021) Roadkill islands: carnivore extinction shifts seasonal use of roadside carrion by generalist avian scavenger. *Journal of Animal Ecology* **90**, 2268–2276. doi:10.1111/1365-2656.13532

Fielding MW, Cunningham CX, Buettel JC, Stojanovic D, Yates LA, Jones ME, Brook BW (2022) Dominant carnivore loss benefits native avian and invasive mammalian scavengers. *Proceedings of the Royal Society B* **289**, 20220521. doi:10.1098/rspb.2022.0521

Fleming PA, Crawford HM, Stobo-Wilson AM, Dawson SJ, Dickman CR, Dundas SJ, Gentle MN, Newsome TM, O'Connor J, Palmer R, Riley J, Ritchie EG, Speed J, Saunders G, Stuart J-MD, Thompson E, Turpin JM, Woinarski JCZ (2021) Diet of the introduced red fox *Vulpes vulpes* in Australia: analysis of temporal and spatial patterns. *Mammal Review* **51**, 508–527. doi:10.1111/mam.12251

Flint PL, Lance EW, Sowl KM, Donnelly TF (2010) Estimating carcass persistence and scavenging bias in a human-influenced landscape in western Alaska. *Journal of Field Ornithology* **81**, 206–214. doi:10.1111/j.1557-9263.2009.00262.x

Forbes SL, Carter DO (2015) Processes and mechanisms of death and decomposition of vertebrate carrion. In 'Carrion ecology, evolution, and their applications'. (Eds ME Benbow, JK Tomberlin, AM Tarone) pp. 13–30. (CRC Press: Boca Raton, FL, USA)

Forsyth DM, Woodford L, Moloney PD, Hampton JO, Woolnough AP, Tucker M (2014) How does a carnivore guild utilise a substantial but unpredictable anthropogenic food source? Scavenging on hunter-shot ungulate carcasses by wild dogs/dingoes, red foxes and feral cats in south-eastern australia revealed by camera traps. *PLoS ONE* **9**, e97937. doi:10.1371/journal.pone.0097937

Grilli MG, Bildstein KL, Lambertucci SA (2019) Nature's clean-up crew: quantifying ecosystem services offered by a migratory avian scavenger on a continental scale. *Ecosystem Services* **39**, 100990. doi:10.1016/j.ecoser.2019.100990

Handler KS, Subalusky AL, Kendall CJ, Dutton CL, Rosi EJ, Post DM (2021) Temporal resource partitioning of wildebeest carcasses by scavengers after riverine mass mortality events. *Ecosphere* **12**, e03326. doi:10.1002/ecs2.3326

Hartig F, Hartig MF (2017) 'Package 'dharma'.' (R Development Core Team: Vienna, Austria)

Heinsohn TE, Barker R (2006) Observations of scavenging carnivory by the common brushtail possum *Trichosurus vulpecula* on macropod carcasses in Namadgi National Park, montane Southeastern Australia. *Australian Zoologist* **33**, 295–305. doi:10.7882/AZ.2006.003

Hopcraft JGC, Holdo RM, Mwangomo E, Mduma SAR, Thirgood SJ, Borner M, Fryxell JM, Olff H, Sinclair ARE (2015) Why are wildebeest the most abundant herbivore in the serengeti ecosystem? In 'Serengeti IV: sustaining biodiverstiy in a coupled human-natural system'. (Eds ARE Sinclair, KL Metzger, SAR Mduma, JM Fryxell) pp. 125–174. (University of Chicago Press: Chicago, IL, USA)

How RA, Hillcox SJ (2000) Brushtail possum, *Trichosurus vulpecula*, populations in south-western Australia: demography, diet and conservation status. *Wildlife Research* **27**, 81–89. doi:10.1071/WR98064

Inagaki A, Allen ML, Maruyama T, Yamazaki K, Tochigi K, Naganuma T, Koike S (2020) Vertebrate scavenger guild composition and utilization of carrion in an East Asian temperate forest. *Ecology and Evolution* **10**, 1223–1232. doi:10.1002/ece3.5976

Jedrzejewska B, Jedrzejewski W (1998) 'Predation in vertebrate communities: the bialowieza primeval forest as a case study.' (Springer Science & Business Media: Heidelberg, Germany)

Jones E, Coman BJ (1981) Ecology of the feral cat, *Felis catus* (L.), in south-eastern Australia I. Diet. *Wildlife Research* **8**, 537–547. doi:10.1071/WR9810537

Jones SC, Strauss ED, Holekamp KE (2015) Ecology of African carrion. In 'Carrion ecology, evolution, and their applications'. (Eds ME Benbow, JK Tomberlin, AM Tarone) pp. 461–491. (CRC Press: Boca Raton, FL, USA)

King NJ, Bagley PM, Priede IG (2006) Depth zonation and latitudinal distribution of deep-sea scavenging demersal fishes of the Mid-Atlantic Ridge, 42 to 53°N. *Marine Ecology Progress Series* **319**, 263–274. doi:10.3354/meps319263

Kinnear JE, Sumner NR, Onus ML (2002) The red fox in Australia: an exotic predator turned biocontrol agent. *Biological Conservation* **108**, 335–359. doi:10.1016/S0006-3207(02)00116-7

Knight MH (1995) Drought-related mortality of wildlife in the southern Kalahari and the role of man. *African Journal of Ecology* **33**, 377–394. doi:10.1111/j.1365-2028.1995.tb01047.x

Kostecke RM, Linz GM, Bleier WJ (2001) Survival of avian carcasses and photographic evidence of predators and scavengers. *Journal of Field Ornithology* **72**, 439–447. doi:10.1648/0273-8570-72.3.439

Krofel M, Kos I, Jerina K (2012) The noble cats and the big bad scavengers: effects of dominant scavengers on solitary predators. *Behavioral Ecology and Sociobiology* **66**, 1297–1304. doi:10.1007/s00265-012-1384-6

Lenth RV (2016) Least-squares means: the R package lsmeans. *Journal of statistical software* **69**, 1–33. doi:10.18637/jss.v069.i01

López-López P, Benavent-Corai J, García-Ripollés C, Urios V (2013) Scavengers on the move: behavioural changes in foraging search patterns during the annual cycle. *PLoS ONE* **8**, e54352. doi:10.1371/journal.pone.0054352

Mann RW, Bass WM, Meadows L (1990) Time since death and decomposition of the human body: variables and observations in case and experimental field studies. *Journal of Forensic Sciences* **35**, 103–111. doi:10.1520/JFS12806J

Mateo-Tomás P, Olea PP, Moleón M, Vicente J, Botella F, Selva N, Viñuela J, Sánchez-Zapata JA (2015) From regional to global patterns in vertebrate scavenger communities subsidized by big game hunting. *Diversity and Distributions* **21**, 913–924. doi:10.1111/ddi.12330

Mateo-Tomás P, Olea PP, Moleón M, Selva N, Sánchez-Zapata JA (2017) Both rare and common species support ecosystem services in scavenger communities. *Global Ecology and Biogeography* **26**, 1459–1470. doi:10.1111/geb.12673

Matuszewski S, Bajerlein D, Konwerski S, Szpila K (2010) Insect succession and carrion decomposition in selected forests of Central Europe. Part 1: pattern and rate of decomposition. *Forensic Science International* **194**, 85–93. doi:10.1016/j.forsciint.2009.10.016

McComb LB, Lentini PE, Harley DKP, Lumsden LF, Antrobus JS, Eyre AC, Briscoe NJ (2018) Feral cat predation on Leadbeater's possum (*Gymnobelideus leadbeateri*) and observations of arboreal hunting at nest boxes. *Australian Mammalogy* **41**, 262–265. doi:10.1071/AM18010

Merritt RW, De Jong GD (2015) Arthropod communities in terrestrial environments. In 'Carrion ecology, evolution, and their applications'. (Eds ME Benbow, JK Tomberlin, AM Tarone) pp. 65–92. (CRC Press: Boca Raton, FL, USA)

Moleón M, Sánchez-Zapata JA, Selva N, Donázar JA, Owen-Smith N (2014) Inter-specific interactions linking predation and scavenging in terrestrial vertebrate assemblages. *Biological Reviews* **89**, 1042–1054. doi:10.1111/brv.12097

Moleón M, Sánchez-Zapata JA, Sebastián-González E, Owen-Smith N (2015) Carcass size shapes the structure and functioning of an African scavenging assemblage. *Oikos* **124**, 1391–1403. doi:10.1111/oik.02222

Moleón M, Selva N, Quaggiotto MM, Bailey DM, Cortés-Avizanda A, DeVault TL (2019) Carrion availability in space and time. In 'Carrion ecology and management'. (Eds PP Olea, P Mateo-Tomás, JA Sánchez-Zapata) pp. 23–44. (Springer: Cham, Switzerland)

Moon DL (2005) A study of the abundance, distribution and daily activities of the australian raven (*Corvus coronoides*) in urban wetland parks. Bachelor of Arts Honours, Edith Cowan University.

Moreno-Opo R, Margalida A (2013) Carcasses provide resources not exclusively to scavengers: patterns of carrion exploitation by passerine birds. *Ecosphere* **4**, 1–15. doi:10.1890/ES13-00108.1

Moseby K, Hodgens P, Bannister H, Mooney P, Brandle R, Lynch C, Young C, Jansen J, Jensen M (2021) The ecological costs and benefits of a feral cat poison-baiting programme for protection of reintroduced populations of the western quoll and brushtail possum. *Austral Ecology* **46**, 1366–1382. doi:10.1111/aec.13091

Newsome TM, Spencer EE (2022) Megafires attract avian scavenging but carcasses still persist. *Diversity and Distributions* **28**, 515–528. doi:10.1111/ddi.13390

Newsome AE, Corbett LK, Catling PC, Burt RJ (1983) The feeding ecology of the dingo. 1. Stomach contents from trapping in south-eastern Australia, and the non-target wildlife also caught in dingo traps. *Wildlife Research* **10**, 477–486. doi:10.1071/WR9830477

Nugent G, Sweetapple P, Coleman J, Suisted P (2000) Possum feeding patterns: dietary tactics of a reluctant folivore. In 'The brushtail possum: biology, impact and management of an introduced marsupial'. (Ed. TL Montague) pp. 10–23. (Manaaki Whenua Press: Lincoln, New Zealand)

O'Brien RC, Larcombe A, Meyer J, Forbes SL, Dadour I (2010*a*) The scavenging behaviour of the Australian raven (*Corvus coronoides*): patterns and influencing factors. *Sylvia* **46**, 133–148.

O'Brien RC, Forbes SL, Meyer J, Dadour I (2010*b*) Forensically significant scavenging guilds in the southwest of Western Australia. *Forensic Science International* **198**, 85–91. doi:10.1016/j.forsciint.2010.01.006

Oksanen J, Simpson G, Blanchet F, Kindt R, Legendre P, Minchin P, O'Hara R, Solymos P, Stevens M, Szoecs E, Wagner H, Barbour M, Bedward M, Bolker B, Borcard D, Carvalho G, Chirico M, De Caceres M, Durand S, Evangelista H, FitzJohn R, Friendly M, Furneaux B, Hannigan G, Hill M, Lahti L, McGlinn D, Ouellette M, Ribeiro Cunha E, Smith T, Stier A, Ter Braak C, Weedon J (2022) vegan: Community Ecology Package. *R package version 2.6-4*. Available at https://CRAN.R-project.org/package=vegan

Owen HJ, Norton DA (1995) The diet of introduced brushtail possums *Trichosurus vulpecula* in a low-diversity New Zealand *Nothofagus* forest and possible implications for conservation management. *Biological Conservation* **71**, 339–345. doi:10.1016/0006-3207(94)00058-X

Pardo-Barquín E, Mateo-Tomás P, Olea PP (2019) Habitat characteristics from local to landscape scales combine to shape vertebrate scavenging communities. *Basic and Applied Ecology* **34**, 126–139. doi:10.1016/j.baae.2018.08.005

Pascoe JH, Mulley RC, Spencer R, Chapple R (2012) Diet analysis of mammals, raptors and reptiles in a complex predator assemblage in the Blue Mountains, eastern Australia. *Australian Journal of Zoology* **59**, 295–301. doi:10.1071/ZO11082

Peisley RK, Saunders ME, Robinson WA, Luck GW (2017) The role of avian scavengers in the breakdown of carcasses in pastoral landscapes. *Emu - Austral Ornithology* **117**, 68–77. doi:10.1080/01584197.2016.1271990

Pereira LM, Owen-Smith N, Moleón M (2014) Facultative predation and scavenging by mammalian carnivores: seasonal, regional and intra-guild comparisons. *Mammal Review* **44**, 44–55. doi:10.1111/mam.12005

Rahmstorf S, Coumou D (2011) Increase of extreme events in a warming world. *Proceedings of the National Academy of Sciences* **108**, 17905–17909. doi:10.1073/pnas.1101766108

Ray R-R, Seibold H, Heurich M (2014) Invertebrates outcompete vertebrate facultative scavengers in simulated lynx kills in the Bavarian Forest National Park, Germany. *Animal Biodiversity and Conservation* **37**, 77–88. doi:10.32800/abc.2014.37.0077

Read JL, Wilson D (2004) Scavengers and detritivores of kangaroo harvest offcuts in arid Australia. *Wildlife Research* **31**, 51–56. doi:10.1071/WR02051

Rees JD, Crowther MS, Kingsford RT, Letnic M (2020) Direct and indirect effects of carrion subsidies in an arid rangeland: carrion has positive effects on facultative scavengers and negative effects on a small songbird. *Journal of Arid Environments* **179**, 104174. doi:10.1016/j.jaridenv.2020.104174

Robertson G (1986) The mortality of kangaroos in drought. *Wildlife Research* **13**, 349–354. doi:10.1071/WR9860349

Rød-Eriksen L, Skrutvold J, Herfindal I, Jensen H, Eide NE (2020) Highways associated with expansion of boreal scavengers into the alpine tundra of Fennoscandia. *Journal of Applied Ecology* **57**, 1861–1870. doi:10.1111/1365-2664.13668

Sakamoto Y, Ishiguro M, Kitagawa G (Ed.) (1986) 'Akaike information criterion statistics' (D. Reidel: Dordrecht, The Netherlands).

Santos RAL, Santos SM, Santos-Reis M, Picanço de Figueiredo A, Bager A, Aguiar LMS, Ascensão F (2016) Carcass persistence and detectability: reducing the uncertainty surrounding wildlife-vehicle collision surveys. *PLoS ONE* **11**, e0165608. doi:10.1371/journal.pone.0165608

Schoenly KG, Michaud J-P, Moreau G (2015) Design and analysis of field studies in carrion ecology. In 'Carrion ecology, evolution, and their applications'. (Eds ME Benbow, JK Tomberlin, AM Tarone) pp. 129–148. (CRC Press: Boca Raton, FL, USA)

Sebastián-González E, Barbosa JM, Pérez-García JM, Morales-Reyes Z, Botella F, Olea PP, Mateo-Tomás P, Moleón M, Hiraldo F, Arrondo E, *et al.* (2019) Scavenging in the anthropocene: human impact drives vertebrate scavenger species richness at a global scale. *Global Change Biology* **25**, 3005–3017. doi:10.1111/gcb.14708

Selva N, Fortuna MA (2007) The nested structure of a scavenger community. *Proceedings of the Royal Society B: Biological Sciences* **274**, 1101–1108. doi:10.1098/rspb.2006.0232

Selva N, Jedrzejewska B, Jedrzejewski W, Wajrak A (2003) Scavenging on European bison carcasses in Bialowieza Primeval Forest (eastern Poland). *Écoscience* **10**, 303–311. doi:10.1080/11956860.2003.11682778

Selva N, Jędrzejewska B, Jędrzejewski W, Wajrak A (2005) Factors affecting carcass use by a guild of scavengers in European temperate woodland. *Canadian Journal of Zoology* **83**, 1590–1601. doi:10.1139/z05-158

Selva N, Moleón M, Sebastián-González E, DeVault TL, Quaggiotto MM, Bailey DM, Lambertucci SA, Margalida A (2019) Vertebrate scavenging communities. In 'Carrion ecology and management'. (Eds PP Olea, P Mateo-Tomás, JA Sánchez-Zapata) pp. 71–99. (Springer: Cham, Switzerland)

Skellam JG (1967) Seasonal periodicity in theoretical population ecology. In 'Proceedings of the 5th Berkeley symposium on mathematical statistics and probability'. (Eds LM Le Cam, J Neyman) pp. 179–205. (University of California Press: Berkeley and Los Angeles, USA)

Somerfield PJ, Clarke KR, Gorley RN (2021) Analysis of similarities (ANOSIM) for 2-way layouts using a generalised anosim statistic, with comparative notes on permutational multivariate analysis of variance (PERMANOVA). *Austral Ecology* **46**, 911–926. doi:10.1111/aec.13059

Sotillo A, Depestele J, Courtens W, Vincx M, Stienen EWM (2014) Consumption of discards by herring gulls *Larus argentatus* and lesser black-backed gulls *Larus fuscus* off the belgian coast in the breeding season. *Ardea* **102**, 195–206. doi:10.5253/arde.v102i2.a9

Spencer E, Newsome T (2021) Dingoes dining with death. *Australian Zoologist* **41**, 433–451. doi:10.7882/AZ.2021.008

Spencer EE, Dickman CR, Greenville A, Crowther MS, Kutt A, Newsome TM (2021) Carcasses attract invasive species and increase artificial nest predation in a desert environment. *Global Ecology and Conservation* **27**, e01588. doi:10.1016/j.gecco.2021.e01588

Subalusky AL, Dutton CL, Rosi EJ, Post DM (2017) Annual mass drownings of the Serengeti wildebeest migration influence nutrient cycling and storage in the Mara River. *Proceedings of the National Academy of Sciences* **114**, 7647–7652. doi:10.1073/pnas.1614778114

Subalusky AL, Dutton CL, Rosi EJ, Puth LM, Post DM (2020) A river of bones: wildebeest skeletons leave a legacy of mass mortality in the Mara River, Kenya. *Frontiers in Ecology and Evolution* **8**, 31. doi:10.3389/fevo.2020.00031

Sweetapple PJ, Fraser KW, Knightbridge PI (2004) Diet and impacts of brushtail possum populations across an invasion front in south westland, New Zealand. *New Zealand Journal of Ecology* **28**, 19–33.

Turner KL, Abernethy EF, Conner LM, Rhodes OE Jr., Beasley JC (2017) Abiotic and biotic factors modulate carrion fate and vertebrate scavenging communities. *Ecology* **98**, 2413–2424. doi:10.1002/ecy.1930

Vernes K, Dennis A, Winter J (2001) Mammalian diet and broad hunting strategy of the dingo (*Canis familiaris dingo*) in the wet tropical rain forests of northeastern Australia. *Biotropica* **33**, 339–345. doi:10.1111/j.1744-7429.2001.tb00185.x

Ward M, Tulloch AIT, Radford JQ, Williams BA, Reside AE, Macdonald SL, Mayfield HJ, Maron M, Possingham HP, Vine SJ, O'Connor JL, Massingham EJ, Greenville AC, Woinarski JCZ, Garnett ST, Lintermans M, Scheele BC, Carwardine J, Nimmo DG, Lindenmayer DB, Kooyman RM, Simmonds JS, Sonter LJ, Watson JEM (2020) Impact of 2019–2020 mega-fires on Australian fauna habitat. *Nature Ecology & Evolution* **4**, 1321–1326. doi:10.1038/s41559-020-1251-1

Whisson DA, Weston MA, Shannon K (2015) Home range, habitat use and movements by the little raven (*Corvus mellori*) in a coastal peri-urban landscape. *Wildlife Research* **42**, 500–508. doi:10.1071/WR15039

White TCR (2011) The significance of unripe seeds and animal tissues in the protein nutrition of herbivores. *Biological Reviews* **86**, 217–224. doi:10.1111/j.1469-185X.2010.00143.x

Wiggins NL, McArthur C, McLean S, Boyle R (2003) Effects of two plant secondary metabolites, cineole and gallic acid, on nightly feeding patterns of the common brushtail possum. *Journal of Chemical Ecology* **29**, 1447–1464. doi:10.1023/A:1024221705354

Wilmers CC, Getz WM (2004) Simulating the effects of wolf-elk population dynamics on resource flow to scavengers. *Ecological Modelling* **177**, 193–208. doi:10.1016/j.ecolmodel.2004.02.007

Wilmers CC, Post E (2006) Predicting the influence of wolf-provided carrion on scavenger community dynamics under climate change scenarios. *Global Change Biology* **12**, 403–409. doi:10.1111/j.1365-2486.2005.01094.x

Wilmers CC, Crabtree RL, Smith DW, Murphy KM, Getz WM (2003) Trophic facilitation by introduced top predators: grey wolf subsidies to scavengers in Yellowstone National Park. *Journal of Animal Ecology* **72**, 909–916. doi:10.1046/j.1365-2656.2003.00766.x

Wilson EE, Wolkovich EM (2011) Scavenging: how carnivores and carrion structure communities. *Trends in Ecology & Evolution* **26**, 129–135. doi:10.1016/j.tree.2010.12.011

Data availability. Data available on request.

Conflicts of interest. Thomas Newsome is an Associate Editor of Wildlife Research but was blinded from the peer-review process for this paper.

Declaration of funding. Funding for this work was provided by the Australian Alps National Parks Cooperative Management Program.

Acknowledgements. We are indebted to the National Parks and Wildlife Service of Kosciuszko National Park for field support and providing park access and accommodation during field work. We are also eternally grateful for the support and hospitality provided by Ted Rowley and Jo Oddie throughout the course of this work. We also thank the numerous field volunteers and members of the Global Ecology Lab for their various contributions. This paper forms part of the first authors (James Vandersteen) MPhil(Sci) thesis entitled 'Scavenging Dynamics of the Australian Alps' (2022).

Author affiliations

[A]School of Life and Environmental Sciences, The University of Sydney, Sydney, NSW 2006, Australia.

[B]School of Biological, Earth, and Environmental Sciences, The University of New South Wales, Sydney, NSW 2052, Australia.

[C]Institute for Marine and Antarctic Studies, University of Tasmania, Battery Point, Tas. 7004, Australia.

[D]Future Regions Research Centre, Federation University, Ballarat, Vic. 3353, Australia.