

Moose (*Alces alces*) hunters subsidize the scavenger community in Alaska

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Abstract In many temperate ecosystems animal carcasses resultant from wildlife harvest can provide a high-quality food source for myriad facultative scavengers. We investigated scavenger use of human-provisioned ungulate carrion from a fall moose (*Alces alces*) hunt during 2010 and 2011 on the Gustavus Forelands, Alaska, USA. Using data from remote cameras, we (1) identified the scavenger species that used these resources and (2) evaluated their spatial and temporal responses to this seasonal resource event by indexing their activity patterns and relative order of arrival at carrion sites. We also quantified the length of time carrion persisted and estimated the amount of moose biomass provisioned to vertebrate scavengers by human hunters. Our results indicated that 11 vertebrate species (five birds and six mammals) scavenged moose carrion. We found that the common raven was the only species documented at all carrion sites and the most abundant species at

moose carrion sites. As a species group, corvids [black-billed magpie (*Pica hudsonia*), common raven (*Corvus corax*); 0.1 ± 2.3 days] were the first to arrive at human-provisioned moose carrion sites, whereas ursids [brown bear (*Ursus arctos*), black bear (*U. americanus*); 1.3 ± 1.0 days] arrived after corvids but sooner than expected and canids [gray wolf (*Canis lupus*), coyote (*C. latrans*); 3.9 ± 3.0] arrived later than expected compared to our null model. On average, carrion persisted >20 days and hunters provided scavengers with a minimum of 2720 kg (82.7 kg/km^2) and 1815 kg (64.8 kg/km^2) of moose carrion during 2010 and 2011, respectively. Understanding how scavengers, particularly large carnivores, interact with human-provisioned moose carrion at the rural–wildland interface is essential for mitigating potential human–wildlife conflicts associated with humans subsidizing predators with a high-quality food resource.

Keywords Canids · Corvids · Carrion · Moose · Scavengers · Subsidies

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Introduction

Consumers exploit diverse food resources using a variety of foraging strategies. Yet the extent to which vertebrate consumers that are characterized as predators engage in facultative scavenging largely has been ignored in studies of community ecology (Wilson and Wokovick 2011; Oro et al. 2013; Moleón et al. 2014; Pereire et al. 2014). However, facultative scavenging can give consumers access to high-quality food without consumers expending energy to chase, capture and kill prey (Wilmers et al. 2003a, b; Haroldson et al. 2004; White 2006), thus scavenging has been identified as a key ecological process in

food web dynamics (DeVault et al. 2003; Selva 2004; Wilson and Wokovick 2011).

In temperate ecosystems, scavenging of animal carcasses resultant from seasonal wildlife harvest—especially ungulates—represents a potentially substantial resource in the form of a resource pulse because hunter kills often are spatially aggregated and occur over relatively short time periods (Wilmers et al. 2003b; Haroldson et al. 2004; White 2006; Mateo-Tomás et al. 2015). Moreover, there is evidence to suggest that human-provisioned carrion could reduce predation rates in the short term by providing predators a resource that does not require additional prey mortality, provided that carrion resources do not result in a positive numerical response by the species scavenging these resources (Wilson and Wokovick 2011; Moleón et al. 2014). Most species that are able to take advantage of human-provisioned ungulate carrion are generalist consumers that are capable of shifting facultatively between predation and scavenging (Wilmers et al. 2003b; White 2006). However, in rural communities where ungulate hunting occurs in close proximity to human establishments, human-provisioned carrion may influence the spatial and temporal patterns of generalist consumers including gray wolves (*Canis lupus*), black bears (*Ursus americanus*) and brown bears (*U. arctos*), which could result in increased incidences of human–large carnivore interactions and conflicts. Yet, data on scavenger community use of human-provisioned carrion are lacking for most terrestrial ecosystems (Mateo-Tomás et al. 2015).

Our goal was to investigate scavenger use of human-provisioned ungulate carrion from a regulated annual fall moose (*Alces alces*) hunt in the Gustavus-Glacier Bay Ecosystem, Alaska, USA. Using remote cameras, we identified the scavenger species that used these resources and evaluated their spatial and temporal responses to this seasonal resource event. For the most common scavenger species documented at moose carrion sites, we indexed their daily activity patterns to better understand temporal patterns in scavenger use of human-provisioned resources. We also assessed the relative order of scavenger species arrival at carrion sites and examined whether any correlations existed between scavenger species at carrion sites. Finally, we quantified the length of time carrion persisted and estimated the amount of moose biomass provisioned to vertebrate scavengers by human hunters.

Materials and methods

Study area

This study was conducted during the annual moose hunt (September 15–October 15, 2010–2011) on the 102 km²

Gustavus forelands (58°24′59.10″N, 35°44′43.81″W; Fig. 1), named for the town of Gustavus (pop. 442; United States Census Bureau 2010) and the flat, coastal topography (i.e., sea level to 36.5 m) in contrast to surrounding mountains. The Gustavus forelands are bordered by Glacier Bay National Park and Preserve (13,289 km²) to the west, north and east and the Pacific Ocean to the south and serve as the winter range for a partially migratory moose population that congregates on the forelands during October through April (winter moose density on the forelands varied between 2.4 and 4.8 moose/km² from 2004 to 2010; White et al. 2014). The forelands are a mosaic of wetlands, forests dominated by Sitka spruce (*Picea sitchensis*), willow (*Salix* spp.) thickets, herbaceous beach meadows and human development (Streveler et al. 2003). Additionally, numerous low-elevation streams support spawning Pacific salmon (*Oncorhynchus* spp.) between July and October in the study area (C. Murdoch, NPS fisheries biologist, personal communications), which may provide important alternative food resources for predators. Typical cool maritime weather conditions prevailed during the study period with September temperatures ranging from 0.6 to 22.2 °C in 2010 and 0.6 to 18.3 °C in 2011 and October temperatures ranging from −2.2 to 13.9 °C in 2010 and −2.2 to 11.7 °C in 2011 (<http://marine.weather.gov>, accessed August 7, 2015).

Moose carrion monitoring

We located remains of hunter-killed moose by communicating directly with hunters, Alaska Department of Fish and Game (ADFG) biologists and Alaska Wildlife Troopers responsible for evaluating whether harvested moose met legal guidelines for the antler-restricted harvest. In 2010, 13 moose were harvested in a 33 km² area, and in 2011, 8 moose were harvested in a partially overlapping 28 km² area (Fig. 1); harvest locations were characterized as wet or upland meadows.

Moose remains often were located while hunters were still present at harvest sites. During 2010, however, there were three cases in which moose remains were not located until >24 h post-harvest due to extreme weather conditions (e.g., winds >63 km/h) and one case in which moose remains were not located until 2–3 days post-harvest. In two of these cases, the sites appeared to be undisturbed by scavengers as evidenced by a lack of hair plucking from the hide, absence of bone fragments, the carrion was in a single heap upon our arrival and there was no evidence of avian or mammalian tracks or feces at these sites. Although in two cases, including the remains located 2–3 days post-harvest, carcasses were evidently scavenged before we located them. For statistical analyses, we excluded the two sites where there was evidence of scavenging activities prior to

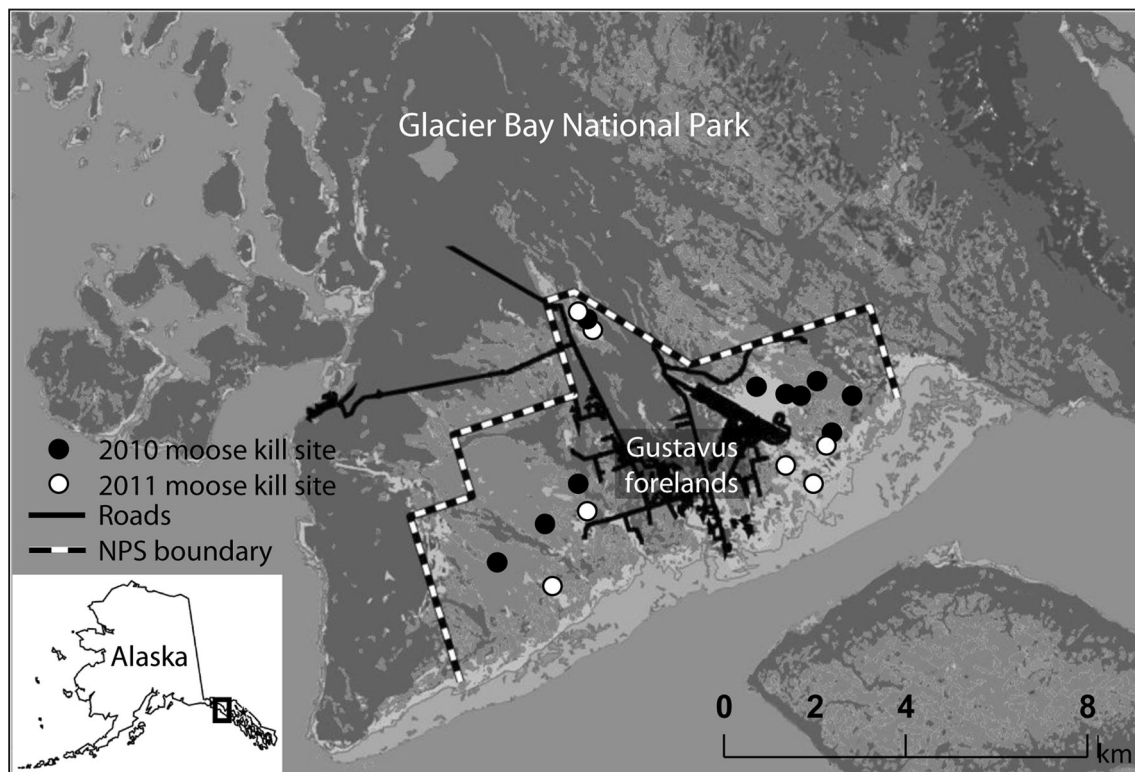


Fig. 1 Gustavus forelands, southeastern Alaska, USA ($58^{\circ}24'59.10''\text{N}$, $135^{\circ}44'43.81''\text{W}$), showing locations of monitored moose (*Alces alces*) carrion during the 2010 (black circles) and 2011 (white circles) hunts

our arrival; data from these sites were used for descriptive purposes only. In addition, one camera malfunctioned resulting in no data. In 2011, we were present during or immediately following (<1 h) field-butchered at all moose harvest sites except one, which we located within a few hours post-harvest. This site appeared undisturbed upon our arrival, although ravens and a bald eagle were observed in the trees near the site (D. Lafferty, personal observations). Additionally, we were unable to locate the remains of one moose in 2010 and one moose in 2011, although we were able to communicate directly with the hunters to gather information about the approximate location and quality/quantity of the remains available to scavengers.

When we arrived at carrion sites, we recorded the location using a global positioning system (GPS) and recorded the harvest date. We classified the carrion as Type 1 or Type 2. Type 1 carrion consisted of viscera, head, vertebral column, lower legs and hide, whereas Type 2 consisted of viscera, viscera and hide, or viscera, hide and lower legs (see below for samples sizes for each carrion type). To monitor the carrion, we deployed a motion-detecting digital camera (Trail Watcher Model 2035) to document scavenger use of carrion 24 h per day; nighttime images were possible via a white flash. Cameras were attached to trees or shrubs 2–4 m from the moose remains

and about 0.5–1 m above ground, set for a 20 s delay between detections and checked every 3–10 days to exchange media cards and replace batteries as needed. For each image obtained, we recorded date, time and number of individuals of each species present that appeared to be scavenging the moose remains. When only skeletal components remained, the resource was assumed depleted when no vertebrates were recorded interacting with the carrion for 10 consecutive days, at which point the camera was removed.

Estimating total hunter provided moose carrion

We estimated the total biomass of human-provisioned moose carrion available to scavengers on the Gustavus forelands using moose weight and harvest data from Titus et al. (2009). When viscera, head, vertebral column, lower legs and hide remained (Type 1), we estimated the amount of carrion available to scavengers to be 300 kg/moose. When Type 2 carrion remained (viscera, viscera and hide, or viscera, hide and lower legs), we estimated the amount of carrion available was 14 % (105 kg; Wilmers et al. 2003b) of moose live weight (750 kg; Titus et al. 2009); thus, our estimates may be conservative. To estimate density of human-provisioned moose carrion per km^2 per

year, we divided estimated moose carrion biomass by the total area within a minimum polygon drawn around the location of moose harvest sites each year.

Statistical analyses

First, we tested whether there were correlations between scavenger species and carcass type (i.e., Type 1, Type 2) as well as all pairwise correlations between species using Pearson product moment correlations with a meaningful correlation cutoff of $|r| > 0.5$ (Dormann et al. 2013). For subsequent analyses, due to the limited number of detections for several species at moose carcass sites, we binned species into three groups: corvid (common raven, magpie), canid (gray wolf, coyote) and ursid (black bear, brown bear). All other species detected at carrion sites were excluded from statistical analysis due to low numbers of detections. For example, although bald eagles were detected at $> 23\%$ of sites, the site where eagles were most active was scavenged before our arrival and deployment of a camera, and thus, data from this site were excluded from statistical analyses because we were unable to assess scavenger arrival times at this site.

We tested whether the arrival time of the first corvid, canid and ursid across carcasses differed using ANOVA of log-transformed arrival times to meet normality assumptions, with time to arrival following human departure at each site as the dependent variable and species group as the independent variable. We also examined whether the distribution of initial arrival times of canids and ursids relative to the first occurrence of corvids at each carcass differed from random and whether occurrence was sooner or later (two-tailed test) than expected from our neutral model. We generated 10,000 random mammal occurrence times per carcass using a uniform distribution bounded by the first and last corvid occurrence at each carcass. We then calculated the lag time between the randomly generated mammal occurrence time and time since the previous corvid was present at the carcass. These data were gamma distributed, and formed our neutral model for mammal lag time following corvids. We fitted both the simulated and observed data to gamma distributions using a generalized linear mixed-effect model using SAS Proc Glimmix (Bolker 2008, SAS Institute, Cary, NC). We tested whether arrival times differed between randomly generated and observed points for canids and ursids separately (Littell et al. 2006). We used individual carcasses as a random effect level to account for the within-carcass correlation for the randomly generated arrival points using an alpha level of 0.05. Statistical tests were performed on logit transformed data, while back-transformed mean estimates and standard error means are reported.

Results

In 2010, 13 harvested moose remains available to scavengers consisted of seven Type 1 and six Type 2 remains (Table 1). In 2011, eight harvested moose remains available to scavengers consisted of five Type 1 and three Type 2 remains. We recorded 9025 images of which 7115 contained wildlife. We recorded 11 vertebrate species (i.e., 5 avian, 6 mammalian) scavenging moose remains; moose as well as domestic dogs accompanied by humans were detected at multiple sites but were excluded from analyses because there were no images that suggested these species scavenged the carrion (Table 2). The number of species recorded foraging at carrion sites ranged from one to five ($\bar{x} = 3.2 \pm 0.2$ SE), and we recorded several instances of multiple species foraging simultaneously such as ravens, magpies and wolves as well as ravens, magpies and brown bear. The most commonly recorded species at carrion sites were common ravens, magpies, brown bear, black bear and wolves as indexed by the number of images per hour across all carrion sites (Fig. 2). Common ravens and magpies were most active during the day from about 9:00 am to 5:00 pm, whereas brown bears and black bears were active throughout much of the day, although black bears exhibited a peak in activity in the late afternoon (Fig. 2). Wolves were most active between midnight and 9:00 am with a second peak in activity around 3:00 pm. Common ravens were the only species detected at every site and were detected in greater numbers (range 1–29) than all other species. On average, the maximum number of ravens foraging concurrently per site was more than twice the maximum number of individuals foraging together for any other species. In addition to scavengers consuming moose tissue and bone, we documented black bears consuming rumen contents and common snipe (*Gallinago gallinago*) foraging in the rumen contents, although we were unable to determine whether the snipe were consuming rumen contents or invertebrates (e.g., insect larvae) associated with the rumen contents.

We found no correlations between scavenger species and carrion type (Type 1, Type 2; $|r|$ range from 0.09 to 0.42), and thus, we did not differentiate carrion type during subsequent analyses. Further, we found no correlations between scavenger species at moose carrion sites. However, arrival times of species groups at carcasses differed ($F_{2,31} = 7.64$, $P = 0.002$); mean first corvid arrival was 0.1 ± 2.3 days, ursid first arrival was 1.3 ± 1.0 days and canid first arrival was 3.9 ± 3.0 days. Although avian scavengers typically arrived sooner at moose carrion sites compared to mammalian scavengers, the arrival time of ursids relative to corvids was sooner than expected based on the null model ($F_{1,69999} = 3.93$, $P = 0.047$). Model

Table 1 Human-provisioned moose carrion by type, approximate size of the harvest area and estimated moose carrion biomass available to scavengers, Gustavus, Alaska, USA, 2010–2011

Year	Moose carrion type			
	Type 1 ^a (300 kg)	Type 2 ^b (105 kg)	Harvest area (km ²)	Estimated carrion biomass (km ²)
2010	7	6	33	2730
2011	5	3	28	1815

Carrion weight estimated based on values from Titus et al. (2009)

^a Type 1 consists of viscera, head, vertebral column, lower legs and hide

^b Type 2 consists of viscera, viscera and hide, or viscera, hide and lower legs

Table 2 Species documented at 17 hunter-harvested moose carrion sites, Gustavus, Alaska, USA, 2010–2011

Species		Percentage of sites	Summary statistics for number of individuals recorded at one time		
Common name	Scientific name		Mean	SE	Range
American robin	<i>Turdus migratorius</i>	11.8	1	–	0–1
Common snipe	<i>Gallinago gallinago</i>	5.9	2	–	0–2
Common raven	<i>Corvus corax</i>	100.0	12.4	1.7	1–29
Magpie	<i>Pica hudsonia</i>	76.5	4.4	0.7	0–9
Bald eagle	<i>Haliaeetus leucocephalus</i>	23.5	1	–	0–1
Short-tailed weasel	<i>Mustela erminea</i>	5.9	1	–	0–1
American marten ^a	<i>Martes americana</i>	5.9	1	–	0–1
Coyote	<i>Canis latrans</i>	11.8	1	–	0–1
Gray wolf	<i>Canis lupus</i>	41.2	1.6	0.4	0–4
Black bear	<i>Ursus americanus</i>	23.5	2.3	0.8	0–4
Brown bear	<i>Ursus arctos</i>	35.3	1	–	0–1
Domestic dog ^a	<i>Canis familiaris</i>	11.8	1	–	0–1
Moose ^a	<i>Alces alces</i>	47.1	1.4	0.2	0–2

Also shown are the percentage of sites at which each species was documented and summary statistics for the mean number of individuals of each species recorded at each carrion site at one time

^a Moose and domestic dogs were recorded at multiple sites but were not recorded scavenging moose carrion. An American marten was recorded in a single image, but we could not discern whether this animal scavenged the moose remains from this image

predicted ursid arrival times following corvids occurred in 0.6 ± 0.3 days, while random expected arrival times for ursids was 1.7 ± 0.5 days. Arrival time of canids was later than expected relative to the initial arrival time of corvids ($F_{1,79999} = 6.10$, $P = 0.012$). Model predicted canid arrival times following corvids was 3.4 ± 2.2 days, while random expected arrival times given the camera trap occurrence of corvids was 1.3 ± 0.6 days.

On average, Type 1 carrion persisted for 34.6 ± 13.2 days and Type 2 carrion persisted for 21.1 ± 4.6 days across years. However, the difference in average persistence time for Type 1 and Type 2 carrion was driven by a single Type 1 carrion site that persisted for >161 days. When this outlier was removed, the differences in the average time Type 1 (20.6 ± 4.4) and Type 2 (21.1 ± 4.6) carrion persisted was small (<0.6 days). When we considered all human-provisioned moose carrion on an annual

basis, carrion persisted for 28.2 ± 9.6 days (range 6–161 days) in 2010 and 22.6 ± 5.6 days (range 5–41) in 2011. In addition, we estimated a minimum of 2720 kg (82.7 kg/km^2) and 1815 kg (64.8 kg/km^2) of human-provisioned moose carrion was available during 2010 and 2011, respectively.

Discussion

In our tightly circumscribed study area, moose hunters provided a substantial and relatively persistent resource subsidy to an assemblage of mammalian and avian scavengers during the fall of 2010 and 2011 as evidenced by the remains of all located harvested moose being scavenged. However, documenting scavenger use and activities at human-provisioned moose carrion sites using remote

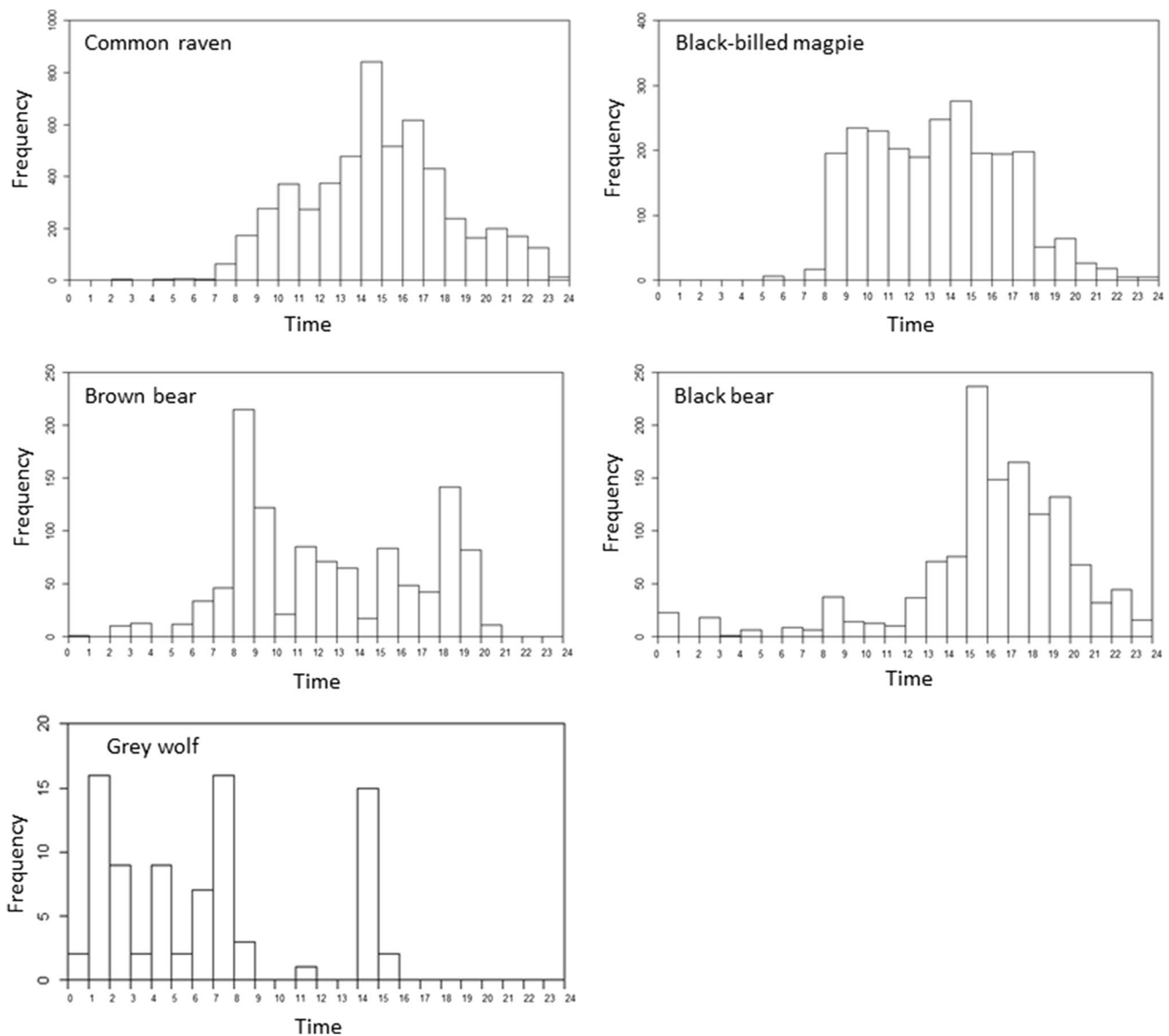


Fig. 2 Index of scavenger species activity patterns at human-provisioned moose (*Alces alces*) carrion based on the number of images per hour by species across all carrion sites, Gustavus forelands, southeastern Alaska, USA

cameras is not with biases despite being a relatively non-invasive approach. Recent studies provide evidence that the noise as well as the flash associated with remote cameras can startle animals and may dissuade some individuals from accessing an area where a camera is active (reviewed by Gibeau and McTavish 2009; Meek et al. 2014, 2015). For instance, the single image we recorded of an American marten (*Martes americana*) at one of our moose carrion sites occurred at night and the white flash seemed to have startled the animal. Further, at multiple sites where wolves were recorded scavenging at night, the wolves initially appeared to be startled by the flash but continued to forage; however, in two instances wolves dragged moose rib cages out of the range of the motion detector after several images

were captured using the white flash. During the day, we also recorded several images in which different species (i.e., common raven, black bear, brown bear, wolves) appeared to respond to the noises emitted from the camera. On one occasion following a series of images of a black bear caching a moose viscera (Type 2 carrion), the animal appeared to be curious about the noises from the camera and subsequently put its entire mount over the camera before returning for the cache pile. On a second occasion, a brown bear appeared to hear noises from the camera and the animal swiped the camera with its paw but then returned to forage on the carrion.

Despite potential biases imposed by the cameras, as expected, avian scavengers typically arrived first at moose

carriage sites. In fact, common ravens, magpies and eagles often were observed in the trees in the immediate area of a harvested moose while humans were present at the sites field-dressing the moose carcasses. Also, it is logical that common ravens were detected at all the monitored moose carriage sites and that this species typically was the first to arrive because common ravens are the vertebrate species most often observed in the study area (D. Lafferty, personal observations). Furthermore, common ravens have large foraging radii and are thought to use social communication to transmit the location of foraging sites at communal roosts (Heinrich 1988, Marzluff et al. 1996). Previous studies also have shown that common ravens are very efficient at locating carriage (Stahler et al. 2002, Selva 2004), whereas White (2005, 2006) demonstrated that common ravens may fly toward gun shots, presumably to gain access to carriage left by hunters. Black-billed magpies on the other hand, which also are common in the study area (D. Lafferty, per. obs) but have relatively small foraging radii (Trost 1999), were observed at 76 % of carriage sites. Although common in the area, bald eagles occur at lower densities than corvids and were observed less frequently in the study area (D. Lafferty, personal observations), and thus, it was not surprising that bald eagles were recorded at only a few sites.

We also recorded images of other avian species at moose carriage sites as well as a few relatively rare images of small- to medium-sized mammals. For example, common snipe were recorded at one site over several nights, whereas American robin were recorded at two sites during the day. However, we were unable to discern whether these avian consumers were foraging on the carriage, rumen content, or invertebrates associated with the decomposing moose carcass. Coyotes were documented at two sites; anecdotally, coyote numbers and/or activity on the Gustavus forelands has declined in recent years due to increased wolf activity (G. Streveler, NPS biologist, retired, personal communications). A short-tailed weasel (*Mustela ermine*) was documented on multiple occasions at a single site. The moose carcass associated with this site was initially located in a meadow within 5 m of a small grove of Sitka spruce trees; however, a brown bear dragged the entire carcass remains into the bank of trees within 24 h, at which time we relocated the camera to the 'new' site. As such, it is possible that we missed the arrival of some species when the brown bear dragged the carcass into the trees. As an interesting note, wolverine (*Gulo gulo*), perhaps the most iconic scavenger species in Alaska, was not detected at any of the carriage sites, although this species is occasionally trapped by fur trappers on the Gustavus forelands (D. Lafferty and K. White, personal observations).

When large-bodied mammalian scavengers were recorded at human-provisioned moose carriage sites, these

species typically arrived after avian scavengers. For example, ursids arrived less than 2 days after the arrival of the first corvids, whereas canids did not arrive at carriage sites until more than 3 days after the arrival of the first corvids. The non-random temporal pattern in ursid and canid activity at moose carcasses may be due to multiple interacting factors. First, the ability for avian species to locate human-provisioned moose carriage may be enhanced by aerial searching, thus allowing avian species the opportunity to exploit these resources before large mammals are able to locate the site. Ursids and canids also occur at much lower densities than avian scavengers. For instance, Pinjuv (2013) estimated the black bear population in the greater Gustavus area to be 27.0/100 km², whereas after being extirpated by homesteaders from southeastern Glacier Bay by the 1960s (NPS 2009), brown bears have only recently begun to recolonizing this area and occur at a minimum density of 6.5/100 km² (Pinjuv 2013). In addition, only one wolf pack of 8–12 wolves and a solitary female wolf were known to include the Gustavus forelands in their home ranges during the 2010 and 2011 study period (wolf density 0.8/100 km²; White et al. 2014). Further, the Gustavus forelands are located at the southern end of the home range of the resident wolf pack (Lafferty et al. 2014) and members of this pack typically were present on the Gustavus forelands for 1–2 days every 10–14 days (D. Lafferty personal observations). As such, wolves may have been absent on the forelands when some of the moose carriage became available, resulting in wolves arriving at carriage sites later than other species.

Since the inaugural moose hunt in 1989, the number of moose harvested on the Gustavus forelands has ranged from 2 to 116 annually. Moreover, bear and wolf hunting seasons coincided with moose hunting season, and ursids and canids (i.e., wolves, coyotes) are opportunistically harvested by moose hunters (personal observations D. Lafferty and K. White). In fact, we documented multiple wolves and black bears being harvested by moose hunters, which contributed additional carriage to scavengers and may have conditioned the observed consumption patterns. Further, ursids and canids may have avoided visiting recently harvested moose carcasses due to the high level of human activity associated with moose harvest locations (e.g., field dressing, other hunters), thus arriving much later than avian scavengers. A large bull moose that was suspected of having died of natural causes (e.g., infection associated with a festering ankle wound; personal communications. A. Achey, DVM, D. Lafferty personal observations) also was found within the study area, although this carcass was not scavenged until after the carcass had been frozen solid during the winter. In addition to human-provisioned carriage, Pacific salmon (*Oncorhynchus* spp.) represent a potentially important food source

for predators and are available in numerous streams on the Gustavus forelands as well as in numerous low-elevation streams in the surrounding national park (C. Murdoch, NPS fisheries biologist, personal communications). Thus, despite relatively small moose harvests during 2010 and 2011 (13 and 8 moose, respectively) and the additional carrion to scavengers (e.g., wolf and bear carcasses), the persistence of human-provisioned moose carrion for >20 days, on average, may have been a result of resource saturation.

Human-provisioned resource subsidies have been shown to lead to increased scavenger activity and densities while the resource persists (Wilmers et al. 2003b). Because most carnivores are facultative scavengers and resource subsidies can influence the distribution of these consumers, scavenging can have a profound effect on community structure and dynamics (reviewed in DeVault et al. 2003; Wilson and Wokovick 2011; Moleón et al. 2014; Pereire et al. 2014). For instance, survival and reproduction in ravens, magpies and bald eagles are correlated with the availability of high-quality food resources (Newton et al. 1982; Swenson et al. 1986). Hilderbrand et al. (1999) found that female bears with access to nutrient-rich foods, such as animal matter, attained larger body sizes, matured earlier and produced larger litters compared to female bears that consumed foods of lower digestible energy and protein (e.g., vegetation). In addition, Beckmann and Berger (2003) showed that access to anthropogenic food (i.e., garbage) resulted in black bear densities in Nevada that were three times greater than historic densities, and that female black bears with access to anthropogenic food at the rural–wildland interface gave birth to three times the number of cubs compared to wildland conspecifics. An increase in human-provisioned carrion could also reduce the impacts of predation by providing predators an alternative high-quality resource, as long as the time frame over which the subsidy is available does not permit a numerical response by the predator population ultimately leading to increased pressure on local prey (Moleón et al. 2014). Although rich but ephemeral carrion resources may be important to a variety of facultative scavengers (DeVault et al. 2003), the ability of individuals and species to exploit human-provisioned ungulate carrion likely is influenced by myriad biotic and abiotic factors including competition among individual scavengers (DeVault et al. 2011).

A potential management concern regarding increased scavenger activity associated with the big game hunting is the possibility for increased large carnivore activities and subsequent carnivore–human conflict in and around rural communities. For instance, fall ungulate hunts in temperate ecosystems coincide with the hyperphagic period for black and brown bears (Nelson et al. 1983), in which bears consume high calorie foods to gain body fat to meet the

physiological demands of reproduction and hibernation (Hilderbrand et al. 2000; Belant et al. 2006). During our study, multiple black bears were killed at homesteads when they attempted to usurp a hunter’s quarry. In the Greater Yellowstone Ecosystem (GYE), grizzly bears (*U. a. horribilis*) make seasonal movements from Yellowstone National Park to adjacent areas during the fall elk (*Cervus elaphus*) hunt, presumably to capitalize on human-provisioned elk carrion (Haroldson et al. 2004). These seasonal movements have resulted in an increase in the number of hunting-related grizzly bear mortalities in the GYE (Haroldson et al. 2004). Observations of brown bears on the Gustavus forelands in the early 2000s coincided with the fall moose hunt during multiple years of intensive moose harvests (\bar{x} number of moose harvested during 2000–2002 = 50.6), in which transient brown bears presumably scavenged the remains of harvested moose (Streveler et al. 2003). In general, data on scavenger communities at human-provisioned carrion, particularly large predators, are lacking for many terrestrial ecosystems (Mateo-Tomás et al. 2015). In Gustavus and other ecosystem at the rural–wildland interface where carrion may persist for extended periods of time, as in our study, understanding the role of human-provisioned carrion in the food web as well as the spatial and temporal patterns exhibited by large carnivores that use these resources is essential for mitigating potential human–wildlife conflicts associated with humans subsidizing large carnivores.

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