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Gifts of an enemy: scavenging dynamics in the presence of wolves (*Canis lupus*)

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Carrion represents an important resource for carnivores. Examining competition for carrion in a risk–reward framework allows for a better understanding of how predator guilds compete for and benefit from carrion. We used trail camera data to compare wintertime carrion use and vigilance behavior of four carnivores in Denali National Park and Preserve. We found that carrion use was dominated by wolves (*Canis lupus*) and wolverines (*Gulo gulo*), followed by red foxes (*Vulpes vulpes*) and coyotes (*Canis latrans*). Wolves and wolverines were twice as likely to visit a carcass as foxes and coyotes, and their visits were longer and more numerous. Our results suggest scavenging animals reduced their risk exposure primarily by reducing their use of carrion, with some evidence of increased vigilance at busy sites. We found that carrion use and behavior at carcass sites were influenced by the mortality type of the carcass, the age of the carcass, and the long-term intensity of wolf use in the area. Our results also suggest that wolves are the "top scavenger," and indicate that intraguild competition for carrion strongly affects which species benefit from carrion, with larger and more aggressive species dominating.

Key words: camera trap, *Canis lupus*, carrion, interspecific competition, risk allocation hypothesis, scavenge

Carrion is a critical food component for "facultative" (i.e., opportunistic) scavengers, and carrion consumption is an important but understudied ecological process (DeVault et al. 2003; Wilson and Wolkovich 2011; Fallows et al. 2013; Moleón and Sánchez-Zapata 2015). The creation of carcasses by top predators which then are used by other species has been termed "carrion provisioning" or "subsidizing." However, most predators, including top or apex predators, also are facultative scavengers, and a large percentage of carrion comes from sources other than predation (DeVault et al. 2003). Carrion creation and utilization therefore is a direct component of both predator–prey dynamics and intraguild predator competition (Wilson and Wolkovich 2011; Moleón et al. 2014). Carnivores engage both in exploitative and interference competition with one another, so carrion likely is a risky resource (Palomares and Caro 1999; Prugh and Sivy 2020). Thus, carrion use deserves further attention as an important pathway of behavioral and ecological interactions in carnivore guilds.

Given the ubiquitous competition for carrion resources, any potential consumer of a carcass, including the original predator, makes decisions about whether and for how long to feed in a risk–benefit framework. Consumers must weigh calories gained against the cost, or potential cost (i.e., risk), of intra- or interspecific competition. For this reason large carnivores should be considered competitive actors in the context of multispecies competition for carrion resources, including on their own threatened, usurped, or abandoned kills. We use the term "carcass competitor" to refer to those individuals or species in competition for carrion resources at a given point in time, regardless of their traditional assignment as "predator" or "scavenger" in relationship to the carcass in question.

According to the risk allocation hypothesis (Lima and Bednekoff 1999), if carcass competitors are at high risk of injury or death while feeding at a carcass site, they should seek to maximize the caloric reward of feeding while minimizing the risk of an antagonistic encounter. These are mutually exclusive prospects, because all risk-mediation strategies limit potential caloric intake. Individuals can mediate risk by 1) selecting carcasses that carry less inherent risk; 2) reducing the amount of time spent at a carcass; 3) increasing their level of vigilance while at the carcass; 4) selecting less risky periods of time in which to scavenge; or 5) through some combination of the above. Conversely, if carcass competitors are not at risk, they should follow optimal foraging strategies that maximize caloric reward gained from scavenging by consuming every carcass fully (Charnov 1976). Quantifying both real and perceived risk can be difficult, and while the risk allocation framework has been widely applied in foraging studies, risk assessments of carrion utilization behaviors remain limited (Verdolin 2006; Luttbeg 2017; Prugh et al. 2019). Existing work confirms carrion as widely used by carnivore guilds, despite apparent increased risk associated with carcass sites (Jones 1998; Switalski 2003; Selva 2004; Merkle et al. 2009; Prugh and Sivy 2020). Temperature, habitat and vegetation, indicators of other species' presence, apex predator population density, source of the carcass, and diel cycle, all have been documented affecting patterns of carrion use and scavenger behavior while feeding (Jones 1998; Selva et al. 2005; Wikenros et al. 2014; Allen et al. 2015; Cunningham et al. 2018; O'Malley et al. 2018)

In this study, we used photo data from trail cameras deployed in Denali National Park and Preserve (DNPP) to document and compare wintertime carrion use and vigilance behavior of wolves (*Canis lupus*), wolverines (*Gulo gulo*), coyotes (*Canis latrans*), and red foxes (*Vulpes vulpes*). We compared measures of ungulate carcass use, vigilance levels, and temporal patterns of activity among all four species of carnivores. We also examined how carrion use and vigilance were affected by environmental and interspecific variables that might change the balance of risk or reward while feeding (Fig. 1). Given that wolves, wolverines, coyotes, and foxes, commonly consume carrion, our null hypothesis was that carrion use by each species would be proportional to the density of each species in the study area (Huggard 1993; Switalski 2003; Selva et al. 2005; Dijk et al. 2008b). Therefore, we expected greater use of carcasses by mesocarnivores than by wolves (see "Materials and Methods" for densities). We also expected that differences in risk sensitivity, if found, would manifest primarily through vigilance behavior. Because body size is a strong predictor of dominance when species compete (Palomares and Caro 1999; Ritchie and Johnson 2009), we expected that a species' sensitivity to risk at carcass sites would increase as body size decreased. Alternately, if carrion consumption is a low-risk high-reward activity ("provisioning"), we expected limited vigilance combined with use patterns driven primarily by resource availability, i.e., decreasing with time as the resource is consumed.

Materials and Methods

Study area.—Our study area comprised the northeast corner of DNPP and adjacent state lands (Fig. 2). The area experiences a subarctic climate with long cold winters and short summers. It is comprised of steep mountain ranges bisected by broad glacial river valleys. The primary vegetative communities are boreal forest, including spruce (*Picea* spp.), aspen (*Populus* spp.), and birch (*Betula* spp.); taiga, which is composed of willow (*Salix* spp.) and dwarf birch (*Betula nana*) with scattered spruce; and alpine tundra. Average annual precipitation is 38 cm and average winter and summer temperatures are −15°C and 12°C, respectively (Sousanes 2016). Average snow depth

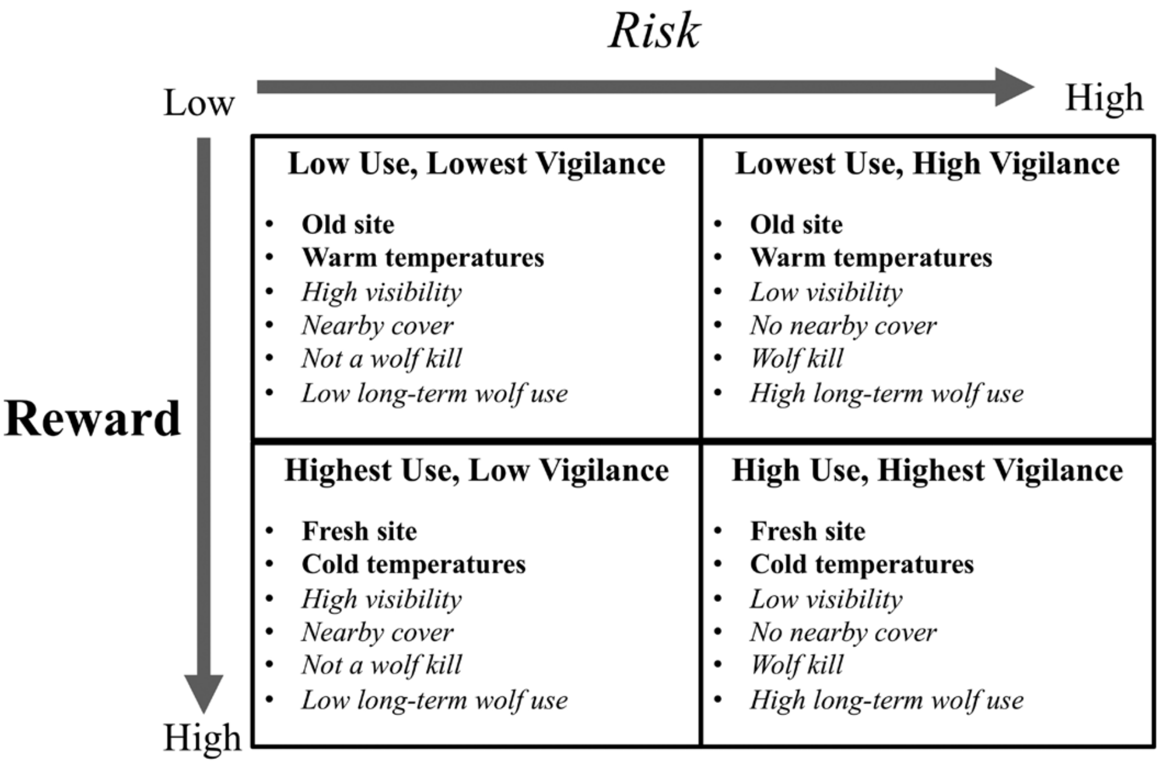

Fig. 1.—Expected relationship between environmental factors dictating risk (italicized) and reward (bold) at ungulate carcass sites, and the associated expected intensity of use and vigilance behavior of mammalian scavengers in the subarctic.

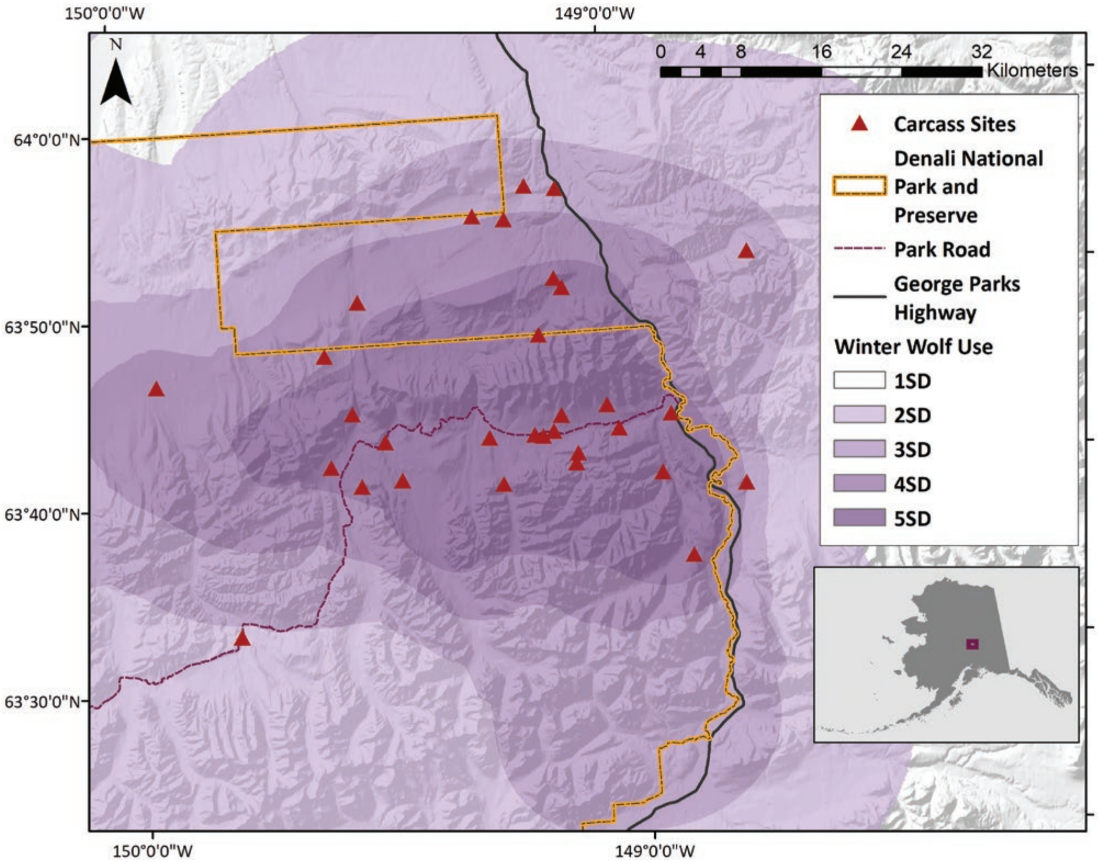

Fig. 2.—Map of study area showing border of Denali National Park and Preserve (yellow dashed line), monitored carcass sites (triangles), area roads, and average winter wolf-use intensity as calculated from combined utilization distributions (purple shading, with each shade representing an increase of 1 *SD* of use intensity, lowest standard deviation shown without color for clarity). Inset shows location of study area within the state of Alaska. Data collected 2013–2017.

during the study period in November–April 2014–2017 was 35 cm, which was measured during concomitant snow-tracking surveys. Wintertime wolf density during our study ranged from 2.76 to 4.73 individuals per 1,000 km^2 (National Park Service Annual Reports, available online). Previous studies estimated mesocarnivore density per 1,000 km^2 in our study area to be 14 for coyotes, 15 for foxes, and 9.5 for wolverines (Alaska Department of Fish and Game 2015; Pozzanghera 2015). Harvest of game and fur-bearing species is allowed on the state lands, which does not affect wolf density (Borg et al. 2015). Data are limited for other furbearers but the scope and intensity of harvest are not likely to significantly reduce populations within the study area. Available ungulate prey species are moose (*Alces alces*), caribou (*Rangifer tarandus*), and Dall sheep (*Ovis dalli dalli*).

Data collection.—We carried out fieldwork from November to April in 2014 – 2017. DNPP staff deployed and maintained one to three GPS collars in all wolf packs in the study area (from 2 to 4 packs depending on the year), generally on breeding animals, as part of the long-term wolf monitoring procedure. DNPP staff darted wolves from helicopters, immobilized them with Telazol, and fitted them with Telonics GPS collars (Telonics, Inc., Mesa, Arizona, multiple models; see Meier et al. 2009 for protocol details). The fix interval of wolf collars varied between four and 24 h. Capture and handling procedures for wolves were approved under National Park Service IACUC protocols ("AKR_YUCH and DENA_Burch_Wolves_2013" and "AKR_DENA_Borg_GrayWolf_2016.A3") and conform to ASM guidelines (Sikes et al. 2016).

We located carcass sites 1) by searching clusters of GPS collar locations that were within 400 m^2 of each other over an 8-h period, 2) from reports of pilots and others in the field, and 3) from field sign and backtracking of carnivores. At each carcass, we documented the prey species and recorded the likely cause of death based on signs such as presence of a chase trail, evidence of hemorrhaging, degree of disarticulation, and orientation of the carcass (Elbroch and McFarland 2019). We categorized causes of death as wolf kill, winterkill, or unknown. Animals not killed by wolves ("winterkill") were presumed to have died of causes such as starvation or disease, as there are no other predators active in winter that regularly kill large ungulates (wolverines have been recorded killing caribou in Alaska, but rarely—Magoun et al. 2019). No road-killed ungulates were detected or included in this study as it was largely a roadless wilderness area. We visually estimated percent shrub and tree cover within a 10-m radius, and measured distance to nearest cover. We defined cover as the nearest object that could provide substantial visual cover for an animal of coyote size, such as mature spruce trees, ravines, and dense thickets. When possible, GPS collar data were used to determine date of death of wolf kills. The date of the first wolf location within 300 m of the carcass site was presumed to represent date of death. We aged remaining sites based on stage of carcass consumption and level of degradation of the remaining tissue, taking into account recent weather patterns and any known activity of carrion consumers at the site (sensu Wilmers et al. 2003b).

We mounted a Reconyx PC900 trail camera (Reconyx, Holmen, Wisconsin) 1–10 m from the center of each site on a tree or post at a height ranging from 0.5 to 1.5 m off the ground. The cameras were set either in default mode (a burst of three photos at a rate of one photo per second when triggered, followed by a 1-s recovery), or in near-video mode (continuous photos at a rate of one per second while sensing movement). This difference was not relevant for the calculation of results because we did not compare raw photo counts between cameras. Any dispersed pieces of the carcass were aggregated in the target zone of the camera but were not anchored in place. For all wolf kills but one, camera deployment occurred after initial abandonment by wolves, and pre-abandonment photos were censored. Cameras were retrieved 2 – 12 months after deployment.

Photo coding.—Each photo of one of the four carnivores was coded for species and number of individuals using Timelapse2 Image Analyzer software (Greenberg and Godin 2015, available at http://saul.cpsc.ucalgary.ca/timelapse/). Because group size varies among wolf packs, which may affect risk levels at carcass sites, we distinguish wolf groups (more than one individual) from lone wolves. We use the term "group" rather than "pack" because "pack" refers to the entire social assemblage, but pack members often split into groups that travel separately from one another (Metz et al. 2011; Benson and Patterson 2015), and many such groups were recorded on camera in this study. We coded behavior of each individual as "feeding," "vigilant," or "other." We defined "feeding" as having food in the mouth, biting or chewing on the carcass, or being positioned with the head down and mouth at the carcass; "vigilant" as head up, ears erect, and gaze directed outward or upward (sensu Atwood and Gese 2008); and "other" including moving around the general area, interacting with conspecifics, or undetermined.

Photos were grouped into "visits," which we defined as beginning when a carnivore appeared on camera and ending either at the last photo of that carnivore before another species appeared, or when a gap of 60 min or greater elapsed between photos of the same species. Sixty minutes was chosen to provide for independence of visits (in contrast to brief intervals off camera while present), and is typical compared to other camera-trap studies of carnivores (Burton et al. 2015). Although both wolves and wolverines are known to remain in the vicinity of carcasses even when not actively feeding (Wright and Ernst 2004; Mech 2011), we assumed an absence of 60 min or greater represented engagement in some alternate behavior (e.g., sleeping, caching, traveling) before returning to actively feed. To ensure that bear (*Ursus* spp.) activity did not bias our results, we truncated data sets at the first appearance of a bear at a carcass or at 1st May (the median date of bear appearance on camera), whichever came first.

Analyses.—We broke down the concept of carcass use into three measurable response variables: 1) presence or absence at a site, 2) number of visits made to a site, and 3) duration (minutes) of visits at a site, with visits of less than 1 min rounded to one. We measured vigilance as the proportion of time an animal exhibited vigilance behavior while on camera, with each photo representing one second of time. In the case of multiple animals on camera, behavior proportions were calculated out of total animal-seconds. For example, a photo of three wolves in which two were feeding and one was vigilant contributed three animal-seconds to the total, two of which were classified as feeding and one classified as vigilant.

We used regression models to test our predictions that attributes of the carcass site would affect the three carcass-use metrics and vigilance behavior (four models total: one per use metric, plus vigilance). We grouped carcass attributes into three categories: 1) caloric need and reward (with temperature as a proxy for caloric need—Selva et al. 2005), 2) visual obstruction and escape ability, and 3) factors that might affect the probability of encountering another carnivore (Table 1). Figure 1 outlines the expected effects of our predictor variables on carcass use and vigilance levels in a risk–reward framework. We expected that higher reward would result in increased use, and that higher risk would result in increased vigilance. To generate wolf utilization distributions (UDs; density maps of probability of use) we used the *kernelUD* function from the package adehabitat (Calenge 2007). We generated kernels for each pack using the ad hoc method for determining reference bandwidth, and a bivariate normal distribution. If a carcass site had a nonzero UD value from multiple packs, the values were summed.

To test for evidence of temporal risk mediation, we looked for evidence of smaller species delaying use of carrion based on the recent presence of larger species. We modeled the gap in time between visits of different species in two ways: 1) comparing gap time between each observed pairing of species, and 2) by comparing gap time between a pair of species to the log-ratio of the body masses of the two species. We calculated the average body mass of each species from capture records of wolves and coyotes in DNPP and published estimates (from Alaska when available; Supplementary Data SD1). We restricted this analysis to gaps of less than 48 h because we assumed the second species was most likely able to detect the presence of the first species during this time window. Both the frequency and predictability of returns by each species could play into the risk landscape for carcass competitors. Therefore, we also calculated the return interval for each species (the average length of time between visits by the same species, regardless of visits by other species in the interim) to estimate how frequently each species returned to carcasses. We additionally examined the coefficient of variation of return intervals to see how predictable their visits were (i.e., if variation in return intervals was low or high).

To examine temporal risk mediation over the diel cycle, we calculated the coefficient of overlap between each species using

Table 1.——Description of predictor variables used in models of scavenging activity and vigilance of mammalian scavengers at ungulate carcass sites in the subarctic. Mean values, with the range of values in parentheses, are shown for each variable. DNPP = Denali National Park and Preserve.

Predictor variables	Mean (range) of values	Description
Caloric need and reward		
Age at deployment	18 (1 – 103) days	Age of the kill in days (day 0 being day of the kill) on the first day the camera was deployed. Measure of site freshness at deployment and thus of the time window captured by the camera.
Site age	46 (1 – 169) days	Age of the kill in days (day 0 being day of the kill) on the day of the visit by an animal. Measure of site freshness during each visit.
Temperature	−12 (−34 – 2) °C	Lowest temperature for the date of visit, degrees Celsius, as recorded at the NOAA weather station at DNPP Headquarters. A proxy for caloric need (https://www.ncdc.noaa.gov/cdo-web/datasets/GHCND/stations/GHCND:USC00505778/detail).
Visual obstruction and escape ability		
Vegetation	61 (0 – 115) %	The sum of percent shrub cover and percent tree cover within a 10-m radius of the kill site. Proxy for visual obstruction.
Distance to cover	6 (0 – 30) m	Distance (m) to nearest object that could provide substantial visual cover for an animal of coyote size.
Encounter risk		
Origin of carcass	N/A	Cause of death of ungulate (wolf kill, winterkill, unknown)
Long-term wolf use	8.7e-10 (0 – 3.0e-09)	Value of wolf utilization distribution for the carcass site, generated for the winter season (October–April) of that year, summed across packs where applicable.
Duration of visit	30 (1 – 319)	Duration (minutes) of the visit. This variable was included only in the model of vigilance proportion while on camera.

the methods described in Ridout and Linkie (2009), as implemented by the *overlapEst* function in the R package *overlap* (Meredith and Ridout 2017). We used the scavenging visit as the unit of replication and used the beginning of the visit as the point in time. We used the kernel estimator Dhat1 as recommended for small sample sizes (Meredith and Ridout 2017). We calculated bootstrapped confidence intervals for the coefficient of overlap with 10,000 samples. We followed Linkie and Ridout (2011) and Lynam et al. (2013) in considering coefficient of overlap values ≥ 0.8 as "high" overlap and values ≤ 0.4 to be "low," with the intervening range considered "moderate."

We used generalized linear models (GLMs) or generalized linear mixed models (GLMMs) for all analyses other than the analysis of time overlap (Table 2). We initially fit each model as a mixed model with carcass site as a random effect, then checked the intraclass correlation coefficient (ICC—Koch 2006) to determine if the random effect was necessary. If the ICC value was at or near zero, which indicates that samples from within sites were no more similar than samples between sites, we proceeded with a fixed-effect modeling framework; otherwise, the random effect of site was retained. Camera duration, the number of days that the camera was out and functioning, was included as a fixed effect in the model of species presence and included as a log-transformed offset in the model of number of visits to account for differing lengths of camera deployment. We coded species as a four-level categorical predictor in the three carcass-use models and the vigilance model, and we included interaction terms between "species" and the other variables (excluding camera duration) to examine species-specific responses. Wolf group and wolf kill were set as the reference levels for species and origin of the carcass because they were generally the most abundant. Continuous variables were scaled to a mean of zero and standard deviation of one to assist in model convergence.

Proportional data, such as our vigilance measures, can be difficult to model, particularly when the data include true zeroes and ones (Bolker et al. 2009). Following Warton and Hui (2011), we adjusted values of zero to 0.006, which corresponded to the smallest nonzero proportion in our data, and values of one were correspondingly adjusted to 0.994. This adjustment may bias coefficient values slightly toward no effect (Warton and Hui 2011), so our vigilance model should be viewed as conservative. We present complete model specifications in Table 2. We assessed model fit by viewing Q–Q plots, examining the distribution of plotted residuals, and calculating *R*-squared values when appropriate. We ran regression models in program R (ver. 3.6.1) using packages lme4 and glmmTMB (Bates et al. 2015; Brooks et al. 2017; R Core Team 2019).

RESULTS

We collected 38,571 photos of wolves (n = 18,886), wolverines (n = 15,392), coyotes (n = 1,281), and red foxes (n = 3012) over 1,384 camera-days from 30 carcass sites. Wolves visited 18 carcass sites, wolverines visited 21 sites, and coyotes and foxes each visited 10 sites. At no time did we observe two species of carnivore in the same photo. Carcasses were primarily moose (n = 26) with the remainder caribou (n = 3) and Dall sheep (n = 1; see Supplementary Data SD2 for carcass site summaries). We classified carcasses as being 16 wolf kills, six winterkills, and eight sites with unknown cause of death. Wolf-killed carcasses were estimated to have an average of 8% (± 10) biomass remaining at camera deployment, winterkill carcasses had 37% (± 28) remaining, and unknown carcasses had 0.5% (± 0.5) biomass remaining.

Wolverines removed substantial parts of the carcass from the field of view in three cases; as a result, our findings may slightly underrepresent wolverine use of carrion. We excluded

Table 2.—Model specifications for models of carcass use, behavior while at carcass, and gap time between visits of mammalian scavengers to ungulate carcasses in the subarctic. GLM = generalized linear models; GLMM = generalized linear mixed models.

Response variable	Model type	*n*	Distribution family	Link	Predictor variables
Presence/absence	GLMM	150[a]	Binomial	logit	camera duration + species * carcass age at deployment + species * vegetation + species * origin of carcass + species * long-term wolf use + (1|site)
Number of visits	GLMM	77[b]	Negative binomial	log	Offset(log(camera duration)) + species * carcass age at deployment + species * vegetation + species * origin of carcass + species * long-term wolf use + (1|site)
Duration of visits	GLM	378	Negative binomial	log	species * carcass age (days) + species * temperature + species * vegetation + species * distance to cover + species * origin of carcass + species * long-term wolf use
Proportion time vigilant on camera	GLM	378	Beta	logit	Species * carcass age (days) + species * temperature + species * vegetation + species * distance to cover + species * origin of carcass + species * long-term wolf use + species * duration of visit
Gap time between visits	GLMM	77	Negative binomial	log	A: species pairing B: log-ratio body size

[a] Five species categories by 30 sites.

[b] For this analysis, number of visits was tabulated only for those species that had appeared at a site.

lynx (*Lynx canadensis*) from analysis as they were captured on camera only four times and were not feeding. We did not observe marten (*Martes americana*) at kill sites although they were present in the study area. Grizzly bears (*Ursus arctos*) only appeared in the late spring and were not active during the majority of camera deployments, and so were excluded from analysis. Avian scavengers including ravens (*Corvus corax*), gray jays (*Perisoreus canadensis*), and American black-billed magpies (*Pica hudsonia*) were recorded scavenging; however, their group sizes were small (typically only one to three birds at a time), unlike reports from lower latitudes (e.g., Stahler et al. 2002; Vucetich et al. 2004; Kaczensky et al. 2005). Because the effect of birds as competitors to mammalian scavengers should be relatively minimal at such low densities, and their risk–reward balance likely differs substantially due to their ability to fly, they were also excluded.

We identified one outlier: one site experienced 34 visits by a fox, 10 higher than the next highest number in the data set and roughly five times higher than the grand mean of site visits, which obscured the ability to examine general trends. To avoid having to exclude the entire site, we changed this value to the mean number of visits made by foxes as calculated without the outlier (six visits) when modeling number of visits. Analysis including the outlier showed no difference in overall trends other than increased variance and inflation of some coefficients driven by the unusually high representation of the characteristics of that site (Supplementary Data SD3).

Utilization of carcass sites across species.—Contrary to our predictions, wolves and wolverines were more than twice as likely as coyotes and foxes to use a carcass site at least once (Fig. 3; Supplementary Data SD4). At visited sites, wolverines made approximately twice as many visits to carcass sites as wolves, foxes, and coyotes (Fig. 3; Supplementary Data SD5). Duration of visits were longest for wolf groups, and shortest for coyotes (Fig. 3; Supplementary Data SD6). In line with our predictions, wolf groups and wolverines dedicated the least time to vigilance behavior, roughly 10%. In comparison, lone wolves and foxes showed slightly higher levels, roughly 15%, and coyotes were twice as vigilant, at about 20% (Fig. 3; Supplementary Data SD7). Although percent of time feeding was variable, on average wolf groups dedicated the most time to feeding ($\bar{x}$ = 40% ± 27), followed by wolverines ($\bar{x}$ = 34% ± 31), lone wolves ($\bar{x}$ = 20% ± 27), coyotes ($\bar{x}$ = 19% ± 27), and foxes ($\bar{x}$ = 16% ± 24).

Effect of site characteristics on use and vigilance.—As predicted, origin of the carcass had strong effects on use; however, it was winterkill carcass sites, not wolf kills, which had the highest number of visits, duration of visits, and vigilance behavior for most species (Fig. 4). Long-term wolf use also had strong effects, as predicted, but the effects varied by species in unexpected ways (Fig. 5). However, in line with our predictions, most of the instances of mesocarnivore scavenging were observed at sites that fell in the lower half of calculated long-term wolf-use values. Increases in temperature generally decreased carcass use and vigilance as we expected (Supplementary Data SD3 – SD7). The age of the site had mixed and inconsistent effects on use across species (Supplementary Data SD3 – SD7). Vegetation around the site and distance to cover had no effect on use for wolves and wolverines, and inconsistent and generally weak effects on use for coyotes and foxes (Supplementary Data SD3 – SD7). Vegetation and distance to cover overall had the weakest and most inconsistent effects on carcass use and vigilance, although there was a slight trend toward smaller species showing greater carrion use at sites with more vegetation and cover (Supplementary Data SD3 – SD7).

Temporal risk mediation.—The comparison of gap time between visits of different species showed no differences by species pairing, by size ranking of the species in the pair, or by the log-ratio of body size (Fig. 6; Supplementary Data SD8 – SD10). All species showed a high or moderate degree of temporal overlap with one another (Table 3). The highest overlap was between wolverines and wolves, both lone or in groups. Coyotes and red foxes showed noticeably lower overlap between one another than did any other pair of species,

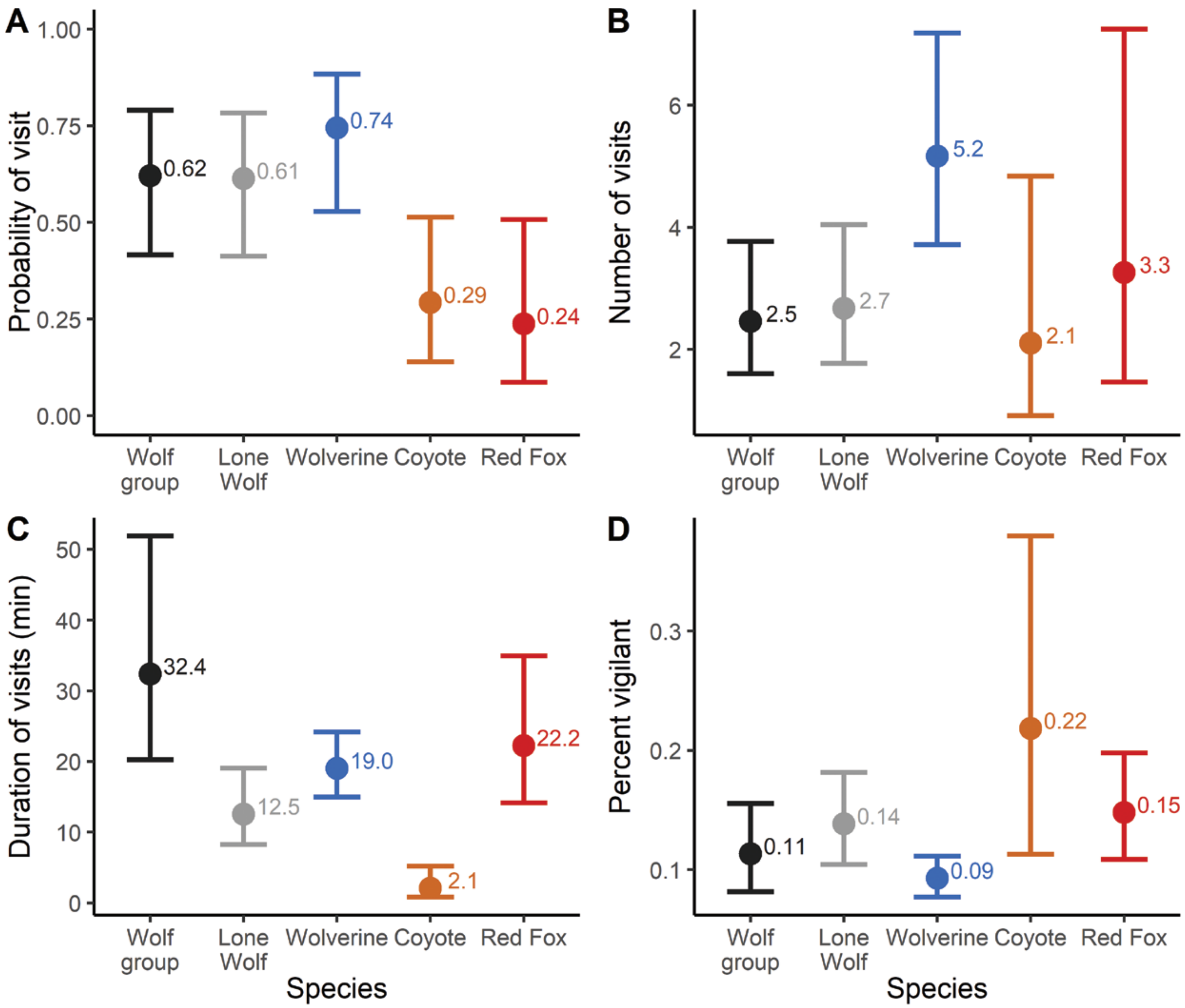

Fig. 3.—Estimates of three metrics of carcass use and of vigilance behavior across four species of scavengers (wolves split by group size) at wintertime ungulate carcass sites in Denali National Park, Alaska, derived from generalized linear models incorporating information about the carcass sites (see "Materials and Methods"; Supplementary Data SD4–SD8). Data collected 2013–2017. (A) probability of a site being visited; (B) number of scavenging visits; (C) duration of scavenging visits; (D) percent of time vigilant. Error bars show 95% *CI*.

but their overlap was still moderate (Supplementary Data SD11). Red foxes showed the strongest diel pattern, appearing to be almost entirely crepuscular or nocturnal, and all species except coyotes showed a dip in activity between approximately 1200 and 1800 h (Fig. 7). A post hoc comparison between coefficient of overlap and log-ratio of body size showed no significant relationship (linear model, $P = 0.464$, $R^2 = -0.048$, $n = 10$) suggesting no evidence of temporal partitioning by relative body size.

Return interval.—Return interval varied by species, with coyotes having the longest ($\bar{x} = 13.5$ days) and red foxes the shortest ($\bar{x} = 2.5$ days; Table 4). Return intervals were unpredictable for all species, with coefficients of variation > 100% for all species (Table 4).

DISCUSSION

Our findings reveal that wolves and wolverines dominate the activity at carcass sites and display little vigilance behavior, whereas foxes and especially coyotes use carcass sites less and are more vigilant, suggesting that carcass use is not proportional to carnivore density. Origin of the carcass, long-term wolf risk, and site age had the greatest overall effects on carcass use and vigilance behavior, suggesting that these factors are important to the risk–reward balance of these carcass competitors. Overall, carcass competitors in this system appear to mediate risk primarily by reducing their use of carrion and in addition, by increasing their vigilance while at carcass sites, but not through temporal partitioning, counter to our prediction that vigilance (not avoidance) would be

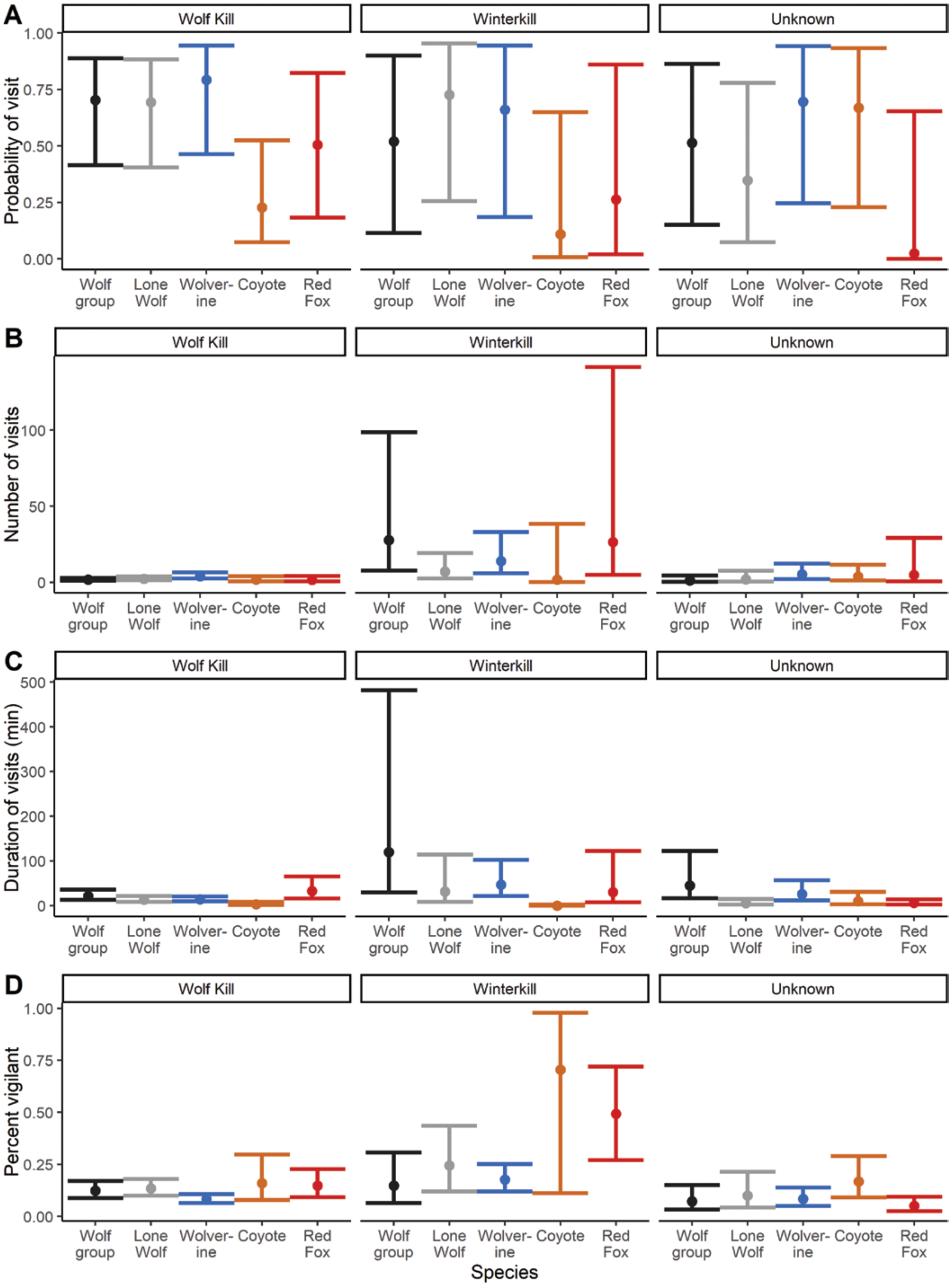

Fig. 4.—Effect of origin of carcass site on three measures of carrion use and vigilance behavior for four scavenging species at wintertime ungulate carcass sites in Denali National Park, Alaska, derived from generalized linear models incorporating information about the carcass sites (see "Materials and Methods"; Supplementary Data SD4–SD8). Data collected 2013–2017. (A) probability of a site being visited; (B) number of scavenging visits; (C) duration of scavenging visits; (D) percent of time vigilant. Error bars show 95% *CI*.

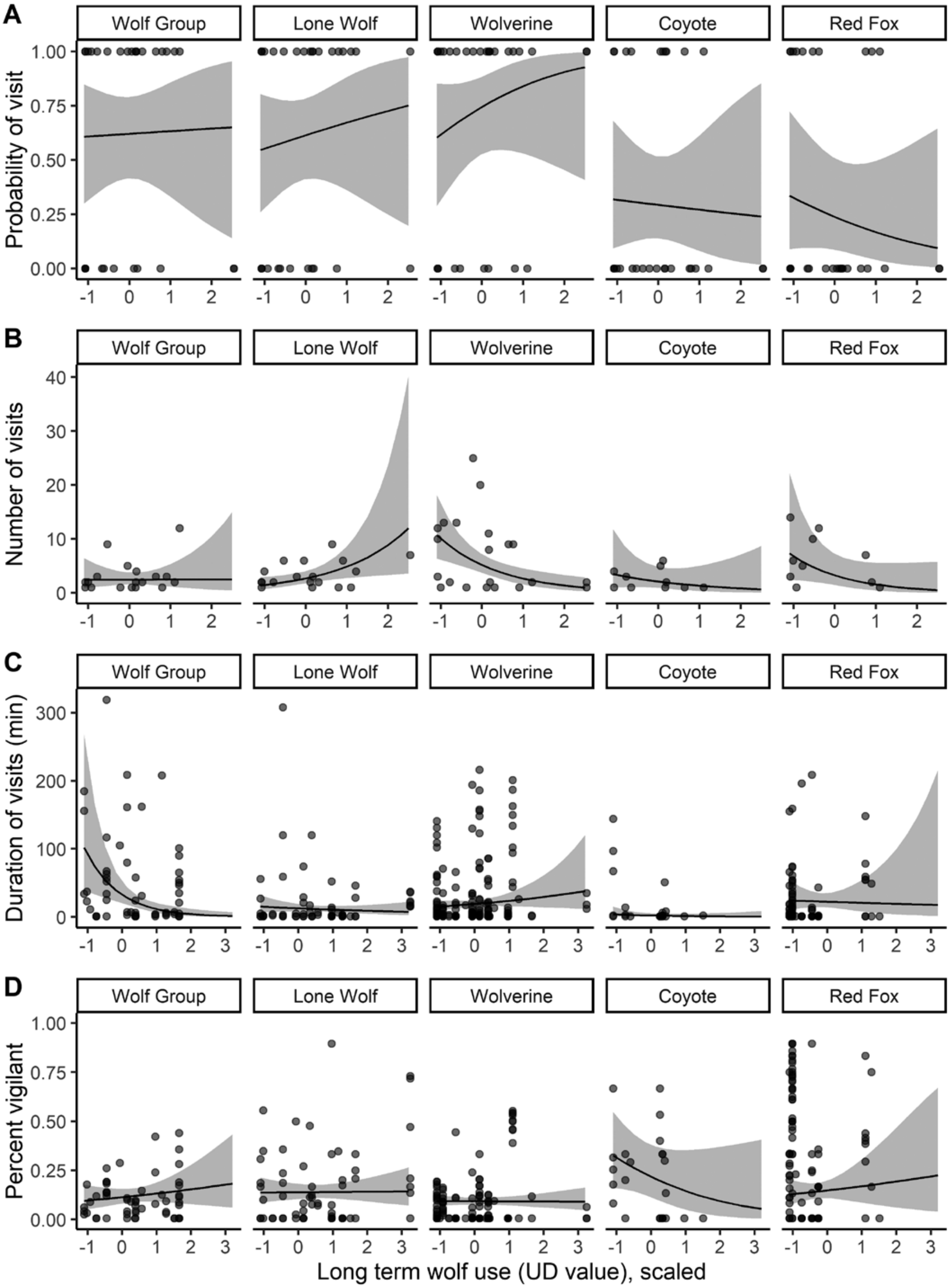

Fig. 5.—Effect of long-term wolf use at carcass location (measured as a value of the combined utilization distribution of multiple packs, scaled) on three measures of carrion use and vigilance behavior, for four scavenging species at wintertime ungulate carcass sites in Denali National Park, Alaska, derived from generalized linear models incorporating information about the carcass sites (see "Materials and Methods"; Supplementary Data SD4–SD8). Data collected 2013–2017. (A) probability of a site being visited; (B) number of scavenging visits; (C) duration of scavenging visits; (D) percent of time vigilant. Shading represents 95% *CI*.

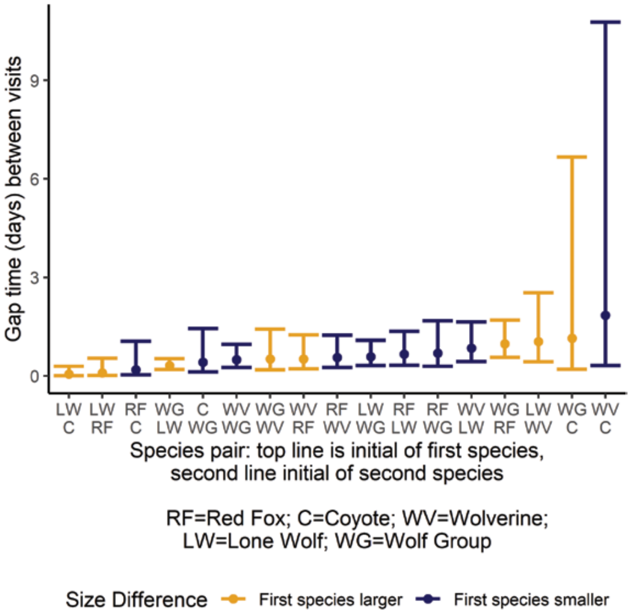

Fig. 6.—The gap time in days between subsequent visits of different scavenging species to the same ungulate carcass. Analysis was restricted to gaps of less than 48 h. Species body mass was taken from published records and Denali National Park and Preserve capture records. Data collected 2013–2017. Error bars show 95% *CI*s.

Table 3.—Temporal overlap values, 95% *CI*s, and overlap classification for pairs of scavenging species visiting ungulate carcass sites in the subarctic winter.

Species combination	Coefficient of overlap	95% *CI*	Degree of overlap
Coyote–red fox	0.55	0.38–0.71	Moderate
Lone wolf–red fox	0.73	0.60–0.84	Moderate
Wolverine–red fox	0.74	0.64–0.84	Moderate
Wolf group–red fox	0.76	0.64–0.88	Moderate
Lone wolf–coyote	0.77	0.67–0.97	Moderate
Wolverine–coyote	0.78	0.68–0.97	Moderate
Wolf group–coyote	0.79	0.70–1.0	Moderate
Wolf group–lone wolf	0.91	0.88–1.0	High
Wolf group–wolverine	0.93	0.92–1.0	High
Lone wolf–wolverine	0.93	0.92–1.0	High

the primary risk-mediation strategy. The high use of carcasses by wolves and wolverines and low use by smaller species supports our hypothesis that carcass sites are subject to guild-wide competition and therefore risky to smaller competitors. Our findings support reframing carrion as a pivotal and coveted resource rather than as a trophic “bonus” (Prugh and Sivy 2020).

Wolverines.—When comparing use and vigilance across carcass competitors, wolverines stood out as dominant among the mesocarnivores. Their high number of visits combined with their relatively high duration of visits and shorter return intervals allowed them to take extensive advantage of carrion resources. Our results corroborate published data indicating that wolverines are accomplished scavengers (Dijk et al. 2008b; Mattisson et al. 2011). Counter to our predictions, however, the very low vigilance of wolverines implies that they do not view wolves or any other carnivore species as a serious threat, despite the frequent presence of wolves at the carcass sites and documented instances of wolves killing wolverines (Palomares and Caro 1999; White et al. 2002). This threat was illustrated in a video recorded at a carcass site in DNPP after the conclusion of this study in which a wolf attacked a scavenging wolverine; the confrontation was brief and the wolverine yielded the carcass (Supplementary Data SD12). Our results support the hypothesis that wolverine abundance may track wolf abundance more closely compared to populations of other mesocarnivores due to their heavy use of carrion (Dijk et al. 2008a). The tendency of wolverines to dominate the activity at carcass sites, combined with their fearless nature, suggests the possibility that wolverines could inhibit coyote and red fox use of carrion as much as, or more than, wolves, especially in environments where wolverine densities exceed those of wolves. Combining high-resolution spatial and temporal data from collared scavengers with camera data at carcass sites would help elucidate the spatial scales at which scavengers interact and defend carcass sites and improve interpretation of camera data sets.

Coyotes and foxes.—Compared to wolverines, coyotes and foxes showed much lower use of carcasses. Coyotes showed the lowest use of all species and had the longest return interval, indicating that one visit was not likely to be followed up by another for nearly 2 weeks on average. This low level of carrion use differs from that recorded in lower latitudes, including Manitoba and the Greater Yellowstone Ecosystem (Paquet 1991; Merkle et al. 2009). The low level of coyote use observed also contrasts with a concurrent (2013 – 2014) study in the same area of DNPP which found that ungulate remains were the most common items in coyote scats, presumably from scavenging (Sivy et al. 2017a). In comparison to coyotes, foxes were found to have less carrion in their scats (Sivy et al. 2017a), yet we recorded a greater use of carrion by foxes in this study. This discrepancy is puzzling, as our cameras only recorded a grand total of approximately 10 min of actual feeding by coyotes. We suggest several hypotheses: 1) caching behavior by coyotes could have extended the presence of ungulate hair in their scat beyond observed feeding, and 2) coyotes could have been targeting carcass conditions poorly represented in our study, such as the period immediately after wolf abandonment, or very fresh winterkills—circumstances that might offer them the greatest caloric benefit per time spent feeding. Finally, it is possible that coyotes were more sensitive to residual human scent than other species, and were therefore deterred from visiting carcasses post-camera deployment. Our results highlight the need for additional research directly linking observed scavenging behavior with subsequent scat and diet analysis.

We found that foxes were the least likely to appear at a carcass site, so their total consumption of carrion was limited in comparison to wolves and wolverines. However, we found that if a fox visited a carcass, their use levels were comparable to wolves and wolverines, although they were much more vigilant than those species. They also had the shortest return intervals, implying frequent use of carcass sites after their discovery. Our finding of the low proportion of carcass sites at which foxes

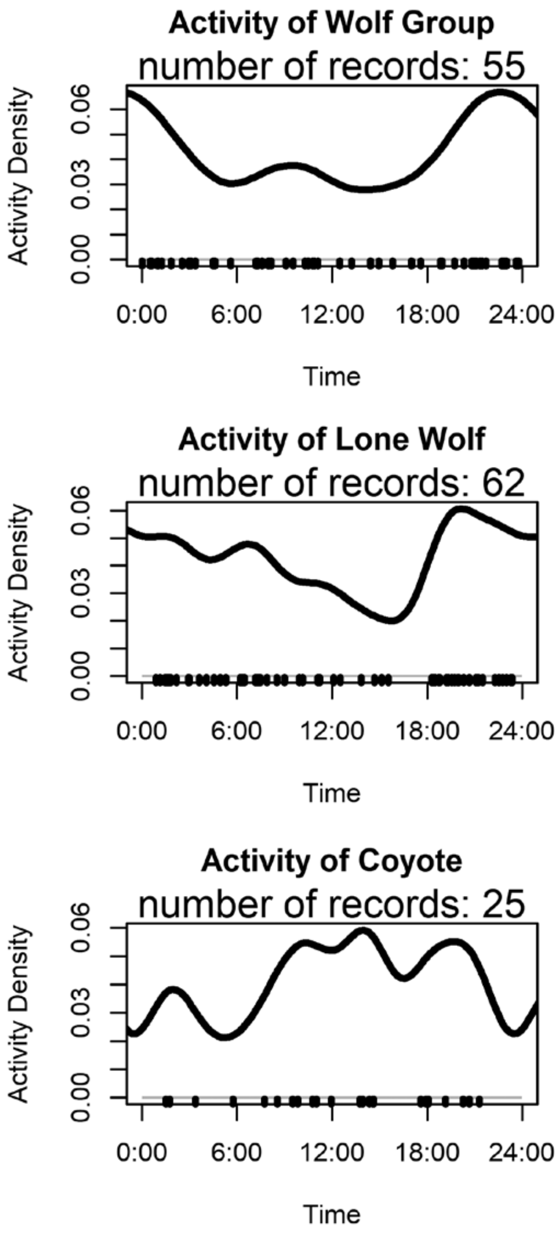

Fig. 7.—Diel patterns of activity of four scavenging species (wolves separated by group size) at wintertime ungulate carcass sites in Denali National Park and Preserve, Alaska. Tick marks along the x-axis (rug values) indicate carcass site visits as captured by trail cameras. Data collected 2013–2017.

were recorded (30%) conflicts with findings in Europe and elsewhere in North America, which reveal red foxes to be one of the most prolific scavengers in those regions, visiting upwards of 80 – 90% of carcasses in some studies (Selva 2004; Scholten 2012; Wikenros et al. 2014; O'Malley et al. 2018). Wikenros et al. (2014) reported foxes displaying slightly higher vigilance levels (22% of time) than what we observed (15% of time). The low use of carrion by coyotes and foxes in this study could be explained by high risk levels at carcass sites for these species, suggesting that coyotes and foxes may perceive carcass sites in this area to be riskier than previously documented in other systems. More research on carrion use is needed to identify the variations in risk or reward which drive differences between our findings and other studies.

Wolves.—Though wolf scavenging and returning to previously abandoned kills is a broadly acknowledged phenomenon, it remains poorly documented (Vucetich et al. 2004, 2012; Selva et al. 2005; Metz et al. 2011). We defined carcass competition by wolves as including returning to feed on their own kills after the initial abandonment of the kill (abandonment in this context refers to leaving the kill site and moving around the territory). There is a large decrease in both quality and quantity of food available after initial abandonment, and the amount of food remaining at old kills is unpredictable (Wilmers et al. 2003a). Caloric intake is therefore not comparable between the two scenarios, and we would not expect similar decision-making processes to govern the use of fresh kills versus old kills (McNamara and Houstoun 1992). This distinction is supported

Table 4.—The average return interval (time between visits) at wintertime carcass sites, *CI*, coefficient of variation (*CV*), and *n* of four mammalian scavengers.

Species	Return interval (days)	95% *CI*	*CV*	*n*
Wolf group	8.0	3.8–13.5	192	37
Lone wolves	10.3	6.4–14.8	144	44
Wolverine	3.4	2.3–4.7	198	126
Coyote	13.5	7.6–21.3	110	15
Red fox	2.5	1.8–3.4	154	79

by evidence that wolves are less likely to return to their old kills when prey vulnerability is high and new kills can be made more easily (Wikenros et al. 2013). Most studies found or implied a comparable rate of wolf visitation to carcasses as our study found, although differences in methods made comparisons of overall carcass use difficult (Palm 2001; Jędrzejewski et al. 2002; Selva 2004; Nordli and Rogstad 2016). However, some studies indicated a much lower use of carcass sites by wolves, suggesting that further standardized research is needed to identify the factors determining wolf carcass-use patterns (Sand et al. 2008; Cortés-Avizanda et al. 2009; Wikenros et al. 2013). In our study, wolves spent more time on camera than the other scavenger species (~50% of all photos), driven largely by the extended duration of visits by groups of wolves, a finding that identifies them as active players in the carcass competitor arena. Lone wolves had slightly higher levels of vigilance than wolf groups, suggesting that wolves likely feel safer in groups, perhaps due to the strength of numerical superiority or because of the "many eyes" effect (Roberts 1996; Cassidy et al. 2015).

Carcass attributes.—The source of the carcass, the degree of long-term wolf use in the area, and carcass age were the most important attributes affecting use and behavior of all four species. Vegetation and distance to cover had mostly weak and inconsistent effects, suggesting they do not strongly influence carcass competitor behavior in this system, a finding that contrasts to similar studies in Europe (Wikenros et al. 2014). We expected wolf kills to be used most heavily because they were already known to the wolves, and because wolf kills generate sounds and odors that can be readily detected by scavengers (Wilmers et al. 2003a). Instead, we found that winterkill carcass sites received greatest use by all species except coyotes. We hypothesize that high use of nonpredated carcasses occurs because these carcasses have more food remaining, unlike wolf kills which are mostly consumed prior to abandonment. In addition, winterkilled carcasses remain enclosed in tough hide and, in cold climates, often freeze before discovery by carcass competitors, meaning additional time is necessary for animals to access and consume them. The fact that even wolves spent the most time at winterkill sites suggests they are monopolizing the caloric benefit from not only their own kills, but from other carcasses as well (Haber 1977). Winterkill sites, with their higher use by all species, were also associated with higher vigilance by the mesocarnivores, offering some evidence of behavioral risk mediation at high-activity sites. Further work surveying a broader array of carcass sources (e.g., by placing carcasses on the landscape or using collar data from multiple predators or prey species to locate carcasses) would help to assess the generality of our findings.

The intensity of wolf activity on the landscape had strong but variable effects on carcass competitors' activity. The unexpected finding that wolf use of carcass sites was not notably higher within core areas of wolf activity might be explained by the fact that these sites were in frequently traveled areas and were therefore quickly consumed. Wolf-use intensity also had mixed effects on wolverine use of carcasses. Wolverines were less likely to revisit carcasses in the core of wolf home ranges, but the likelihood of at least one visit was actually higher and duration of visits were longer in these core areas. This pattern may indicate an increase in feeding intensity by wolverines, to make up for fewer visits at higher-risk sites. The decrease in use by coyotes and foxes at sites with greater long-term wolf use is consistent with a pattern in which coyotes and foxes mediate risk of wolf-caused mortality when scavenging. This contrasts with earlier findings of spatial association between mesocarnivores and wolves in this system (Sivy et al. 2017b), suggesting that if spatial association between mesocarnivores and wolves is carrion related, it may be that mesocarnivores are assessing opportunities to scavenge but in many cases not electing to do so.

Optimal foraging theory predicts that resource use should decline as the marginal gains from foraging decrease (Charnov 1976). As predicted, higher temperatures decreased the duration of feeding events and vigilance behavior for all species, supporting our hypothesis that carrion is a less critical (and therefore less contested) resource at higher temperatures. However, the effect of site age was inconsistent across use metrics and species, suggesting that either caloric availability is a poor predictor of carrion use, or that site age is a poor predictor of caloric availability. We found that food availability did not steadily decrease with age at several sites due to environmental conditions that temporarily affected access to the carcass, including overflow and snow drifting. As a result, time may not be a good proxy for caloric availability, as we assumed. Similar environmental conditions could have added uncertainty to our initial age estimates for carcasses found opportunistically; however, cameras generally tracked carcasses for months, and any inaccuracies in our initial estimates of carcass age likely had minimal effects on our results. Direct measurement of carcass biomass is advised to better address the relationship between carrion use and available biomass.

Temporal patterns.—Most species had very similar activity patterns throughout the day, indicating that temporal partitioning was not a primary mechanism of competition avoidance at carcass sites. Our results also indicate that the presence of other species at a carcass during the previous 48 h does not impact how long a second species will wait to approach the carcass. We found that the average gap was 14 h, and this overall low encounter rate could have meant there were limited cases where a carcass competitor arrived at a carcass soon enough after the previous visitor for it to matter. Alternately, an initial approach followed by the decision not to visit a carcass could happen outside the limited field of view of the camera. We found that the greatest differences in the temporal analysis, and in some other analyses such as use of carcass types, appeared between coyotes and foxes. These two species may be the closest resource competitors among the four species, and foxes may thus aim principally to avoid coyotes at carcasses (Sargeant et al. 1987; Harrison et al. 1989; Gosselink et al. 2003; Levi and Wilmers 2012).

Implications.—Relatively low densities of mesocarnivores combined with a relatively small sample size of carcasses could have skewed results if not all the carcasses were encountered by representatives of each species. However, this seems unlikely given the extended monitoring periods, and concurrent snow-tracking surveys indicated all species were well dispersed throughout the study area (Sivy et al. 2017b). Low mesocarnivore population density was driven in part by the relative scarcity of small mammal prey, a factor we were not able to directly incorporate into our assessment. Snowshoe hares (*Lepus americanus*) were at the lowest part of their cycle during the study period, while rodent populations fluctuated (Schmidt et al. 2018; Sivy et al. 2017a). It is difficult to predict how a dramatic increase in the abundance of small prey (and thus mesocarnivore populations) would affect carcass competition: carrion use could decline due to food switching, or the increase in mesocarnivore populations could increase the pressure to scavenge as competition for prey increases (Needham et al. 2014; Mattisson et al. 2016). Higher population densities could also result in higher rates of intra- and interspecific encounters, and consequently we might expect temporal partitioning to play a larger role under these circumstances. Further work during other phases of the hare cycle, when mesocarnivore populations are higher, could shed light on the role of mesocarnivore population density in mediating activity levels and behaviors at carcass sites.

Large carnivore kills often are described as carrion that is “provided” by large carnivores, since large live ungulates are a resource generally not accessible to scavenging species. However, all prey animals must die eventually, and it is therefore possible that ungulate carrion biomass would be greater in the absence of large carnivores. The net effect of predation on the creation of carrion is a complex set of interrelationships between population densities of predator and prey, prey fitness, kill rate, and severe weather (Wilmers and Getz 2004). Previous studies suggested that although wolves may decrease total annual carrion biomass, they may increase the carrion available to scavengers by smoothing out the annual distribution of carrion from a pulse in late winter to more consistent availability year-round (Wilmers et al. 2003a; Wilmers and Getz 2004). However, these studies did not take into account the subsequent effect of wolves as carcass competitors. Our findings show that wolves dominate carcass site activity at both their own kills and winterkills. This suggests that wolves reduce the wintertime availability of carrion resources to mesocarnivores in the subarctic by successfully competing with them for both wolf-killed and winterkilled carrion, and by causing carcass sites to be high-risk. This competition with wolves would be additive to the reduction in late-winter carrion associated with wolf presence (Wilmers and Getz 2004). Our results suggest that competition with wolves has the greatest limiting effects on foxes and coyotes and the least influence on wolverines.

Our findings indicate that a framework in which top carnivores are situated as providers of carrion and mesocarnivores as benefactors is not appropriate for subarctic systems in North America. Instead, we demonstrated that carrion is a resource subject to guild-wide competition, and one that is dominated by wolves and wolverines. Consequently, carrion consumption is a risky activity for animals in this system, especially for smaller species like coyotes and foxes, resulting in decreased use of carrion by these species, and increased vigilance, especially at high-activity sites. Wolverines’ high use of carrion resources and low vigilance despite being of comparable size to coyotes indicates that risk sensitivity and competition for carrion is driven by behavior as well as body mass (Briffa et al. 2015; Toscano et al. 2016). We did not find evidence of temporal partitioning or temporal risk mediation by scavengers. The high level of wolf use recorded here suggests wolves are the “top scavenger” and the top predator in this system during the winter months. The potential for a species to hold such a position may bear further investigation in this and other systems, and traditional views of the trophic role of carrion may need to be revised. Scavenging and carrion use deserve further attention, particularly in harsh environments, as an important food resource, and thus a key arena of intraguild competition.

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SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Sources for carnivores’ body mass.

Supplementary Data SD2.—Summary information on monitored carcass sites.

Supplementary Data SD3.—Model output of regression assessing number of visits made by red fox, when including the outlier, to ungulate carcass sites in Denali National Park and Preserve.

Supplementary Data SD4.—Model output of regression assessing likelihood of visitation to an ungulate carcass site by four mammalian scavengers in Denali National Park and Preserve.

Supplementary Data SD5.—Model output of regression assessing number of visits made by four mammalian scavengers to ungulate carcass sites in Denali National Park and Preserve.

Supplementary Data SD6.—Model output of regression assessing duration of visits made by scavenging species to ungulate carcass sites in Denali National Park and Preserve.

Supplementary Data SD7.—Model output of regression assessing proportion of time spent vigilant at ungulate carcass site by four mammalian scavengers in Denali National Park and Preserve.

Supplementary Data SD8.—Model output of linear model comparing gap time between visits of different species.

Supplementary Data SD9.—Generalized negative binomial linear model comparing gap time between visits to an ungulate carcass across log-ratio body mass of subsequent species at carcass sites in Denali National Park and Preserve.

Supplementary Data SD10.—The gap time (days) between scavenging visits as an effect of log-ratio body mass of scavenging species pairs.

Supplementary Data SD11.—Diel overlap between coyotes and red foxes.

Supplementary Data SD12.—Video of interaction between a wolverine and wolf at a carcass.

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