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Prey availability and ambient temperature influence carrion persistence in the boreal forest

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Abstract

1. Scavenging by vertebrates can have important impacts on food web stability and persistence, and can alter the distribution of nutrients throughout the landscape. However, scavenging communities have been understudied in most regions around the globe, and we lack understanding of the biotic drivers of vertebrate scavenging dynamics.
2. In this paper, we examined how changes in prey density and carrion biomass caused by population cycles of a primary prey species, the snowshoe hare *Lepus americanus*, influence scavenging communities in the northern boreal forest. We further examined the impact of habitat and temperature on scavenging dynamics.
3. We monitored the persistence time, time until first scavenger, and number of species scavenging experimentally-placed hare carcasses over four consecutive years in the southwestern Yukon. We simultaneously monitored hare density and carrion biomass to examine their influence relative to temperature, habitat, and seasonal effects. For the primary scavengers, we developed species-specific scavenging models to determine variation on the effects of these factors across species, and determine which species may be driving temporal patterns in the entire community.
4. We found that the efficiency of the scavenging community was affected by hare density, with carcass persistence decreasing when snowshoe hare densities declined, mainly due to increased scavenging rates by Canada lynx *Lynx canadensis*. However, prey density did not influence the number of species scavenging a given carcass, suggesting prey abundance affects carrion recycling but not necessarily the number of connections in the food web. In addition, scavenging rates increased in warmer temperatures, and there were strong seasonal effects on the richness of the vertebrate scavenging community.
5. Our results demonstrate that vertebrate scavenging communities are sensitive to changes in species' demography and environmental change, and that future assessments of food web dynamics should consider links established through scavenging.

KEYWORDS
boreal forest, carrion, community ecology, food web, nutrient cycling, scavenging

1 | INTRODUCTION

Scavenging by vertebrates is an overlooked food web interaction that could impact the structure and stability of ecological communities (Barton, Cunningham, Lindenmayer, & Manning, 2013). Carrion can be a valuable resource for a multitude of species, and can drive the population dynamics of both obligate and facultative scavengers (Pain et al., 2003; Wilmers, Crabtree, Smith, Murphy, & Getz, 2003). Vertebrates can consume up to 90% of available carrion, which alters the distribution and availability of nutrients in comparison to carrion colonized by invertebrates and microbes (DeVault, Olson, Beasley, & Rhodes, 2011). Given the propensity for animals to consume carrion, scavenging contributes to a reticulate food web through the creation of numerous weak connections (Wilson & Wolkovich, 2011), which can stabilize community dynamics by dampening the destabilizing effects of strong consumer-resource interactions (McCann, 2000). Coupled with the retention of energy at higher trophic levels, vertebrate scavengers could have an important impact on food web stability and persistence (Dunne, Williams, & Martinez, 2002; Rooney, McCann, Gellner, & Moore, 2006). Despite this potential importance, classic food web theory has often ignored scavenging (Wilson & Wolkovich, 2011), and there remains a paucity of work examining the multitude of potential factors driving vertebrate scavenging dynamics.

Predator-prey dynamics are often drivers of carrion availability in ecosystems, which could influence scavenger behaviour (Perrig, Donadio, Middleton, & Pauli, 2017; Wilmers et al., 2003). Species commonly alter foraging strategies when food availability shifts, and vertebrates switch to consuming carrion to take advantage of an abundant food source (Gleason, Hoffman, & Wendland, 2005). Therefore, changes in carrion biomass associated with predator-prey dynamics may have an important influence on carrion recycling rates, or the number of scavengers in the community (Allen, Elbroch, Wilmers, & Wittmer, 2015; Wilmers et al., 2003). Scavenging rates for predator species, however, are likely dependent on changes in the abundance of their prey, where carrion represent an alternate caloric resource when prey are scarce (Mattisson et al., 2016; Needham, Odden, Lundstadsveen, & Wegge, 2014). If a predator species has a relatively large impact on the scavenging community, or multiple predators behaviourally respond to the same prey, temporal variation in prey density could be an important driver of vertebrate scavenging dynamics. The effects of landscape-wide changes in prey or carrion availability on the vertebrate scavenging community remain unknown (Beasley, Olson, & Devault, 2018), in part because of the limited studies estimating temporal variation in carrion biomass (Barton et al., 2019; Moleón, Selva, & Sánchez-Zapata, 2020).

Along with biotic factors, scavenging rates can be modulated by abiotic conditions, such as habitat and temperature (Smith, Laatsch, & Beasley, 2017; Turner, Abernethy, Conner, Rhodes Jr., & Beasley, 2017). Acquisition of carrion by vertebrates is reduced as temperature increases, due to increased microbial and invertebrate activity at the carcass (DeVault, Brisbin Jr., & Rhodes Jr., 2004). Forest openings also increase carrion detection and consumption, as dense canopy cover can obscure visibility from certain avian scavengers (Selva, Jędrzejewska, Jędrzejewski, & Wajrak, 2005; Turner et al., 2017). However, the generality of these abiotic effects across a diverse range of ecosystems has not been tested (Sebastián-González et al., 2019), and species in a community likely differ in their response to these variables (Selva et al., 2005). Furthermore, the importance of abiotic variables on scavenging rates could be minor relative to changes in species density or carrion biomass, as studies have measured the effects of abiotic conditions without considering temporal changes in species demography. Understanding these dynamics is important to forecast how future changes in the density of species, as well as climate and habitat change will impact food web structure (Bartley et al., 2019).

The boreal forest of North America is characterized by large-scale fluctuations of a dominant prey species, the snowshoe hare *Lepus americanus*. Snowshoe hares undergo population cycles with an 8–11 year periodicity, with densities varying by over two orders of magnitude across the cycle (Krebs, Boonstra, Boutin, & Sinclair, 2001). Snowshoe hares can account for >50% of the vertebrate biomass in the boreal forest, and their fluctuations drive the behaviour and abundance of several predator species (Boutin et al., 1995; Krebs, 2011). Although the impact of these cycles on predator-prey dynamics and community interactions have been thoroughly investigated (Krebs, 2011; Krebs et al., 2014), little is known about the impacts of snowshoe hare population dynamics on scavenging communities (O'Donoghue et al., 1998). Snowshoe hare carcasses likely represent an important food source for numerous species, but changes in snowshoe hare carrion and biomass associated with their population cycles may be important drivers of temporal variation in scavenger efficiency and the diversity of vertebrate scavengers.

Scavenging dynamics in the boreal forest have been relatively understudied in comparison to other ecosystems around the globe (Sebastián-González et al., 2019). At high latitudes, abiotic conditions could be comparatively important predictors of scavenging behaviour (Selva et al., 2005), and may impact scavenging rates differently than other systems given the relatively limited activity of invertebrates, particularly during winter months. The vertebrate community in the boreal forest also changes among seasons due to the arrival and departure of migrating and hibernating species (Krebs, 2011), which could cause strong seasonal patterns in the richness of vertebrate scavengers and scavenging rates (Sebastián-González et al., 2019). Understanding the influence of these factors on the vertebrate scavenging community of the boreal forest is critical, especially given the rapid increase in temperatures at northern latitudes due to climate change, and the potential destabilization of animal populations displaying cyclic patterns in abundance (Ims, Henden, & Killengreen, 2008; Streicker, 2016).

In this study, we monitored vertebrate scavengers over four consecutive years in the boreal forest of southwestern Yukon, a region where scavenging dynamics have not yet been considered in studies of community interactions. The extensive research on the snowshoe hare cycle in this region provides a unique opportunity to examine the influence of changing prey abundance and carrion biomass on community and species-specific scavenging rates. We monitored the density of snowshoe hares, as well as the availability of their carcasses, to test whether prey and carrion availability influence vertebrate scavenging communities relative to temperature, habitat, and seasonal effects. For the primary scavengers, we developed species-specific scavenging models to examine variation on the effects of these factors across species, and we determined which predator/scavenger species may be driving temporal patterns in the entire community. This research provides important insight into the mechanisms driving changes in the boreal forest food web, a system where scavenging communities have not been thoroughly examined (Sebastián-González et al., 2019).

2 | MATERIALS AND METHODS

2.1 | Study area

This study was conducted in the Kluane lake region (350 km^2) of southwestern Yukon, Canada (61 N, 138 W), in a broad glacial valley bounded by alpine areas and bisected by the Alaska Highway (Krebs, Boutin, & Boonstra, 2001). The boreal forest in this area is comprised primarily of white spruce *Picea glauca* with smaller amounts of trembling aspen *Populus tremuloides* and balsam poplar *Populus balsamifera*, and the shrub layer is dominated by areas of gray willow *Salix glauca* and dwarf birch *Betula glandulosa* (Douglas, 1974). The climate is cold continental, with snow cover occurring from October to May, with July being the only snow free month, and temperatures in February averaging −14.0°C during the 4 years of our study (between 2015 and 2018). During this study, the snowshoe hare population increased, peaked, and declined, with densities ranging from 0.49 to 1.82 snowshoe hares per hectare (Krebs, Boonstra, & Boutin, 2018).

2.2 | Field methods and camera analysis

We opportunistically deployed 98 snowshoe hare carcasses during field-work in the region between January 2015 and May 2018. Carcasses were located during fieldwork (e.g. road-kill) or were donated from local trappers and/or researchers and were deployed continuously between September and May. We used carcasses immediately following discovery, or froze and later thawed them prior to deployment. Most carcasses were whole but some had external damage due to the cause of death, and carcasses used had no evidence of previous scavenging. We deployed carcasses in forested or non-forested areas consisting of willow and open-fields. To limit pseudo-replication, we did not simultaneously deploy multiple carcasses within 1 km of each other, and no deployment occurred in the same location as a previous carcass (Turner et al., 2017). When carcasses were deployed, we recorded the time of deployment, habitat type (broad categories above), and canopy closure at the carcass to the nearest 10% measured using a spherical densiometer.

We monitored each carcass with one remote-sensing camera (no-glow, infrared PC900 Hyperfire^{TM} RECONYX, Inc., Holmen) set on a tree or shrub approximately 2–4 m from the carcass and 0.5 m off the ground. We set cameras to take three rapid-fire photographs when triggered, with a 15 s delay between subsequent triggers. We checked carcasses regularly (every 2–4 days) and left them in place until the carcass was removed or minimal edible remains were left. We did not secure carcasses to the ground to allow species to move the carcass to cover for consumption. If carcasses were moved slightly off-camera by a scavenger species, we adjusted the carcass position during our checks to ensure scavenging species were being detected on camera.

We downloaded images from the cameras after the conclusion of each deployment (i.e. once carcass was consumed or removed by a scavenger) and uploaded them to the Alberta Biodiversity Monitoring Institute website (www.abmi.ca) for image classification and analysis. In each photo, we identified the scavenger species and whether or not they were scavenging. We classified the observation as unknown if we could not determine the exact species responsible for the scavenging event. We further classified micromammals (*Myodes* sp., *Peromyscus* sp. and *Sorex* sp.) together as "small mammals" given the difficulty of distinguishing these species in photographs. We defined a scavenging event as any time a vertebrate consumed any part of the carcass, or if a disturbance or movement of the carcass was observed between two consecutive photos. For the latter, we attempted to eliminate instances that resembled solely carcass investigation. However, to an unknown degree some events where carrion consumption did not occur may have been classified as scavenging if the animal repeatedly moved the carcass. For larger species such as Canada lynx *Lynx canadensis* or coyote *Canis latrans*, we considered scavenging events to be either (a) consumption of the carcass on site, or (b) the carcass being carried off-screen by the scavenger (see Figure S1). If the carcass was removed between a series of rapid-fire photos, we assumed the scavenger removed it during the 15-s delay. From the photographs, we also recorded the date and time of the first scavenging event on a given carcass, and when each carcass was removed or consumed. We did not attempt to quantify or describe any data on invertebrate scavengers. We acknowledge that scavenging rates in our study may be dependent on carcass condition (i.e. opened) and human presence at the site. However, these factors were not confounded across carcasses, and our primary goal was to determine how biotic and abiotic factors influenced changes in scavenging community efficiency and richness.

2.3 | Monitoring snowshoe hare densities and carrion biomass

We calculated monthly hare carrion biomass in our study area throughout the 4 years as a function of biomass in g/km^2 using the following equation:

$$\text{Monthly hare carrion biomass}\,(g/km^2) = \text{hare density}\,(km^2) \times \text{monthly mortality percentage} \times \text{average carcass remaining}\,(g).$$

We obtained density estimates for snowshoe hares from the Community Ecological Monitoring Program (CEMP; https://www.zoology.ubc.ca/~krebs/kluane.html), which has estimated the density of species in the Kluane Lake study area over the last four decades (Krebs et al., 2014, 2018). Hare density was monitored each autumn and spring using mark-recapture (see methods described in Krebs, Boonstra, et al., 2001). Between January 2015 and May 2018, we captured snowshoe hares continuously in Tomahawk live-traps (Tomahawk Live Trap Co.), and we fitted snowshoe hares weighing over 1,100 g with VHF collars equipped with mortality sensors (Model SOM2380, Wildlife Materials Inc., or Model MI-2M). Over the course of the study, we monitored a total of 458 individual snowshoe hares with VHF telemetry and checked their status near daily. VHF collars weighed <40 g and were below the threshold of 5% of the individual body weight. The University of Alberta Animal Care and Use Committee (Protocol: AUP00001973) approved handling and collaring procedures. From these data, we calculated monthly survival rates using the Kaplan Meier estimator in the SURVIVAL package in R (Therneau, 2019). Our average sample size for calculating monthly survival was 70 individuals (range 33–116). When a mortality signal was detected, we located the kill site to determine cause of death based on predator tracks and other field sign, and estimated the proportion of the carcass remaining (nearest 10%). In the above calculation, density was re-estimated at the beginning of each month based on the previous month's density and survival rate. We determined the average carcass remaining in grams for each year by multiplying the proportion remaining estimate by an approximate average mass of an adult snowshoe hare (i.e. 1,500 g).

2.4 | Scavenger species richness and community efficiency

First, we calculated the number of species observed scavenging in each season, and the percentage of carcasses each species was observed scavenging (i.e. carcasses a given species was observed scavenging/total number of carcasses). Seasons were defined as: autumn (September–November), winter (December–February), and spring (March–May).

We then examined the drivers of scavenging efficiency (i.e. carcass persistence and time until first scavenger) and scavenger species richness (i.e., the number of species scavenging during a single deployment) using GLM with a gamma or Poisson distribution in the program R (3.3.1.; R Core Team, 2018). Time until first scavenger and carcass persistence were defined as the duration of time in decimal days between carcass placement and either the first scavenging event, or time at which all available flesh was consumed or the carcass was removed by a large scavenger. For each analysis, we removed carcasses where cameras failed prior to complete carcass consumption. We used an information theoretic approach to determine which variables best characterized community scavenging dynamics. Models consisted of combinations of the daily temperature on deployment date, canopy closure (nearest 10%), season (autumn, winter, spring), snowshoe hare density, and carrion biomass. We selected the top models using Akaike's Information Criterion, corrected for small sample sizes (AICc; Burnham & Anderson, 2002) and examined relative variable importance from the entire model set using the MuMIn package in R (Barton, 2019). We then excluded candidate models that contained uninformative parameters (Leroux, 2019), which were identified when the addition of a parameter to a simpler nested model had no improvement on model fit (i.e. log-likelihood), and increased AICc by approximately the penalty of two (as in Cunningham, Johnson, Hollings, Kreger, & Jones, 2019). We then calculated model-averaged coefficients and included models with $\Delta AIC < 4$ to retain the most information (Burnham, Anderson, & Huyvaert, 2011). Model selection tables containing uninformative parameters are included in the Supporting Information.

Covariates used for our analyses had a Pearson's correlation coefficient <0.60 (Dormann et al., 2013). For our analysis of scavenger richness, we further included time until carcass removal to the nearest day as a covariate, as carcasses that persisted longer could have a larger number of species scavenging (Turner et al., 2017).

2.5 | Drivers of species-specific scavenging

For our most frequent avian and mammalian scavengers (species that scavenged >10 carcasses; see below) we constructed species-specific models to determine the factors driving their scavenging rates. We determined the effects of covariates on whether or not that species scavenged a carcass using a GLM with a binomial distribution and a logit link. For each avian species (i.e. black-billed magpie *Pica hudsonia*, common raven *Corvus corax* and Canada jay *Perisoreus canadensis*) we considered models using every combination of season, temperature, canopy closure, and carrion biomass and selected the top models for scavenging rates based on AICc (Burnham & Anderson, 2002).

For the most frequent mammalian scavengers (i.e. Canada lynx, North American red squirrels *Tamiasciurus hudsonicus*, and snowshoe hares), we included biotic variables in addition to abiotic variables, since reliable data for these species were available through concurrent ecological monitoring. For snowshoe hares, we included season, temperature, forest, and snowshoe hare density in our model selection, with models in our candidate set having a maximum of three covariates due to the smaller sample size (i.e. 12 scavenging events, Murray, Bastille-Rousseau, Hornseth, Row, & Thornton, 2020). For Canada lynx we included temperature, season, lynx density and prey density in our model selection. Indices of lynx abundance in the Kluane Lake region are determined each year through track transects, where tracks are counted along a 25-km transect that traversed our study area, on days after fresh snowfalls while tracks were distinguishable (Boutin et al., 1995). We considered food availability for Canada lynx as the density of snowshoe hares, determined using mark-recapture as mentioned above. We included a mid-winter density estimate (1 January) as the average between fall and spring densities of that winter, and assigned a snowshoe hare density to each carcass based on the nearest density estimate to the deployment date.

For red squirrels, candidate models included combinations of season, forest, temperature, squirrel density and food availability. Squirrel density was monitored in the fall and spring using mark-recapture as part of the CEMP (Krebs, Boonstra, et al., 2001). Food availability for red squirrels is primarily determined by white spruce cone production (Steele, 1998). Each autumn, cone production is measured in the region by counting the number of cones in the top three meters of 100 individual trees on six different study grids according to the sampling protocol outlined and calibrated in LaMontagne, Peters, and Boutin (2006). In our red squirrel model, we estimated food availability for each deployment as the mean cone production per tree in the previous summer. This is because red squirrels cache cones throughout the autumn as a food resource over the winter (Steele, 1998). For species-specific models, we did not examine the time spent scavenging or time at carcass (as in Allen et al., 2015). Although we believe these variables are informative, time at the carcass in our study would be strongly dependent on whether or not an individual consumed the carcass on camera, or removed the carcass out of camera view. As above, we excluded candidate models for each species that contained uninformative parameters to calculate model weights (Leroux, 2019), and calculated model-averaged coefficients using models with ΔAIC < 4 (Burnham et al., 2011). We plotted the effect of variables with >0.5 relative variable importance for each species.

3 | RESULTS

3.1 | Community scavenging dynamics

In total, 24 different vertebrate species scavenged snowshoe hare carcasses during the 4 years we monitored carcasses. The top avian scavengers in our system, determined as the proportion of carcasses that they scavenged, were Canada jays (61.1%), common ravens (60.0%), and black-billed magpies (40.0%). Top

FIGURE 1 Common avian and mammalian scavengers in the Kluane Lake region, Yukon during our study including, (a) Canada jay *Perisoreus canadensis*, (b) common raven *Corvus corax*, (c) black-billed magpie *Pica hudsonia*, (d) North American red squirrel *Tamiasciurus hudsonicus*, (e) Canada lynx *Lynx canadensis* and (f) snowshoe hare *Lepus americanus*

mammalian scavengers were red squirrels (51.6%), Canada lynx (25.3%), and snowshoe hares (12.6%; Figure 1). The number of scavenger species changed between seasons, with 11, 11, and 21 different species observed scavenging in the autumn, winter, and spring, respectively (Table 1). Average monthly carrion biomass of snowshoe hares was 5.33 kg/km^2 (95% CI = 4.08–6.57) during our study but varied substantially across months (range 1.02–13.34 kg/km^2; Figure 2). This large variation was caused by changes in hare density (Figure 2), monthly survival rate (0.70–0.98), and the average percent of the carcass remaining across study years (15%–51%; average carcass remaining = 26.7%; 95% CI = 22.6–30.8).

Mean persistence of carcasses was 5.53 days (95% CI = 3.98–7.08; *n* = 87). Our top model explaining carcass persistence consisted of snowshoe hare density, temperature, and season (*w* = 0.34), and the only other models within 2 ΔAICc included snowshoe hare density and season (*w* = 0.21), or solely temperature (*w* = 0.17, see Table S1). Temperature had the highest relative variable importance (0.69), followed by season (0.68) and hare density (0.65). Carcass persistence time was the highest during the winter compared to spring and autumn (Figure 3), decreased with increasing temperature (−0.03 ± 0.02; model averaged estimate ± *SE*), and increased at higher snowshoe hare density (0.63 ± 0.58; Figure 4).

The average time until first scavenger was 1.11 days (95% CI = 0.72–1.50; *n* = 83) and were most often Canada jays (36.4%), red squirrels (19.3%), and common ravens (17.0%). The top model explaining time until first scavenger consisted of canopy closure and season (*w* = 0.22). However, season was the only variable included in all models within 2 ΔAICc (see Table S3), and had the highest relative variable importance (0.99; see Table S4). The time until first scavenger was longer in winter (1.32 ± 0.36) and spring (1.08 ± 0.30) relative to the autumn. The mean number of species scavenging per carcass was 3.05 (95% CI = 2.78–3.35). The top model explaining the number of scavenger species consisted solely of carcass persistence

TABLE 1 Percent of snowshoe hare carcasses scavenged (*n*) by season for each species observed scavenging between January 2015 and May 2018 in the Kluane Lake region, Yukon

		Season		
Species	**Overall (95)**	**Autumn (34)**	**Winter (21)**	**Spring (40)**
Avian				
Bald eagle *Haliaeetus leucocephalus*	4.2 (4)	9.0 (3)	0.0 (0)	2.5 (1)
Black-billed magpie *Pica hudsonia*	40.0 (38)	47.1 (16)	57.1 (12)	25.0 (10)
Black-capped chickadee *Poecile atricapillus*	1.1 (1)	0.0 (0)	0.0 (0)	2.5 (1)
Boreal chickadee *Poecile hudsonicus*	1.1 (1)	0.0 (0)	0.0 (0)	2.5 (1)
Common raven *Corvus corax*	60.0 (57)	73.5 (25)	57.1 (12)	25.0 (20)
Golden eagle *Aquila chrysaetos*	1.1 (1)	0.0 (0)	0.0 (0)	2.5 (1)
Canada jay *Perisoreus Canadensis*	61.1 (58)	70.6 (24)	66.7 (14)	50.0 (20)
Northern goshawk *Accipiter gentilis*	7.4 (7)	8.8 (3)	9.5 (2)	5.0 (2)
Northern harrier *Circus cyaneus*	4.2 (4)	0.0 (0)	0.0 (0)	10.0 (4)
Northern hawk-owl *Surnia ulula*	1.1 (1)	0.0 (0)	0.0 (0)	2.5 (1)
Red-tailed hawk *Buteo jamaicensis*	1.1 (1)	0.0 (0)	0.0 (0)	2.5 (1)
Mammal				
Arctic ground-squirrel *Spermophilus parryii*	1.1 (1)	0.0 (0)	0.0 (0)	2.5 (1)
Black bear *Ursus americanus*	1.1 (1)	0.0 (0)	0.0 (0)	2.5 (1)
Canada lynx *Lynx canadensis*	25.3 (24)	8.8 (3)	42.8 (9)	30.0 (12)
Coyote *Canis latrans*	4.2 (4)	0.0 (0)	9.5 (2)	5.0 (2)
Grizzly bear *Ursus arctos*	3.2 (3)	8.8 (3)	0.0 (0)	0.0 (0)
Least chipmunk *Tamias minimus*	1.1 (1)	0.0 (0)	0.0 (0)	2.5 (1)
Northern flying squirrel *Glaucomys sabrinus*	2.1 (2)	0.0 (0)	9.5 (2)	0.0 (0)
Red squirrel *Tamiasciurus hudsonicus*	51.6 (49)	67.6 (23)	52.4 (11)	37.5 (15)
Small mammals *Myodes*; *Peromyscus*; *Sorex*	8.4 (8)	17.6 (6)	0.0 (0)	5.0 (2)
Snowshoe hare *Lepus americanus*	12.6 (12)	11.8 (4)	28.6 (6)	5.0 (2)
Short-tailed weasel *Mustela ermine*	9.5 (9)	8.8 (3)	14.3 (3)	7.5 (3)
Wolverine *Gulo gulo*	2.1 (2)	0.0 (0)	4.8 (1)	2.5 (1)

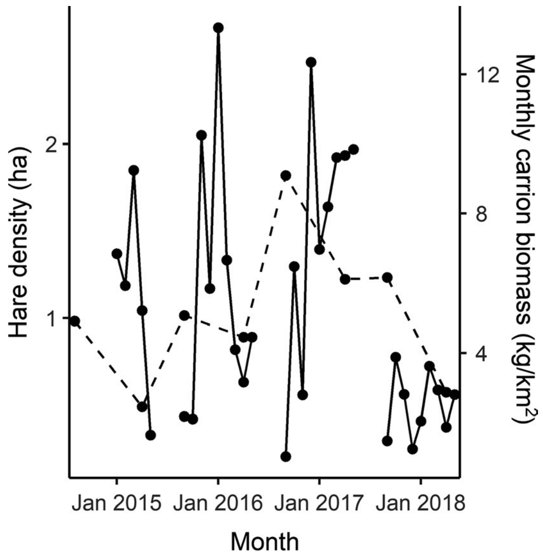


FIGURE 2 Snowshoe hare *Lepus americanus* density (dashed), and estimated monthly carrion biomass (solid) in the Kluane Lake region, Yukon, during the 4 years of our study. Gaps represent summer months when carrion biomass and community scavenging dynamics were not examined

time (w = 0.19; Table S5), which had a relative variable importance of 0.69, and was the only variable with relative variable importance >0.5 (Table S6). Longer carcass durations supported more species at the carcass (0.01 ± 0.01).

3.2 | Species-specific scavenging

Abiotic and biotic factors driving scavenging dynamics differed between species. For the common raven, the top model predicting scavenging rates consisted of season, canopy closure, and monthly carrion biomass on the landscape (w = 0.41). Carrion biomass was the only variable included in all models within 2 ΔAICc (Table S7), and had the highest relative variable importance (0.84), followed by canopy closure (0.74) and season (0.60). Scavenging probability for ravens was lowest in the winter (0.81 ± 0.87) and spring (−0.71 ± 0.72) relative to autumn, decreased in more closed canopy (−0.11 ± 0.23), and increased when there was more biomass of carrion on the landscape (0.0002 ± 0.0001; Figure 5a,b). Several models were within 2 ΔAICc for predicting magpie scavenging (Table S9), however, season was included in most of the top models and was the only variable with >0.5 relative variable importance (Table S10). Magpie scavenging was the highest during the autumn (Table 1). Canada jay scavenging was best supported by the null model, which suggests none of the covariates included in our model describe Canada jay scavenging (see Table S11).

The top model explaining red squirrel scavenging included season and squirrel density (w = 0.22). These were the only covariates included in every model with ΔAICc < 2, and had relative variable importance of 0.86 and 0.74, respectively (Tables S13 and S14). Scavenging by red squirrels was highest in autumn, relative to winter (−0.89 ± 0.74) and spring (−1.34 ± 0.67), and increased when their densities were high (0.87 ± 0.70; Figure 5). The top supported model for Canada lynx scavenging consisted of season, daily temperature, and snowshoe hare density (w = 0.47), with season and snowshoe hare density being the only variables included in all models with ΔAICc < 2 (Table S15). Hare density had the highest relative variable importance (0.98), followed by season (0.88) and temperature (0.63; Table S16). Canada lynx scavenging was highest in the winter (2.26 ± 1.19), decreased at higher hare density (−4.04 ± 1.58), and increased during warmer temperatures (0.05 ± 0.05; Figure 5). Our top model for scavenging by snowshoe hares included only daily temperature (w = 0.61), and was the only model within 2 ΔAICc (Table S17). Scavenging by hares decreased with increasing temperature (−0.08 ± 0.05; Figure 5).

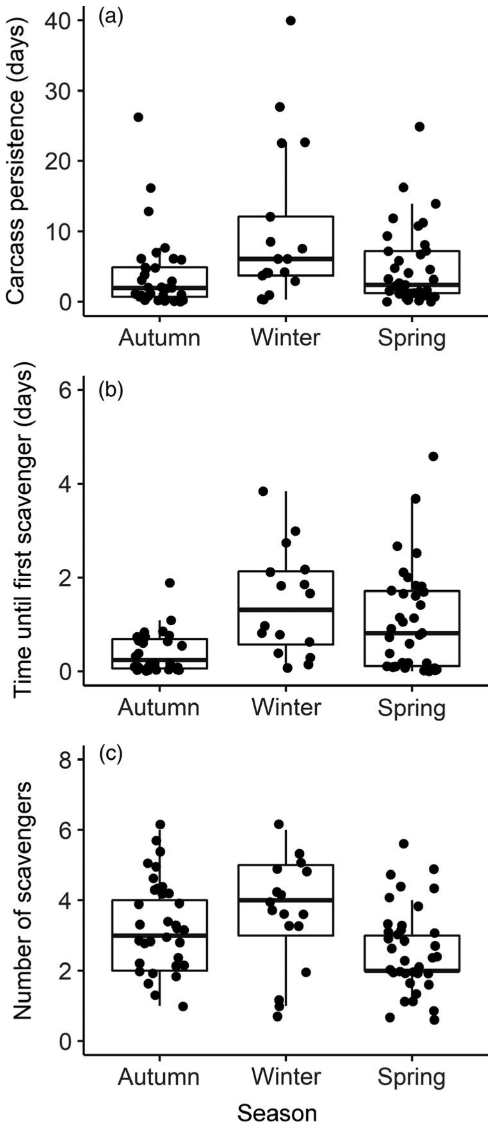


FIGURE 3 Boxplot and values for each carcass deployment comparing seasonal differences in (a) carcass persistence time (days), (b) time until the first scavenger (days) and (c) number of scavenger species per carcass

FIGURE 4 Modeled effect of (a) daily temperature, and (b) snowshoe hare *Lepus americanus* density on carcass persistence (days) during the winter based on model-averaged coefficients from models within 4 ΔAICc. All other variables are held at their mean value and confidence bars represent predicted response standard errors. Data points represent each individual carcass deployment from all seasons

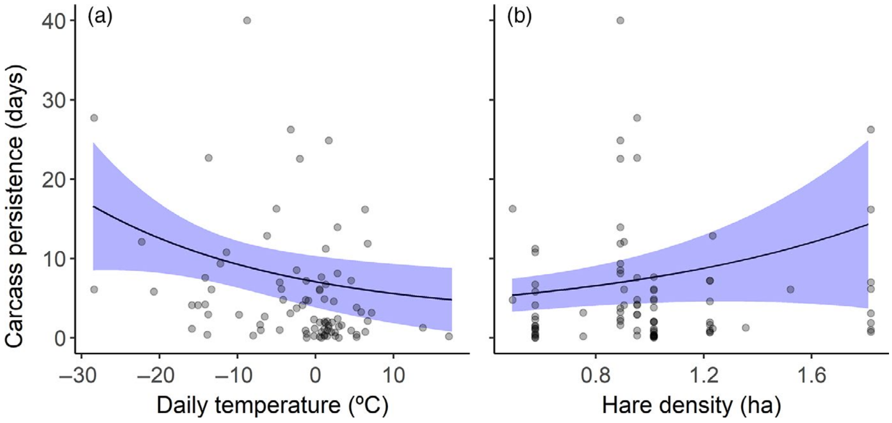
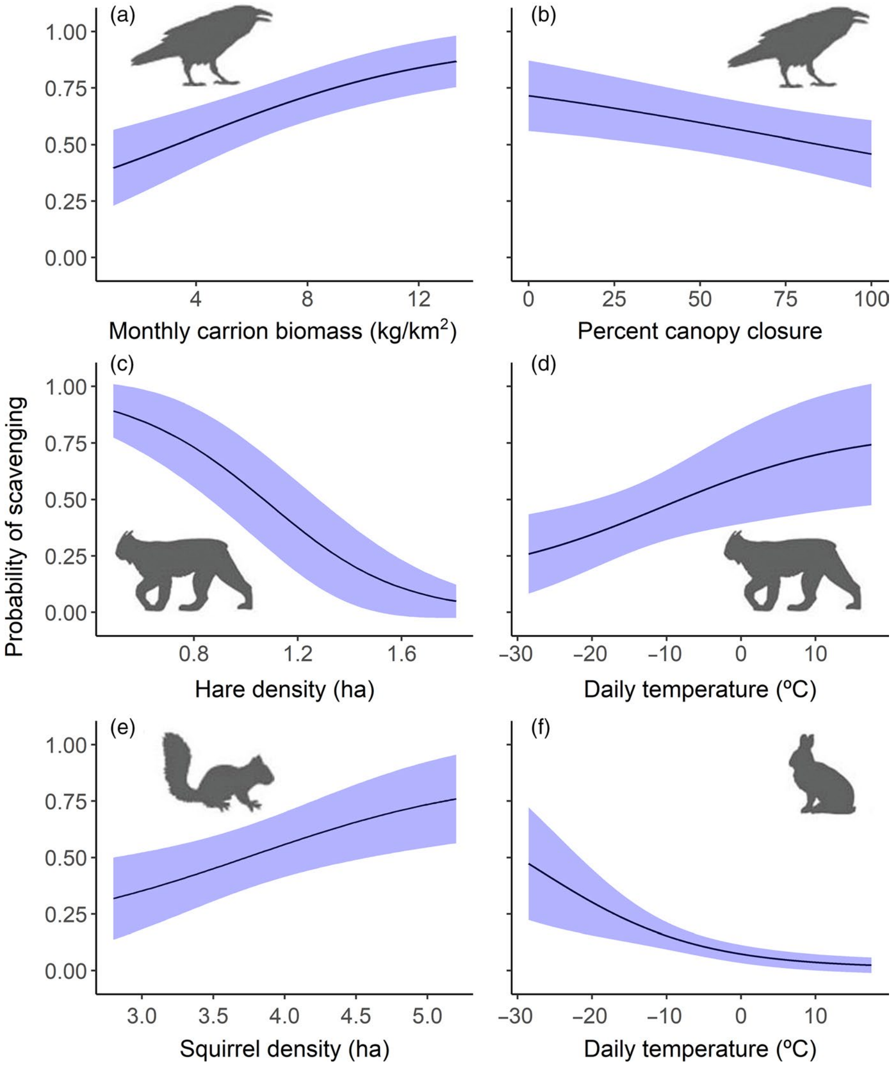


FIGURE 5 Modeled effect of biotic and abiotic predictors on the probability of scavenging for (a and b) common raven *Corvus corax*, (c and d) Canada lynx *Lynx canadensis*, (e) red squirrel *Tamiasciurus hudsonicus* and (f) snowshoe hare *Lepus americanus* during the winter season using model-averaged coefficients from models within 4 ΔAICc. All other variables are held at their mean value and confidence bars represent predicted response standard errors



4 | DISCUSSION

The role of scavenging in vertebrate food webs may be described by the efficiency at which carrion is consumed by vertebrates, as well as the number of species that scavenge (Dunne et al., 2002; Wilson & Wolkovich, 2011). We demonstrate that population cycles of a primary prey species can influence the efficiency of carrion recycling through their impact on vertebrate scavenging communities. Carrion persistence in our system decreased when snowshoe hare densities declined, likely through increased scavenging rates by their predators, in particular Canada lynx (Figure 5). Although hare carrion may not impact lynx demography (O'Donoghue et al., 2001), change in lynx scavenging behaviour may reduce carrion available for other vertebrate species over-winter (Allen, Elbroch, Wilmers, & Wittmer, 2014; Cunningham et al., 2018), and may indirectly alter predation rates on prey (Moleón, Sánchez-Zapata, Selva, Donázar, & Owen-Smith, 2014). Changes in prey abundance can therefore have a greater influence on food web dynamics than expected from purely a predator-prey framework, and these results may be broadly applicable as prey availability has been shown to impact the scavenging rates of several predator species (Mattisson et al., 2016; Needham et al., 2014). However, snowshoe hare density did not influence scavenger richness at each carcass, indicating prey density primarily affects carrion recycling efficiency rather than the number of connections in the food web established through scavenging. Vertebrate scavenger communities are therefore variable, and dependent on biological changes in the broader ecological community (Cunningham et al., 2018; see DeVault et al., 2011).

Changes in hare carrion biomass was not a strong predictor of scavenging rates. Even though snowshoe hares are a large proportion of available prey biomass in the system, the majority of snowshoe hare mortalities are from predation, and predators consume a large percentage of their carcasses (Feierabend & Kielland, 2015; Hodges, 2000). This suggests hares may only represent a minor portion of total carrion in our system relative to larger herbivores which have more biomass remaining from predator-killed carcasses (Allen et al., 2015; Moleón, Sánchez-Zapata, Sebastián-González, & Owen-Smith, 2015). Although carrion biomass has rarely been quantified (Moleón et al., 2020), the biomass estimated in our study was relatively low in comparison to the biomass estimated across terrestrial systems (Barton et al., 2019). Therefore, temporal variation in carrion biomass from snowshoe hares may have less of an impact on changes in the efficiency at which carrion is consumed by vertebrates. That being said, the influence of snowshoe hare carrion may be more apparent during the low phase of their population cycle, when hares occur at such low densities that carcasses will be nearly absent from the landscape. Irrespective of the effect on community scavenging dynamics, our data demonstrates large temporal variation in carrion biomass (Figure 2) that should be considered in future estimates (Moleón et al., 2020).

Temporal changes in snowshoe hare carrion did influence the scavenging rates of ravens, through either behavioural or demographic changes (Figure 5). Raven densities are correlated with snowshoe hare cycles (Boutin et al., 1995), and during peak densities predator-killed snowshoe hare carcasses may represent a consistent food source for ravens throughout the winter (Wilmers et al., 2003). Many organisms use carrion as either a principle food source or a buffer when primary resources decline, and changes in consistent carrion can impact the demography of both obligate and facultative scavengers (Pain et al., 2003; Wilmers et al., 2003). In total, 24 species scavenged hare carcasses during our study, indicating snowshoe hares may impact a plethora of vertebrate scavengers in the boreal forest not commonly associated with their population cycles (Table 1). Although we were strict in classifying scavenging events, we acknowledge the potential that instances considered scavenging may have represented carcass investigation. Regardless, our findings add to a growing body of research indicating that an omission of scavenging might substantially underestimate the connectedness of vertebrate food webs (Wilson & Wolkovich, 2011). Future assessments of the boreal forest community should consider links established through scavenging, given the potential importance of weak interactions in food web stability (McCann, 2000; McCann & Rooney, 2009), coupled with the rich assemblage of scavengers documented in our study area relative to other systems (see Sebastián-González et al., 2019).

Several studies have demonstrated that carrion acquisition by vertebrates is highly influenced by temperature, with warmer temperatures decreasing vertebrate scavenging rates because of increased microbial and invertebrate activity (DeVault et al., 2004; Turner et al., 2017). As a result, it has been postulated that climate change may increase carrion decomposition rates (Parmenter & Macmahon, 2009), and reduce the amount of carrion available to vertebrate scavengers (Beasley, Olson, & Devault, 2012). In our system, however, vertebrate scavenging rates actually increased with increasing temperatures, which is likely driven by decreased accessibility to carrion at cold temperatures (i.e. less than −20°C), as well as minimal competition with invertebrates over winter at northern latitudes. Our results indicate decreased carrion persistence with warmer temperatures, suggesting vertebrate scavenging may actually increase during the winter under climate change in the northern boreal forest. Although warmer temperatures also favour microbial and invertebrate activity (DeVault et al., 2004; Turner et al., 2017), the subsequent increase in vertebrate scavenging during the winter may reduce the proportion of carcasses that persist to the summer. This would limit the amount of carrion available for decomposers, however, the influence of temperature on the competitive interactions between vertebrates and decomposers in this system warrants further investigation.

As documented in other systems, we found strong seasonal differences in scavenging dynamics with carcasses persisting longer during the winter, likely driven by the influence of temperature (Turner et al., 2017). The longer persistence of carcasses during winter explained why winter supported more scavenger species per carcass, as persistence time was the strongest predictor of the number of species scavenging (see Table S5). Detection times were lowest during the autumn season, which coincides with increasing scavenging rates for avian species and red squirrels (Table 1). The richness of the vertebrate scavenging community also varied among seasons. As would be expected, hibernators such as arctic ground squirrels *Spermophilus parryii* and black bears *Ursus americanus*, and migratory birds such as Northern harriers *Circus cyaneus* and red-tailed hawks *Buteo jamaicensis* were never observed scavenging in the winter (Table 1). However, most of these species were still present but did not scavenge in autumn, indicating carrion may be a resource used by migrating or hibernating species prior to green up, when their primary food sources become more abundant. That being said, we did not monitor carcasses over the summer, limiting inference on the scavenging behaviour of these species. Regardless, the seasonal changes we observed in the scavenging community are likely consistent throughout the boreal forest, and could be incorporated into multi-season perspectives of food web dynamics in temperate ecosystems (see Humphries, Studd, Menzies, & Boutin, 2017).

Although the processes governing scavenging rates within a community can be complex, they are not random and dependent on several extrinsic factors (Selva & Fortuna, 2007; Selva et al., 2005; Turner et al., 2017). That being said, there was large variability in scavenging rates, and the number of species scavenging across predictor variables (Figure 4), potentially due to variance among species in the primary drivers of their behaviour (Figure 5). For instance, while warmer temperatures increased scavenging rates for the community, snowshoe hares scavenged more during colder periods (see Videos 1 and 2) which could be due to lower protein content of the woody browse species consumed in winter (Peers, Majchrzak, Konkolics, Boonstra, & Boutin, 2018). This high rate of cannibalistic scavenging is particularly interesting, given that other species (i.e. carnivores) generally avoid scavenging conspecifics to prevent disease transmission (Moleón et al., 2017), and certain pathogens may persist longer in colder environments (Rossi, Interisano, Deksne, & Pozio, 2019). This suggests the risk of disease transmission through carrion is generally low in this species. Carrion consumption for Canada lynx, red squirrels, and ravens was dependent on biotic factors that differed among species (Figure 5). Canada lynx appear to increase their use of carrion when resources decline (i.e. snowshoe hare), however, red squirrel scavenging was not related to white spruce cone abundance. In combination, this indicates that spatial and temporal patterns in community scavenging rates may be challenging to forecast, particularly in systems comprised of a diverse assemblage of facultative scavengers. This further implies that biotic variables not included in our models, such as the density of avian species, may be important predictors of species behaviour and could influence community scavenging rates across the boreal forest.

Our results demonstrate that in a community dominated by facultative scavengers, biotic and abiotic factors can modulate vertebrate scavenging dynamics. In particular, lower prey density on the landscape and warmer temperatures increased carrion recycling efficiency, indicating vertebrate scavenging communities are sensitive to changes in species' demography and environmental change (Beasley et al., 2018), and that increased access to carrion may buffer the negative impacts on climate change for certain species. Given that biotic factors influenced scavenging behaviour for multiple species considered here, scavenging rates in most systems are likely dependent on the population dynamics of species in the community (Cunningham et al., 2018; see DeVault et al., 2011). Scavenging rates established in previous studies are therefore dependent on the biotic conditions during the time of their study, and understanding the full suite of factors driving vertebrate scavenging communities across the globe requires continued investigation. Future studies should examine the influence of changes in prey density and carrion biomass on community scavenging rates, particularly for species that may contribute substantially to overall carrion abundance.

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AUTHORS' CONTRIBUTIONS

All authors contributed to the conception of the study and assisted with data collection either in the field or through the assessment of trail camera images. M.J.L.P., S.M.K., C.T.L. analysed the data; M.J.L.P. drafted the manuscript, and all authors critically revised the manuscript.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.g1jwstqnr (Peers et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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