Canadian Journal of Zoology
Revue canadienne de zoologie

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Journal:	<i>Canadian Journal of Zoology</i>
Manuscript ID	cjz-2016-0268.R2
Manuscript Type:	Article
Date Submitted by the Author:	16-Jul-2017
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Keyword:	Carrion, predator-prey, ecology of fear, FORAGING < Discipline, giving-up density, non-consumptive effects, trophic cascade

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Scavenging and the ecology of fear: Do animal carcasses create islands of risk on the landscape?

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ABSTRACT

Many vertebrate scavengers function as predators in ecosystems, suggesting that the presence of scavengers and occurrence of predator effects may be intertwined near carcasses. We tested for risk effects near a series of experimentally placed carcasses by measuring small mammal foraging in a Before-After Control-Impact design. Validation efforts revealed low levels of food loss from stations due to human error and invertebrate foraging, and habituation to stations occurred after two weeks. Increased perceived predation risk by small mammals relative to controls occurred in three of seven trials. The effect was observed across tested carcass types (beaver *Castor canadensis* Kuhl, 1820 and white-tailed deer *Odocoileus virginianus* Zimmermann, 1780) and seasons (summer and fall). However, small mammals also increased foraging relative to controls in two of seven trials, and foraging reached a ceiling in two other trials that prevented inference on a response. Taken together our results suggest that scavenger recruitment to carcasses can in some instances create islands of risk for prey on the landscape, but the effect is not likely to be universal. Where small mammal foraging does decrease, further work will be necessary to determine if risk effects cascade to adjacent trophic levels through enhanced seed and seedling survival.

25 **KEY WORDS**

26 Carrion, predator-prey, ecology of fear, foraging, giving-up density, non-consumptive
27 effects, trophic cascade

28

Draft

INTRODUCTION

When an animal dies on the landscape, an intense competition begins for the nutrients in its body (DeVault et al. 2003). The first organisms to capitalize on nutrients in a carcass are the microbes that existed inside the animal when it died (Carter et al. 2007; Zhou and Byard 2011). The process of microbial decomposition can create well defined ‘islands’ (Carter et al. 2007) of primary production in terrestrial landscapes as carcass nutrients are incorporated into nearby vegetation (Towne 2000; Bump et al. 2009). Nutrient efflux is one of the primary paths by which carcasses effect a landscape (Danell et al. 2002; Payne and Moore 2006; Melis et al. 2007; Parmenter and MacMahon 2009).

However, the by-products of microbial decomposition also attract invertebrate and vertebrate competitors to carcasses (Tomberlin et al. 2011). Invertebrates act to dampen the intensity of primary production spurred by carcass decomposition to some extent, because insects incorporate carcass resources, pupate, and carry nutrients away from the carcass (Carter et al. 2007). Lastly, the signal of local nutrient flux from a carcass is further attenuated when vertebrates feed, because vertebrate scavengers can consume the carcass, sometimes along with their invertebrate and microbial competitors (Janzen 1977; Burkepile et al. 2006), and move away to interact with the broader landscape (Towne 2000; Payne and Moore 2006; Barton et al. 2012). The direct effects of a carcass on the landscape are therefore mediated in part by the animals that recruit to feed on it. Often, carcasses affect the landscape through some combination of microbial, invertebrate, and vertebrate action (Beasley et al. 2015).

Scavengers are animals that feed on animal carcasses that they did not kill (DeVault et al. 2003). Typically, scavengers are categorized into two groups, obligate or facultative scavengers, based on the species’ level of dependence on carrion as a food source. Scavenging behavior is best understood for the obligate scavengers; these are scavengers that require carrion for their

53 survival and include species of old and new world vultures (DeVault et al. 2003). Facultative
54 scavengers, on the other hand, belong to a broader category of animals that do not depend on
55 carrion for their survival but will feed on a carcass if the opportunity presents itself (DeVault et
56 al. 2003; Moleon et al. 2014). The list of facultative scavengers is diverse, and includes many
57 animals that are not typically viewed as carrion-feeders (Dudley 1996; DeVault and Krochmal
58 2002; Kapfer et al. 2011; Olson et al. 2016). In general, however, most vertebrate facultative
59 scavengers and those most commonly observed feeding on carrion also function as predators in
60 their ecosystems (DeVault et al. 2003; Selva et al. 2003; Selva et al. 2005; Wilson and
61 Wolkovich 2011; Pereira et al. 2014; Moleon et al. 2014; Allen et al. 2015).

62 Because many vertebrate scavengers also function as predators in their ecosystems, the
63 presence of scavengers and the occurrence of predator effects could be intertwined (Schmitz et
64 al. 2008; Wilson and Wolkovich 2011; Moleon et al. 2014). Specifically, animal carcasses may
65 serve to focus predator effects temporally and spatially as predator-scavengers recruit to feed on
66 a carcass. Cortés-Avizanda et al. (2009a) found evidence for this interaction in an observational
67 study where the presence of a carcass increased the probability of researchers finding tracks in
68 the snow of several species of vertebrate scavenger, and negatively influenced the probability of
69 researchers finding tracks of a prey species (brown hare *Lepus europaeus* Pallas, 1778).
70 Similarly, artificial nest studies indicate that the probability of nest predation increases in the
71 presence of carrion and its associated vertebrate scavengers (Cortés-Avizanda et al. 2009b; Rees
72 et al. 2015). These results provide support for the notion that vertebrate scavengers maintain their
73 roles as predators even while engaged in the search for carrion. From the perspective of prey
74 species near a carcass, an influx of scavengers could therefore enhance predation risk (Cortés-
75 Avizanda et al. 2009a).

Predators can influence ecosystems through two types of effects on prey. Predators affect prey numerically by direct killing, but importantly can also cause the alteration of prey traits, such as prey behavior or physiology (i.e., risk effects, Creel and Christianson 2008; non-consumptive effects, Orrock et al. 2008), when prey perceive a risk of predation (Lima and Dill 1990). These numerical and behavioral (i.e., trait-mediated) effects of predators on prey can sometimes propagate within ecosystems to impact more distant trophic levels (Estes and Palmisano 1974; McInnes et al. 1992; Huang and Sih 1991; Werner and Peacor 2003). For example, Ripple and Beschta (2012) describe cascading effects of wolf (*Canis lupus* L. 1758) reintroduction on elk (*Cervus canadensis* Erxleben, 1777) herbivory and aspen (*Populus tremuloides* Michx.) and willow (*Salix spp.*) recruitment in the Yellowstone National Park, USA, ecosystem. While the depth of potential trophic cascades likely depends on a variety of factors specific to the predator, prey, their interactions, and their ecosystem, both numerical and risk effects may be involved (Creel and Christianson 2007). Comparisons of the strength of numerical and risk effects in the literature indicate that risk effects can be at least as important as numerical effects in terms of a cumulative impact (McPeck and Peckarsky 1998; Creel and Christianson 2007).

Optimal foraging theory holds that prey animals face a tradeoff when deciding to forage or engage in antipredator behaviors to reduce their predation risk (i.e., avoidance or vigilance), and that foraging effort should be reduced in environments where predation risk is greater (Brown 1988). Brown (1988) exploited the concept of giving up density (GUD) to propose the use of depletable food stations for the measurement of perceived predation risk. To use this method, researchers deploy a number of physically identical foraging stations that include identical amounts of substrate and food (i.e., metabolic and missed opportunity costs of foraging

are standardized), and the amount of food remaining in a station after foraging is interpreted as a willingness to ‘give up’ additional foraging opportunities in that station in exchange for a safer microhabitat (Brown 1988). Foraging and risk are inversely related in this system, and GUD measurements could provide the opportunity to assess predation risk perceived by small mammals under scenarios of scavenger presence. However, to our knowledge no study has empirically tested if or how frequently carcasses and their scavengers focus risk effects on the landscape.

In this study we used repeated experiments to test for risk effects caused by scavenger recruitment to carcasses. Specifically, we determined if the presence of a carcass, and the consequent presence of vertebrate scavengers, affected foraging behavior of small mammals near the carcass. Small mammals are important in terrestrial landscapes in part because they eat seeds and seedlings, a role in which their abundance and foraging behavior ultimately influences the composition of forest ecosystems (Ostfeld et al. 1997). Therefore, any force that consistently alters the abundance or foraging patterns of small mammals is of broad interest ecologically. We hypothesized that small mammal foraging would decrease (i.e., GUD would increase) after scavengers recruited to a carcass, and that this effect would be consistent across carcasses.

MATERIALS AND METHODS

Study Area

The study was conducted within two forested sites, approximately 100 and 150 ha in size, respectively, near the University of New England in southern Maine, U.S.A. (N43°27'17'' W70°26'27'' and N43°27'18'' W70°24'36''). Landowner permission for access was granted prior to the study. Sites consisted of contiguous tracts of mature upland transition hardwood forest habitat (Westveld 1956). The small mammal community in southern Maine includes North American deer mouse *Peromyscus maniculatus* Wagner, 1845, white-footed mouse *Peromyscus*

123 *leucopus* Rafinesque, 1818, southern red-backed vole *Myodes gapperi* Vigors, 1830, meadow
124 vole *Microtus pennsylvanicus* Ord, 1815, woodland vole *Microtus pinetorum* Le Conte, 1830,
125 woodland jumping mouse *Napaeozapus insignis* Miller, 1891, and, more rarely, southern bog
126 lemming *Synaptomys cooperi* Baird, 1858 (Godin 1977).

127 **Field Methods**

128 We used depletable food stations to measure foraging behavior of small mammals
129 (Brown 1988). Stations consisted of an aluminum tray (30cm x 23cm x 6cm) equipped with a
130 clear plastic lid to protect against precipitation and forest debris, and 4.00 g of dried, hulled
131 millet seed distributed randomly throughout a substrate of 500 mL sifted sand. Three rectangular
132 entrances (2cm x 15cm on two long sides and 2cm x 10cm on one short side) were cut in the tray
133 sides to allow access for foragers. These entrances allowed target species to access the stations
134 but prevented foraging by larger species (e.g., Eastern grey squirrel *Sciurus carolinensis* Gmelin,
135 1788).

136 A Before-After Control-Impact design (BACI) was used to assess the effects of carcass
137 treatment on local small mammal foraging (Green 1979; Stewart-Oaten et al. 1986). Food
138 stations were deployed simultaneously in two 5 × 5-station or 6 × 6-station grids in similar
139 habitat within a site and with 10-m spacing between stations. At least 200 m separated the two
140 grids within the site to ensure that individual small mammals were not foraging in both grids,
141 and all trials used different grid locations (except Trials 3 and 4, see below). After a habituation
142 period (i.e., prebaiting; Chitty and Kempson 1949) that allowed time for small mammals to
143 discover and become accustomed to stations (see Field Validation below), we randomly assigned
144 one of the two grids to the treatment condition using a coin flip, except for Trial 4 where we
145 intentionally used the same grids as Trial 3 but reversed the experimental conditions (i.e., from

Treatment to Control and vice versa) to determine if any effect would also reverse. Trials were conducted during 2014 ($n = 3$) and 2015 ($n = 5$).

A beaver (*Castor canadensis* Kuhl, 1820; ~12-14 kg) or white-tailed deer (*Odocoileus virginianus* Zimmermann, 1780; ~35-50 kg) carcass was used to attract scavengers to a treatment grid. Control grids received no carcass. Carcasses were held in place in the center of treatment grids with cable snares and trapping stakes to prevent complete removal by scavengers. We counted scavenger visits to all grids using images from a remote camera. Cameras (Reconyx HC600, Holmen, WI, USA) were positioned about 2-m high on a tree bole and angled slightly down toward the carcass (treatment) or the ground (control; same angle as treatment) to ensure that the cameras were monitoring approximately the same area in each grid. Cameras were programmed to capture three images after being triggered by a combination of heat and motion (i.e., an approaching scavenger), with no delay between images or triggers. Scavenger activity was recorded as a new visit if the same species had not been documented in the previous five minutes.

Foraging was measured twice during the week before and twice during a week after carcass placement and scavenger recruitment. Measurements were made on the same days in both grids by the same personnel, and stations were exposed to either one or two nights of foraging per measure across the study. Millet that remained unconsumed in each station (i.e., Giving Up Density or GUD; Brown 1988) was sifted from the substrate using window screen and returned to the laboratory, sorted to remove debris, dried overnight at 37.7°C, and then weighed using an analytical balance. No attempt was made to blind researchers to experimental conditions during the study, because millet mass was considered to be sufficiently objective as to minimize the potential for observer bias.

Statistical Analyses

We used linear mixed effects models to compare average GUD (that is, a per-station average of the two measures made per time period) across levels of the experimental design (see Lewis 1997; McDonald et al. 2000). We analyzed data separately for each trial, where a trial incorporated the pre- and post-carcass measurements from a control and a treatment grid. We chose to use separate analyses for each trial because scavenger recruitment to carcasses could not be standardized (e.g., local scavenger guilds vary among carcasses, Olson et al. 2016). Thus, we considered each carcass placement to be a new experiment.

Station position was used as a random effect to account for repeated measures in each model, whereas Time (i.e., before and after), Treatment (i.e., treatment and control), and the interaction of Time $\times$ Treatment were fixed effects. A significant interaction term would indicate that the carcass and scavengers had an impact on small mammal foraging. Post hoc (tukey) tests were used to further examine significant interactions to determine the direction of the effect. Mixed effect models are robust to unbalanced designs (Laird and Ware 1982) that might be caused by a delay in scavenger arrival or stations being excluded due to damage, excessive moisture, or human error.

In addition to the main analysis, we also used two separate procedures to assess GUD data for distance effects. We tested all trials for 1) a risk island smaller than a full grid by performing BACI analysis as above but excluding data from stations farther from the grid center (see below), and 2) a linear effect of distance (from grid center to station in meters) on GUD in Treatment grids. After carcass deployment using linear mixed effect models with station as a random effect. For the smaller risk island tests, we used GUD data from the 9 central stations when grid size was 5- $\times$ 5-stations. The 6- $\times$ 6-station grids could be split into inner (4 stations),

middle (12 stations), and outer (20 station) rings, and we repeated the BACI analyses excluding the outer rings first, then again excluding the outer and middle rings.

Scavenger visits were compared qualitatively between treatment and control grids, and before and after treatment. Statistical analyses were conducted in R version 2.15 (R Core Development Team 2012) with $\alpha = 0.05$.

Field validation methods

Depletable food stations have been used extensively to measure foraging behavior of small mammals in desert or grassland habitats (Brown 1988; Morris 1997; Jacob and Brown 2000), but are less commonly used in forested ecosystems probably because of the difficulties posed by frequent precipitation and an abundance of forest debris (although see e.g., Orrock et al. 2004). We validated the use of depletable food stations to measure small mammal foraging in a temperate forested landscape by 1) determining measurement error, 2) documenting the rate of invertebrate foraging, 3) identifying vertebrate foragers, 4) determining an appropriate length of time for habituation, and 5) documenting any evidence of animals using the stations more extensively than for foraging. Measurement error was assessed using stations without entrance holes. These stations were deployed in 2×2 grids adjacent to experimental grids already in use. All field and measurement procedures were otherwise identical. Average millet loss was calculated and attributed to human error. We assessed the scope of invertebrate foraging in stations after we observed slugs (Mollusca, Gastropoda) and in some cases ants (Arthropoda, Insecta, family Formicidae) removing small numbers of millet seeds from stations. To measure invertebrate foraging, additional GUD stations were modified by covering entrances with 0.25-inch steel hardware cloth (6.35-mm openings) to prevent small mammals from entering while allowing invertebrate access. Invertebrate-only stations were also deployed in 2 x 2 grids

adjacent to experimental grids, and all field and measurement procedures were followed as above. Average millet loss from these trials was attributed to foraging by invertebrates, but also included human error.

To verify that target vertebrates (i.e., small mammals) were using the stations, we monitored six randomly-chosen GUD stations with remote cameras (Bedoya-Perez et al. 2013). Cameras were placed ~30 cm from stations, viewing it from above (we used special tree mounts or t-post mounts to achieve the view), and images were used to count any species using the stations. We recorded a new foraging bout if the same species had not been documented at the station in the previous five minutes. We determined the appropriate length of time needed for small mammals to habituate to the stations. We calculated the average proportion of stations with small mammal tracks by week to determine when foraging stabilized. Lastly, we noted any instances of nesting or nest material that might indicate animals perceived the stations as refuge habitats as opposed to foraging habitats, as this could affect our ability to document behavioral responses to predation risk.

RESULTS

Trials 1 and 2 yielded significant Time x Treatment interaction terms (Table 1). In Trial 1, post hoc tests revealed that GUD in the Treatment grid decreased more from before (mean $\pm$ SE; 1.51 $\pm$ 0.26 g) to after (0.03 $\pm$ 0.26 g) carcass placement ($t_{2,4}=4.06$, $P = 0.04$) than did GUD in the Control grid from before (0.51 $\pm$ 0.26 g) to after (0.02 $\pm$ 0.26 g) carcass placement ($t_{2,3}=1.35$, $P = 0.29$). Similarly, in Trial 2 post hoc tests revealed that GUD in the Treatment grid decreased more from before (1.50 $\pm$ 0.15) to after (0.19 $\pm$ 0.15) carcass placement ($t_{2,7}=6.13$, $P = 0.012$) than did the Control grid from before (0.25 $\pm$ 0.15 g) to after (0.02 $\pm$ 0.15 g) carcass placement ($t_{2,7}=1.11$, $P = 0.356$).

Trials 3 and 4 also yielded significant interaction terms (Table 1). However, in Trial 3 the

treatment grid GUD (3.61 ± 0.11 g) did not change after the addition of the carcass (3.47 ± 0.11 g; $t_{210} = 1.24$, $P = 0.217$), while the control grid GUD decreased ($t_{211} = 7.87$, $P < 0.001$) from 3.04 ± 0.11 g to 2.10 ± 0.11 g. In Trial 4, GUD in the Treatment grid decreased ($t_{354} = 3.20$, $P = 0.002$) from before (0.62 ± 0.12 g) to after (0.24 ± 0.10 g) carcass placement, but GUD in the control grid decreased ($t_{354} = 12.64$, $P < 0.001$) more from 2.14 ± 0.12 g to 0.63 ± 0.09 g (Fig. 1).

Trials 5 and 6 were characterized by intense small mammal foraging across all levels of the BACI design (Fig. 1). Average trial-wide GUD for Trial 5 was 0.04 ± 0.004 g, and 0.02 ± 0.002 g for Trial 6. These trials did not yield significant Time $\times$ Treatment interaction terms (Table 1). In response to the intense level of foraging by small mammals in Trials 5 and 6, we decreased the foraging period in Trial 7 from 2 nights to 1 night. Trial 7 yielded a significant interaction term (Table 1), with GUD increasing ($t_{212} = -4.32$, $P < 0.001$) in the Treatment grid from before (0.28 ± 0.13 g) to after (0.78 ± 0.13 g) carcass placement while GUD in the control grid remained unchanged through time (before = 0.34 ± 0.13 , after = 0.51 ± 0.13 , $t_{213} = -1.48$, $P = 0.14$).

The tests for smaller risk islands using the BACI experimental design yielded results similar to, and interpretations in agreement with, those acquired from our full data sets, with the exception that Trial 7 did not yield a significant Time $\times$ Treatment interaction in the reduced data sets (see Supplementary Materials). In Trial 1 ($\text{GUD} = -0.0046(\text{Dist}) + 0.075$, $t_{41} = -2.525$, $P = 0.015$, $r^2 = 0.09$) and Trial 7 ($\text{GUD} = -0.041(\text{Dist}) + 1.721$, $t_{34} = -2.237$, $P = 0.032$, $r^2 = 0.13$), GUD decreased (i.e., foraging increased) as distance from the carcass increased, but these relationships were relatively weak (see Supplementary Materials).

Vertebrate scavengers recruited to all carcasses, and scavenging visits increased qualitatively in all treatment grids after carcasses were added. Scavengers included turkey vulture *Cathartes aura* L., 1758, gray fox *Urocyon cinereoargenteus* Schreber, 1775, red fox

Vulpes vulpes L., 1758, raccoon *Procyon lotor* L., 1758, and coyote *Canis latrans* Say, 1823 (Table 2). Remote cameras captured several other species passing through the grids (white-tailed deer, North American porcupine *Erethizon dorsatum* L., 1758, and wild turkey *Meleagris gallopavo* L., 1758), but these animals did not interact with carcasses, are not predators, and we suspect that such infrequent visitors would not have altered small mammal perceptions of predation risk.

Field Validation

Measurement error was 0.16 ± 0.01 g ($n = 32$ measurements). Invertebrate presence led to a loss of 0.66 ± 0.06 g ($\sim 17\%$, $n = 56$) of millet on average and was consistent across experiments. Slug trails were present in stations pervasively regardless of precipitation events. White-footed mouse ($n = 59$ foraging bouts), southern red-backed vole ($n = 30$), *Microtus* spp. ($n = 26$), and woodland jumping mouse ($n = 3$) were documented foraging at stations monitored with remote cameras over a combined 66 camera nights across the six stations. We recorded five additional bouts where we could not discriminate beyond identifying foragers as small mammals (i.e., a total of 123 bouts). Eight bouts (6.5% of total) included two animals foraging simultaneously. There was only one instance in which a non-target species (a raccoon) accessed millet from a station during validation trials. This particular data point was thrown out, but other instances would have been recognizable even without evidence from a remote camera because the station was destroyed and raccoon tracks were visible in the remaining sand substrate.

The proportion of stations with small mammal tracks increased through the end of two weeks of habituation before stabilizing after 3 weeks (Fig. 2). Trials 1-4 were conducted with two weeks of habituation before the experiment, and Trials 5-7 were conducted with 3 weeks or more. Lastly, no nesting material or other evidence of long-term occupancy (e.g., mice inside the

station when the lid was removed) was identified during the study, indicating that animals were in fact using the stations for foraging rather than as refuges.

DISCUSSION

Animal carcasses can affect ecosystems in a number of ways. Carcasses can be rich sources of nutrients for local soil and foliar communities upon their decomposition, can serve as reproductive resources for invertebrates, act as foci for competition and disease transmission, and provide vertebrate scavengers with food (Towne 2000; DeVault et al. 2003; Melis et al. 2007; Bump et al. 2009; Parmenter and MacMahon 2009; Wilson and Wolkovich 2011; Barton et al. 2012; Pereira et al. 2014; Allen et al. 2015; Barton 2015; Beasley et al. 2015). Our study extends previous knowledge of carrion ecology by experimentally demonstrating that carcasses can also in some instances create islands of risk for vertebrate prey species by recruiting scavengers that focus predator effects on the landscape. However, this effect was not consistently observed across our experiments.

Carcasses attracted vertebrate scavengers in all our trials, and small mammal foraging did decrease (i.e., GUD increased) relative to controls in three of seven trials (Trials 3, 4, and 7). Increased perceived predation risk by small mammals relative to controls occurred across tested carcass types (beaver and white-tailed deer) and seasons (summer and fall). However, small mammals unexpectedly increased foraging (i.e., GUD decreased) relative to controls in two other trials (Trials 1 and 2), and foraging intensified to reach a ceiling in two trials (Trials 5 and 6) which limited our ability to make inference on a response to scavenger presence. Thus, although scavenger recruitment to carcasses appears to affect small mammal foraging in some instances, our results suggest that the creation of risk islands as a function of scavenger recruitment is not universal.

Similarly, any risk island that is formed will likely vary in size and shape (Matassa and Trussell 2011). We assumed that a risk island would be larger than our grid sizes because our grids approximated the size of a small mammal home range (white-footed mouse; Lackey et al. 1985) and had a width within the perceptual range of a small mammal (white-footed mouse; Zollner and Lima 1997). When we analyzed data from subsets of stations closer to the center of each grid, no additional trials emerged with the pattern of GUD increase that met our expectations for the formation of a risk island. We still detected the expected pattern of GUD increase at smaller spatial scales in Trials 3 and 4, but not in Trial 7 where GUD differences among BACI units were likely too small to detect with lower station numbers. Separately, we detected a negative linear relationship between GUD and distance from the carcass in Trials 1 and 7. Interpretation of Trial 1 results is difficult, because foraging increased after carcass placement yet a weak negative association with distance from the carcass was also present. We speculate that the risk island was larger than our grids in Trials 3 and 4, where no distance effect was detected, and approximately grid-sized in Trial 7 leading to diminishing risk effects near the edge of the grid. However, additional research will be required to better understand the shape and size of risk islands in this study system.

The species of scavenger that recruited to a carcass may also have influenced the chance of a risk island being formed, although any pattern was not straightforward. Facultative scavenging canids (coyote and red fox) were present in two of the trials in which risk islands were identified by our measures, whereas only obligate scavenging turkey vultures were recruited in the third such trial. Coyote and red fox are documented predators of small mammals (Bekoff 1977; Lariviere and Pasitschniak-Arts 1996) whose nocturnal habits could be expected to increase perceived predation risk by nocturnal small mammals via increased predator lethality

(Brown et al. 1999). Turkey vultures, however, forage diurnally and are not efficient predators (Campbell 2015), and their ability to shift foraging decisions by small mammals in the experiment was surprising. Turkey vulture activity at carcasses was intense (Table 2), and it is possible that small mammals responded more generally to that increased activity in the treatment grid. Results from Trial 1 further complicate an attempt to generalize our results, because the combined scavenging of gray fox (a nocturnal predator of small mammals; Fritzell and Haroldson 1982) and turkey vultures did not result in an increase in perceived predation risk by small mammals. Thus, neither the presence of a canid nor the presence of scavenger activity in general was fully predictive of a response by the small mammal community.

Local vertebrate scavenger guilds, or the species that assemble to forage on a particular carcass (*sensu* Fauth et al. 1996), have been shown to vary spatially and temporally (Killengreen et al. 2012; Olson et al. 2016) with patterns in guild membership driven to some extent by foraging decisions of individual animals (Olson et al. 2016), to some extent by species traits (Selva et al. 2003, 2005; Allen et al. 2014, 2015), and to a greater extent simply by the background communities of species available to recruit to the carcass where it falls (Killengreen et al. 2012). For example, Killengreen et al. (2012) documented neighborhood effects on local scavenger guilds by monitoring carcasses in adjacent habitats that sampled different vertebrate communities. Similarly, seasonal migrations remove migratory vultures from competitions for carrion resource during colder months in temperate zones (DeVault et al. 2004; Selva et al. 2005; Olson et al. 2016). If small mammals are responding to specific scavengers much as they can respond to specific predators (Jedrzejewski et al. 1993), it is possible that predator effects at carcasses could change geographically or seasonally in concert with structural changes to local scavenger guilds (e.g., seasonal shifts in threat; Brown 1999).

We chose to conduct trials in warmer seasons (summer and fall; average daily temperatures ~15-20 °C) for two reasons. First, GUD measurements could be challenging in colder seasons when snowpack creates opportunities for small mammals to forage in subnivean spaces. Second, we assumed that predator effects would be lower in warmer seasons and that our trials would therefore provide a conservative test of our hypotheses. Facultative scavenger efficiency and activity changes seasonally (DeVault et al. 2003; Selva et al. 2005), in part because invertebrates monopolize progressively more carrion as temperatures rise, which limits vertebrate scavenging at higher temperatures (DeVault et al. 2004; Selva et al. 2005; DeVault et al. 2011). Many vertebrate predators also shift to use carrion more heavily during lean seasons. For example, in colder weather pine martens (*Martes martes* L., 1758) altered their movement behavior to make consistent use of den sites with access to large ungulate carcasses in the Białowieża National Park, Poland (Zalewski 1997). Similarly, coyotes also spent more time at carrion during winter months in the western United States (Gese et al. 1996). Such focused use of carcasses by facultative scavengers would increase prey encounter rates with predators near carcasses, enhance any risk effects, and might affect adjacent trophic levels if predator effects are large enough to cascade (Brown 1999; Cortés-Avizanda et al. 2009a).

On the other hand, resource scarcity for prey species can decrease the effect size of any behavioral response to predation risk, making the response more difficult to detect (Luttbeg et al. 2003). Our study occurred during resource rich seasons for small mammals in general (summer and fall), although we did not measure resource levels in the environment as part of our study. Similarly, the energetic state and abundance of prey animals (Luttbeg et al. 2003), the magnitude of predation risk relative to existing resource levels (Gilliam and Fraser 1987), and the spatial arrangement of the depletable food stations relative to the island of risk (Matassa and Trussell

2011) may all shape the magnitude of risk effects. Although our experimental design used paired treatment and control sites to account for many potential confounds, such as temporal changes in risk (see Lima and Bednekoff 1999, Jacob and Brown 2000, Sundell et al. 2004), lower effect sizes could have reduced the power of our experimental design to detect behavioral changes if they were present. Further experimental work will be necessary to determine if a response by small mammals to scavengers can indeed cascade to adjacent trophic levels (i.e., seed or seedling survival) in those cases where risk effects are observable.

Experimental and theoretical work have also shown that risk effects can persist independent of direct predator stimuli (Orrock et al. 2004; Orrock et al. 2008; Peckarsky et al. 2008). Orrock et al. (2004) found that terrestrial small mammals made foraging decisions based on indirect cues to predation risk rather than a direct olfactory cue to the actual presence of a predator (urine of various predators; Orrock et al. 2004). Such results would seem to minimize the role of chemosensory modalities in assessments of predation risk by terrestrial small mammals, although there are data to suggest the opposite (see Kats and Dill 1998). In some systems, predators may even deprive prey of information concerning their risk of attack by using ‘purposeful unpredictability’ in their movements (Roth and Lima 2007). Uncovering the cues used by prey to gauge predation risk is an active field of research, and the use of carrion to attract otherwise elusive predators to an experimental plot may hold promise for future studies. Lastly, an important finding from our study is that small mammals did not make consistent use of stations immediately, but foraged predictably by the third week of station deployment. Future work should consider habituation time in experimental design of studies employing a GUD framework.

ACKNOWLEDGEMENTS

We thank the University of New England (UNE) and one private landowner for providing access to field sites. This work was made possible by a grant from the UNE. CMS, CAW, and XR were supported by Summer Undergraduate Research Experience fellowships from UNE. This study was conducted with the approval of UNE's Institutional Animal Care and Use Committee under protocol #UNE-20130502OLSOZ.

REFERENCES

- Allen, M.L., Elbroch, L.M., Wilmers, C.C., and Wittmer, H.U. 2014. Trophic facilitation or limitation? Comparative effects of pumas and black bears on the scavenger community. *PLoS One*, 9:e102257. doi: 10.1371/journal.pone.0102257
- Allen, M.L., Elbroch, L.M., Wilmers, C.C., and Wittmer, H.U. 2015. The comparative effects of large carnivores on the acquisition of carrion by scavengers. *Am. Nat.* 185:822–833. doi: 10.1086/681004
- Baril, L.M. 2009. Change in deciduous woody vegetation, implications of increased willow (*Salix* spp.) growth for bird species diversity and willow species composition in and around Yellowstone National Park's northern range. Thesis, Montana State University.
- Barton, P.S. 2015. The role of carrion in ecosystems. *In* Carrion ecology, evolution, and their application. Edited by M.E. Benbow, J. Tomberlin, and A. Tarone. CRC Press, Boca Raton, Fla. pp. 273-290.
- Barton, P.S., Cunningham, S.A., Lindenmayer, D.B., and Manning, A.D. 2012. The role of carrion in maintaining biodiversity and ecological processes in terrestrial ecosystems. *Oecologia*, 171:761-772
- Beasley, J.C., Olson, Z.H., and DeVault, T.L. 2015. Ecological role of vertebrate scavengers. *In* Carrion ecology, evolution, and their application. Edited by M.E. Benbow, J. Tomberlin, and A. Tarone. CRC Press, Boca Raton, Fla. pp. 107-128

- 424 Bedoya-Perez, M.A., Carthey, A.J.R., Mella, V.S.A., McArthur, C., and Banks, P.B. 2013. A
425 practical guide to avoid giving up on giving-up densities. *Behav. Ecol. Sociobiol.*
426 67:1541-1553.
- 427 Bekoff, M. 1977. *Canis latrans*. *Mamm. Species*, No. 79:1-9.
- 428 Beschta, R.L., and Ripple, W.J. 2012. The role of large predators in maintaining riparian plant
429 communities and river morphology. *Geomorphology*, 157-158:88-98.
- 430 Brown, J.S. 1988. Patch use as an indication of habitat preference, predation risk, and
431 competition. *Behav. Ecol. Sociobiol.* 22:37-47.
- 432 Brown, J.S., Laundre, J.W., and Gurung, M. 1999. The ecology of fear: Optimal foraging, game
433 theory, and trophic interactions. *J. Mammal.* 80:385-399.
- 434 Bump, J.K., Peterson, R.O., and Vucetich, J.A. 2009. Wolves modulate soil nutrient
435 heterogeneity and foliar nitrogen by configuring the distribution of ungulate carcasses.
436 *Ecology*, 90:3159-3167.
- 437 Burkepile, D., Parker, J., and Woodson, C. 2006. Chemically mediated competition between
438 microbes and animals: microbes as consumers in food webs. *Ecology*, 87:2821-2831.
- 439 Campbell, M.O. 2015. *Vultures: Their evolution, ecology and conservation*. CRC Press, London.
- 440 Carter, D.O., Yellowlees, D., and Tibbett, M. 2007. Cadaver decomposition in terrestrial
441 ecosystems. *Naturwissenschaften*, 94:12-24.
- 442 Chitty, D., and Kempson, D.A. 1949. Prebaiting small mammals and a new design of live trap.
443 *Ecology*, 30:536-542.
- 444 Cortés-Avizanda, A., Carrete, M., Serrano, D., and Donázar, J.A. 2009a. Carcasses increase the
445 probability of predation of ground-nesting birds: A caveat regarding the conservation
446 value of vulture restaurants. *Anim. Conserv.* 12:85-88.

- 447 Cortés-Avizanda, A., Selva, N., Carrete, M., and Donázar, J.A. 2009b. Effects of carrion
448 resources on herbivore spatial distribution are mediated by facultative scavengers. *Basic*
449 *Appl. Ecol.* 10:265-272.
- 450 Creel, S., and Christianson, D. 2008. Relationships between direct predation and risk effects.
451 *Trends Ecol. Evol.* 23:194-201.
- 452 Danell, K., Berteaux, D., and Brathen, K.A. 2002. Effect of muskox carcasses on nitrogen
453 concentration in tundra vegetation. *Arctic*, 55:389-392.
- 454 DeVault, T., and Krochmal, A. 2002. Scavenging by snakes: an examination of the literature.
455 *Herpetologica*, 58:429-436.
- 456 DeVault, T.L., Brisbin Jr., I.L., and Rhodes Jr., O.E. 2004. Factors influencing the acquisition of
457 rodent carrion by vertebrate scavengers and decomposers. *Can. J. Zool.* 82:502-509.
- 458 DeVault, T.L., Rhodes Jr, O.E., and Shivik, J.A. 2003. Scavenging by vertebrates: behavioral,
459 ecological, and evolutionary perspectives on an important energy transfer pathway in
460 terrestrial ecosystems. *Oikos*, 102:225-234.
- 461 DeVault, T.L., Olson, Z.H., Beasley, J.C., and Rhodes Jr, O.E. 2011. Mesopredators dominate
462 competition for carrion in an agricultural landscape. *Basic Appl. Ecol.* 12:268-274.
- 463 Dudley, J.P. 1996. Record of carnivory, scavenging and predation for *Hippopotamus amphibius*
464 in Hwange National Park, Zimbabwe. *Mammalia*, 60:486-488.
- 465 Estes, J.A., and Palmisano, J.F. 1974. Sea otters: their role in structuring nearshore communities.
466 *Science*, 185:1058-1060.
- 467 Fauth, J.E., Bernardo, J., Camara, M., Resetarits Jr., W.J., Van Buskirk, J., and McCollum, S.A.
468 1996. Simplifying the jargon of community ecology: A conceptual approach. *Am. Nat.*
469 147:282-286.

- 470 Fritzell, E.K., and Haroldson, K.J. 1982. *Urocyon cinereoargenteus*. Mamm. Species, No. 189:1-
471 8.
- 472 Gese, E.M., Ruff, R.L., and Crabtree, R.L. 1996. Foraging ecology of coyotes (*Canis latrans*):
473 the influence of extrinsic factors and a dominance hierarchy. Can. J. Zool 74:769-783.
- 474 Gilliam, J. F., and D. F. Fraser. 1987. Habitat selection under predation hazard: test of a model
475 with foraging minnows. Ecology, 68:1856-1862.
- 476 Godin, A.J. 1977. Wild mammals of New England. Johns Hopkins University Press.
- 477 Green, R.H. 1979. Sampling design and statistical methods for environmental biologists. Wiley,
478 New York.
- 479 Huang, C., and Sih, A. 1991. Experimental studies on direct and indirect interactions in a three
480 trophic-level stream system. Oecologia, 85:530-536.
- 481 Jacob, J., and Brown, J.S. 2000. Microhabitat use, giving-up densities and temporal activity as
482 short- and long-term anti-predator behaviors in common voles. Oikos, 91:131-138.
- 483 Janzen, D. 1977. Why fruits rot, seeds mold, and meat spoils. Am. Nat. 111:691-713.
- 484 Jedrzejewski, W., Rychlik, L., and Jedrzejewska, B. 1993. Responses of bank voles to odours of
485 seven species of predators: experimental data and their relevance to natural predator-vole
486 relationships. Oikos, 68:251-257.
- 487 Kats, L.B., and Dill, L.M. 1998. The scent of death: chemosensory assessment of predation risk
488 by prey animals. Ecoscience, 5:361-394.
- 489 Kapfer, J., Gammon, D., and Groves, J. 2011. Carrion-feeding by Barred Owls (*Strix varia*). The
490 Wilson J. Ornithol. 123:646-649.

- 491 Killengreen, S.T., Strømseng, E., Yoccoz, N.G., and Ims, R.A. 2012. How ecological
492 neighbourhoods influence the structure of the scavenger guild in low arctic tundra. Div.
493 Distr. 18:563-574.
- 494 Lackey J.A., Huckaby D.G., and Ormiston B.G. 1985. *Peromyscus leucopus*. Mamm. Species,
495 No. 247:1-10.
- 496 Laird, N.M., and Ware, J.H. 1982. Random-effects models for longitudinal data. Biometrics
497 38:963-974.
- 498 Larivière, S., and Pasitschniak-Arts, M. 1996. *Vulpes vulpes*. Mamm. Species, No. 537:1–11.
499 doi: 10.2307/3504236
- 500 Lewis, A.R. 1997. Effects of experimental coral disturbance on the structure of fish communities
501 on large patch reefs. Mar. Ecol. Prog. Ser. 161:37-50.
- 502 Lima, S.L. and Bednekoff, P.A. 1999. Temporal variation in danger drives antipredator behavior:
503 the predation risk allocation hypothesis. Am. Nat. 153:649-659.
- 504 Lima, S.L., and Dill, L.M. 1990. Behavioral decisions made under risk of predation: a review
505 and prospectus. Can. J. Zool. 68:619–640.
- 506 Luttbeg, B., Rowe, L., and Mangel, M. 2003. Prey state and experimental design affect relative
507 size of trait- and density-mediated indirect effects. Ecology, 84:1140-1150.
- 508 Matassa, C.M., and Trussell, G.C. 2011. Landscape of fear influences the relative importance of
509 consumptive and nonconsumptive predator effects. Ecology, 92:2258-2266.
- 510 McDonald, T.L., Erickson, W.P., and McDonald, L.L. 2000. Analysis of count data from before-
511 after control-impact studies. J. Agric. Biol. Environ. Stat. 5:262-279.

- 512 McInnes, P.F., Naiman, R.J., Pastor, J., and Cohen, Y. 1992. Effects of moose browsing on
513 vegetation and litter of the boreal forest, Isle Royale, Michigan, USA. *Ecology*, 73:2059–
514 2075.
- 515 McPeck, M.A., and Peckarsky, B.L. 1998. Life histories and the strengths of species interactions:
516 combining mortality, growth, and fecundity effects. *Ecology*, 79:867–879.
- 517 Melis, C., Selva, N., Teurlings, I., Skarpe, C., Linnell, J.D.C., and Andersen, R. 2007. Soil and
518 vegetation nutrient response to bison carcasses in Białowieża Primeval Forest, Poland.
519 *Ecol. Res.* 22:807–813. doi: 10.1007/s11284-006-0321-4
- 520 Moleon, M., Sanchez-Zapata, J.A., Selva, N., Donazar, J.A., and Owen-Smith, N. 2014. Inter-
521 specific interactions linking predation and scavenging in terrestrial vertebrate
522 assemblages. *Biol. Rev. Camb. Philos. Soc.* 89:1042–1054. doi: 10.1111/brv.12097
- 523 Morris, D.W. 1997. Optimally foraging deer mice in prairie mosaics: a test of habitat theory and
524 absence of landscape effects. *Oikos*, 80:31–42.
- 525 Olson, Z.H., Beasley, J.C., and Rhodes Jr., O.E. 2016. Carcass type affects local scavenger
526 guilds more than habitat connectivity. *PLoS One*, 11:1–19. doi:
527 10.1371/journal.pone.0147798
- 528 Orrock, J.L., Danielson, B.J., and Brinkerhoff, R.J. 2004. Rodent foraging is affected by indirect,
529 but not by direct, cues of predation risk. *Behav. Ecol.* 15:433–437. doi:
530 10.1093/beheco/arh031
- 531 Orrock, J.L., Grabowski, J.H., Pantel, J.H., Peacor, S.D., Peckarsky, B.L., Sih, A., and Werner,
532 E.E. 2008. Consumptive and nonconsumptive effects of predators on metacommunities
533 of competing prey. *Ecology*, 89:2426–2435.

- 534 Ostfeld, R.S., Manson, R.H., and Canham, C.D. 1997. Effects of rodents on survival of tree
535 seeds and seedlings invading old fields. *Ecology*, 78:1531-1542.
- 536 Parmenter, R., and MacMahon, J. 2009. Carrion decomposition and nutrient cycling in a
537 semiarid shrub-steppe ecosystem. *Ecol. Monogr.* 79:637-661.
- 538 Payne, L.X., and Moore, J.W. 2006. Mobile scavengers create hotspots of freshwater
539 productivity. *Oikos*, 115:69–80. doi: 10.1111/j.2006.0030-1299.14899.x
- 540 Peckarsky, B.L., Abrams, P.A., Bolnick, D.I., Dill, L.M., Grabowski, H., Luttbeg, B., Orrock,
541 J.L., Peacor, S.D., Preisser, E.L., Schmitz, O.J. and Trussell, G.C. 2008. Revisiting the
542 classics: Considering nonconsumptive effects in textbook examples of predator-prey
543 interactions. *Ecology*, 89:2416–2425.
- 544 Pereira, L.M., Owen-Smith, N., and Moleón, M. 2014. Facultative predation and scavenging by
545 mammalian carnivores: seasonal, regional and intra-guild comparisons. *Mammal Rev.*
546 44:44–55. doi: 10.1111/mam.12005
- 547 Rees, J.D., Webb, J.K., Crowther, M.S., and Letnic, M. 2015. Carrion subsidies provided by
548 fishermen increase predation of beach-nesting bird nests by facultative scavengers. *Anim.*
549 *Conserv.* 18:44–49. doi: 10.1111/acv.12133
- 550 Ripple, W.J., and Beschta, R.L. 2012. Trophic cascades in Yellowstone: The first 15 years after
551 wolf reintroduction. *Biol. Conserv.* 145:205–213. doi: 10.1016/j.biocon.2011.11.005
- 552 Roth, T.C., and Lima, S.L. 2007. Use of prey hotspots by an avian predator: purposeful
553 unpredictability? *Am. Nat.* 169:264–273. doi: 10.1086/510605
- 554 Schmitz, O.J., Jones, H.P., and Barton, B.T. 2008. Scavengers. *In* *Encyclopedia of ecology.*
555 *Edited by* S.E. Jorgensen and B. Fath. Elsevier, Netherlands, pp. 3160-3164

- Selva, N., Jedrzejewska, B., and Jedrzejewski, W. 2003. Scavenging on European bison carcasses in Bialowieza Primeval Forest (eastern Poland). *Ecoscience*, 10:303–311.
- Selva, N., Jedrzejewska, B., Jedrzejewski, W., and Wajrak, A. 2005. Factors affecting carcass use by a guild of scavengers in European temperate woodland. *Can. J. Zool.* 83:1590–1601.
- Stewart-Oaten, A., Murdoch, W.W., and Parker, K.R. 1986. Environmental impact assessment: “pseudoreplication” in time? *Ecology*, 67:929–940. doi: 10.2307/1939815
- Sundell, J., Dudek, D., Klemme, I., Koivisto, E., Pusenius, J., and Ylönen, H. 2004. Variation in predation risk and vole feeding behaviour: a field test of the risk allocation hypothesis. *Oecologia*, 139:157–16.
- Tomberlin, J.K., Mohr, R., Benbow, M.E., Tarone, A. M. and VanLaerhoven, S. 2011. A roadmap for bridging basic and applied research in forensic entomology. *Annu. Rev. Entomol.* 56:401–21. doi: 10.1146/annurev-ento-051710-103143
- Towne, E.G. 2000. Prairie vegetation and soil nutrient responses to ungulate carcasses. *Oecologia*, 122:232–239. doi: 10.1007/PL00008851
- Werner, E.E., and Peacor, S.D. 2003. A review of trait-mediated indirect interactions in ecological communities. *Ecology*, 84:1083–1100.
- Westveld, M. 1956. Natural forest vegetation zones of New England. *J. Forest.* 54:332–338.
- Wilson, E.E., and Wolkovich, E.M. 2011. Scavenging: how carnivores and carrion structure communities. *Trends Ecol. Evol.* 26:129–35.
- Zalewski, A. 1997. Patterns of resting site use by pine marten *Martes martes* in Bialowieza National Park (Poland). *Acta Theriol.* 42:153–168.

- 578 Zhou, C., and Byard, R.W. 2011. Factors and processes causing accelerated decomposition in
579 human cadavers - An overview. *J. Forensic Legal Med.* 18:6-9.
- 580 Zollner, P.A., and Lima, S.L. 1997. Landscape-level perceptual abilities in white-footed mice:
581 perceptual range and the detection of forested habitat. *Oikos*, 80:51-60.
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Table 1

Details pertaining to each trial including start date, the type of carcass that was deployed into the treatment grid, the number of depletable food stations used per grid, the length of the foraging period measured in nights, an indication of whether the experimental effect (i.e., the Time x Treatment interaction) was statistically significant, and the relative direction of the effect if any. Our expectation was that GUD would increase (i.e., more millet left behind) in Treatment relative to Control conditions after carcass deployment.

	Trial 1	Trial 2	Trial 3	Trial 4	Trial 5	Trial 6	Trial 7
Start Date	7/1/14	7/15/14	6/8/15	6/22/15	7/6/15	7/20/15	10/8/15
Carcass Type	Beaver	Beaver	Beaver	Deer	Deer	Deer	Deer
# Stations per Grid	25	25	36	36	36	36	36
Length of Foraging Period (nights)	2	2	2	2	2	2	1
Time x Treatment interaction	yes $F_{1,176}=24.84$ $P<0.001$	yes $F_{1,192}=44.93$ $P<0.001$	yes $F_{1,210}=22.25$ $P<0.001$	yes $F_{1,355}=44.64$ $P<0.001$	no $F_{1,245}=0.623$ $P=0.430$ 5	no $F_{1,213}=1.62$ $P=0.20$ 4	yes $F_{1,212}=3.94$ $P=0.048$
Change in Treatment relative to Control	GUD decreased	GUD decreased	GUD increased	GUD increased	-	-	GUD increased

Table 2

Scavengers documented with remote camera images in treatment and control grids before and after a carcass was deployed. Number of ‘visits’ by that species are in parentheses. A new visit occurred if that species had not been pictured in the preceding 5 minutes

Trial	Carcass	Before		After	
		Control	Treatment	Control	Treatment
1	Beaver		Coyote (1)		Gray fox (2), Turkey vulture (5)
2	Beaver				Turkey vulture (23)
3	Beaver				Coyote (2)
4	Deer				Turkey vulture (17)
5	Deer				Raccoon (1), Turkey vultures (26)
6	Deer				Turkey vulture (21)
7	Deer				Turkey vulture (4), Red fox (1)

Figure 1. Average Giving Up Density (GUD) was assessed across seven trials in which small mammal foraging was measured before and after carcass deployment in paired treatment (carcass = T) and control (C) grids. Results for Trial 6 are not shown separately because foraging was similarly intense in Trials 5 and 6.

Figure 2. Average proportion of depletable food stations that had small mammal tracks after two nights of foraging. Data were accumulated during trials 3, 5, and 6.

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Figure 1

612 Figure 2

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