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REPORT

Resource dispersion and consumer dominance: scavenging at wolf- and hunter-killed carcasses in Greater Yellowstone, USA

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Abstract

The Greater Yellowstone Ecosystem in the northern Rocky Mountains provides the context for a natural experiment to investigate the response of consumers to resources with differing spatial and temporal dispersion regimes. Grey wolves (*Canis lupus*) and human hunters both provide resource subsidies to scavengers by provisioning them with the remains of their kills. Carrion from hunter kills is highly aggregated in time and space whereas carrion from wolf kills is more dispersed in both time and space. We estimated the total amount of carrion consumed by each scavenger species at both wolf and hunter kills over 4 years. Species with large feeding radii [bald eagles (*Haliaeetus leucocephalus*) and ravens (*Corvus corax*)], defined as the area over which a consumer can efficiently locate and integrate resources, dominated consumption at the highly aggregated hunter kills whereas competitively dominant species [coyotes (*Canis latrans*)] dominated at the more dispersed wolf kills. In addition, species diversity and the evenness of carrion consumption between scavengers was greater at wolf kills than at hunter kills while the total number of scavengers at hunter kills exceeded those at wolf kills. From a community perspective, the top–down effect of predation is likely to be stronger in the vicinity of highly aggregated resource pulses as species with large feeding radii switch to feeding on alternative prey once the resource pulse subsides.

Keywords

Carrion, community diversity, foraging behaviour, resource pulse, sage grouse, scavengers, subsidy, wolves.

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INTRODUCTION

A predictive food-web theory requires that we quantify the effects of spatio-temporal resource fluctuation on animal distributions and abundance. To this end, ecologists have recently begun to articulate the effects of temporal resource pulses on local animal populations such as mast fruiting by trees (Kelly 1994; Gonzalez & Donoso 1999), irruptions of insects (Ito 1998), and marine subsidies to terrestrial communities (Rose & Polis 1998). Consumer species that are able to respond to these sudden pulses, such as mice on acorns (Jedrzejewska & Jedrzejewski 1998), insectivorous birds on insects (Folkard & Smith 1995) and coyotes on beached whales (Rose & Polis 1998), are usually generalist species that can support themselves on alternative resources in the absence of a pulse. Positive numerical responses by consumers to such pulsed resources are often observed either through increased population growth or migration, and may have strong trophic consequences (Ostfeld & Keesing 2000). Once a pulse has dissipated, high consumer densities frequently lead to high levels of predation on alternative prey and increased competition with hetero-specifics (Ostfeld & Keesing 2000). While the temporal aspect of resource pulses has been well explored (Ostfeld & Keesing 2000), little is known regarding the response of multiple consumers to the spatial dispersion of resource pulses that have a periodic temporal component.

The 72 800 km^2 greater Yellowstone ecosystem (GYE) provides the context for a natural experiment to investigate this question. Grey wolves in the GYE provide resource subsidies to scavengers in the form of carrion from their kills (Wilmers *et al.* 2003). As the ratio of wolf pack size to prey size decreases and/or snow depth increases (thus weakening ungulate populations) wolves become

increasingly likely to abandon their kills before entirely consuming the carcass (Wilmers *et al.* 2003). A number of avian and terrestrial scavengers are then rewarded with left over muscle meat, bone and hide. Human hunters also provide such subsidies to scavengers when they leave behind the entrails of their kills. The majority of carrion biomass provided by human hunters comes from the Gardiner Late Hunt, a permit-issued elk (*Cervus elaphus*) hunt running from early January to mid-February (Lemke *et al.* 1998). This hunt, which primarily targets 'antler-less' elk (cows and calves) migrating from Yellowstone National Park (YNP), often produces an annual harvest exceeding 1000 individuals (Lemke *et al.* 1998). Whether provided by wolves or hunters, carrion is an ephemeral resource that is often consumed within hours. The spatial and temporal distribution of these two carrion sources differs markedly, however. Hunter kills are aggregated in both time and space, as hunting takes place in a tightly circumscribed area over a narrow time horizon. In contrast, wolf kills are highly dispersed in time and space, as they occur throughout the year and over the entire ecosystem.

A carcass, or group of gut piles, will initially attract scavengers from the local area. If the total amount of carrion is small, then it will be consumed primarily by those scavengers that are the first to arrive and/or competitively dominant. If the amount of carrion is larger than that which can be consumed immediately by local scavengers, then consumers should continue to recruit from more distant areas. Certain species, however, will be more capable of recruiting than others. Those species that can recruit from large geographical distances, therefore, will predominate at highly aggregated resources.

The primary winter scavengers in Greater Yellowstone are, in order of dominance at carcasses, coyote, golden eagle (*Aquila chrysaetos*), bald eagle, raven and magpie (*Pica pica*) (see Magoun 1976 for similar dominance relationships). These species differ in their relative foraging radii, defined as the distance over which an animal can locate and integrate a resource in a given period of time. Within the group of the scavengers mentioned above, we characterize bald eagles and ravens as having the largest feeding radii because they both have excellent long distance flying capabilities (Heinrich 1988; Buehler 2000) and often roost communally where information about resource locations may be transferred (Marzluff *et al.* 1996; Buehler 2000; Dall 2002). Coyotes and magpies are characterized as having relatively small feeding radii because they are limited in their abilities to cover large distances quickly (Bekoff & Andrews 1978; Trost 1999). Golden eagles have similar flying capabilities to bald eagles, however unlike bald eagles, they are relatively solitary and sedentary (LeFrank Jr & Clark 1983). As such we characterize them as having smaller feeding radii than bald eagles and ravens because they lack the degree of social interaction that enhances information transfer concerning resource locations.

Here we investigate this question of resource dispersion and consumer dominance on the northern Yellowstone winter range of the GYE. Specifically, we estimate the total carrion biomass provided to scavengers by both wolves and hunters, and investigate how each species of scavenger responds to different spatial and temporal resource regimes. We hypothesize that the highly concentrated hunter-kills should be dominated by wide-ranging consumers that can track ephemeral resources over a broad geographical area, whereas the more dispersed wolf kills should be tracked most efficiently by competitively dominant local consumers.

STUDY AREA

This study was conducted in north-western Wyoming and southern Montana, USA on the 1530 km^2 northern Yellowstone winter range of the GYE, so named for the large aggregations of ungulates that winter along the Yellowstone River (Houston 1982). Elevations range from 1500 to 3400 m and the climate is characterized by short, cool summers and long, cold winters, with most of the annual precipitation falling as snow. Mean annual temperature is 1.8°C, and mean annual precipitation is 31.7 cm (Houston 1982). Large open valleys of grass meadows and shrub steppe dominate the landscape, with coniferous forests occurring at higher elevations and on north facing slopes.

During the course of the investigation, three to six packs of wolves held territories in the study area. The northern range supports seven species of native ungulates: elk, mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), moose (*Alces alces*), bison (*Bison bison*), bighorn sheep (*Ovis canadensis*) and pronghorn antelope (*Antilocapra americana*); and one non-native ungulate, mountain goat (*Oreamnos americanus*). Five species of native large carnivores also exist: coyote, wolf, cougar (*Puma concolor*), grizzly bear (*Ursus arctos*), and black bear (*U. americanus*). Elk are the primary prey species of both wolves (Mech *et al.* 2001) and hunters (Lemke *et al.* 1998), as well as the primary source of scavenge for many of the ecosystem's meat-eating species (Murie 1940; Gese *et al.* 1996; Crabtree & Sheldon 1999a). It is important to note that hunting occurs in a subset of the larger area used by wolves. As such, the hunting area occurs within the same range of elevation and vegetation as the larger area used by wolves, and is populated by the same suite of scavenger species.

METHODS

We conducted the wolf component of the study from November 1998 to July 2001, excluding summer periods from 15 July to 15 October when wolf predation occurs at

higher elevations, tall grasses preclude observation, ungulate mortality is low (Gese *et al.* 1996), alternate foods are available to scavengers, and smaller prey packages are fed on, attracting fewer scavengers. Hunter-kills were observed during the Gardiner Late Hunt, which in recent years has accounted for >80% of annual hunter take (Lemke *et al.* 1998), in January and February 2001 and 2002. Wolf-killed carcasses (see Mech *et al.* 2001 for cause of death determination) were located on a daily basis by tracking wolves to their kill sites using radio telemetry. Hunter gut piles were located by communicating with hunters, scanning the landscape for blood stains in the snow and searching for aggregations of birds. We observed all kills and gut piles from the time they were located until they were either fully consumed, dragged out of view or it became too dark to distinguish behaviour. We used 15–45× spotting scopes during the day and an infra-red attachment when possible at night to observe feeding activity from observational vantage points located throughout Yellowstone's northern range (for sampling details see Wilmers *et al.* 2003).

Estimating total wolf provided carrion

Total wolf-killed elk biomass available to scavengers on the northern range was estimated by sampling total biomass to scavengers for the majority of northern range wolf packs and then extrapolating to packs that we did not sample. Specifically, if we let D_m be the number of days in each month m, $K_{\rho,\mathrm{m}}$ the monthly wolf kill rate (kg/wolf/day) for each pack ρ, $W_{\rho,\mathrm{m}}$ the number of wolves in each pack by month, $Q_{\rho,\mathrm{m}}$ the percentage of each carcass consumed by wolves and assume that only 68% of each carcass is edible (Wilmers *et al.* 2003), then the total carrion $C_{\rho,\mathrm{m}}$ to scavengers in the months December to March is given by,

$$C_{\rho,\mathrm{m}} = K_{\rho,\mathrm{m}} \cdot W_{\rho,\mathrm{m}} \cdot D_m \cdot (1 - Q_{\rho,\mathrm{m}}) \cdot 0.68. \qquad (1)$$

The kill rates of each sampled pack were estimated by the National Park Service from 15 November to 15 December and 1 to 31 March of each year (Smith *et al.* in press). We use the former period as our November kill rate and the latter as our March kill rate. Kill rates for December to February were linearly interpolated between the November and March rates. Mean percent consumption (and SE) by each wolf pack was calculated from previously reported multiple regression equations (Wilmers *et al.* 2003) using wolf pack size and snow-water equivalent (SWE) as dependent variables.

Total carrion to scavengers from non-sampled packs and for all packs in April and May was then estimated based on multiple linear regressions relating total carrion $C_{\rho,\mathrm{m}}$ to pack size and SWE. We did not extrapolate beyond May because wolf kill rates for the summer months are poorly documented. While wolves continue to kill adult elk that are then scavenged, they also begin killing newborn calves in June which they generally consume entirely. The percentage of their kills that are newborns vs. adults is not currently known making it hard to extrapolate the total carrion biomass they provide to scavengers.

Estimating total wolf-killed carrion to each scavenger species

We then set out to determine the total wolf-killed elk biomass consumed by each scavenger species during the winter period of January to March for comparison with hunters. To do so, we used $s = 1,\ldots,7$ to index the seven common consumer species (1, wolves; 2, grizzly bears; 3, coyotes; 4, golden eagles; 5, bald eagles; 6, ravens and 7, magpies) and $c = 1,\ldots,4$ to represent the stage of consumption (1, eviceration of organs; 2, major muscle; 3, minor muscle and 4, brain and hide) of carcass i. We then sampled *in situ* feeding times to estimate the total time (individual hours) $F^s_{c,i}$ spent by each species at wolf kills and multiplied this by species and stage-specific consumption rates R^s_c (Wilmers & Stahler 2002; Wilmers *et al.* 2003). The proportion $P^s_{c,i}$ of each stage of a carcass i's edible biomass, $B_{c,i}$, consumed by each species s is then given by,

$$P^s_{c,i} = \frac{R^s_c F^s_{c,i}}{B_{c,i}}, \quad \text{where} \quad \sum_{s=1}^{7} P^s_{c,i} = 1. \qquad (2)$$

We determined ungulate age from its incisors and used this to determine $B_{c,i}$ using previously determined weight by stage relationships (see Wilmers *et al.* 2003).

We then pooled each species-specific stage proportion $P^s_{c,i}$ for carcass i and calculated the mean in order to get an overall estimate of the percentage of each stage that a species consumed during the winter. Because sampling effort varied between carcasses, percentages from heavily sampled carcasses were more likely to represent the true division of carrion than those from lightly sampled carcasses. Since sampling variance in estimating means is proportional to the reciprocal of the square root of sample size, we weighted each proportion by the square root of the number of samples n_i taken from carcass i in our pooling procedure. Specifically, mean per cent consumption $\mathbf{\Omega}^s_c$ of stage c by species s is given by

$$\mathbf{\Omega}^s_c = \frac{\sum_i P^s_{c,i}\sqrt{n_i}}{\sum_i \sqrt{n_i}}. \qquad (3)$$

For each species, s, we then sum mean percent consumption across all stages c, weighting each stage's contribution to total carcass biomass in order to get the total percent of an average carcass consumed by each species to obtain,

$$\Omega_T^s = \frac{0.14}{0.68}\Omega_1^s + \frac{0.31}{0.68}\Omega_2^s + \frac{0.15}{0.68}\Omega_3^s + \frac{0.08}{0.68}\Omega_4^s. \quad (4)$$

(Wilmers *et al.* 2003)

Total carrion biomass H_{m}^s consumed by a species per month is then,

$$H_{\mathrm{m}}^s = \Omega_T^s \cdot \sum_{\rho} C_{\rho,\mathrm{m}}. \quad (5)$$

Estimating total hunter provided carrion

The total number of elk killed by hunters is reported each year by Montana, Fish, Wildlife and Parks. In order to estimate the total amount of elk carrion provided by hunters to scavengers, we assumed that all hunters field-dressed their carcass thus leaving behind the entrails. We used sex and age information from each kill (Lemke 2001, 2002) to estimate that animals live weight based on a model (Murphy *et al.* 1997). Gut weights (not including the rumen) were assumed to be 14% of live weight based on Wilmers *et al.* (2003). Total carrion to scavengers was then equal to the sum of each kill multiplied by its live weight and by 0.14.

In order to estimate the proportion of this total going to each scavenger species, we used the same procedure as we did for wolf kills except for there was only one stage of consumption. Additionally, we periodically checked all known gut piles each morning for animal tracks to account for potential consumption by nighttime foragers, such as coyotes.

Analysing spatial distribution

In order to test for a difference in spatial distribution between wolf- and hunter-killed elk, we first estimated the centre of both wolf and hunter kills, respectively. To do this, we found the average x and y location for wolf kills and then did the same for hunter kills. We then calculated the distance of each wolf kill to its centre and the distance of each hunter kill to its corresponding centre. A Wilcoxon rank sum test was then used to test for a difference in distribution between the two sets of distances.

RESULTS

We observed 202 wolf-killed carcasses and 28 hunter-killed gut piles for a total of 83 325 and 5775 min, respectively. In 1998–1999 and 1999–2000, we sampled three of the four existing northern range wolf packs while in 2000–2001, we sampled four of six. Multiple regression analysis revealed that SWE and the square of wolf pack size accounted for 59% of the variance in carrion abundance to scavengers. We used this relationship to estimate mean monthly carrion from wolf-killed elk to scavengers ± residual SE (Fig. 1). Mean seasonal (November to May) carrion provided to scavengers from wolves on the northern range was 13 220 ± 383.9 kg. Hunters provided significantly more carrion to scavengers (January to mid-February) at 33 203 ± 993 kg (Wilcoxon rank sum test, $P < 0.05$). We documented 12 scavenger species feeding at wolf kills and four species feeding at hunter kills (Table 1). We sub-sampled the wolf kills by randomly selecting 28 wolf kills at a time to investigate the effects of sample size on common species present. This did not have an effect on the presence of common species at wolf kills. We could not determine whether the presence or absence of rare species at wolf vs. hunter hills was because of a sampling artefact or biology.

The distribution of hunter provided carrion was highly aggregated in both space (Fig. 2) and time (Fig. 1) compared

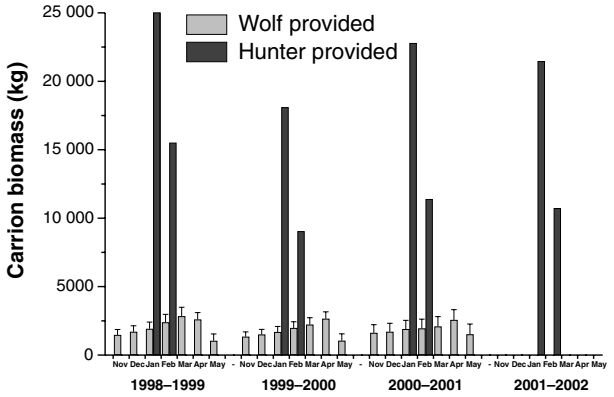

Figure 1 Estimated carrion provided to scavengers by wolves and hunters respectively for the 7 months from November to May (mean ± SE). Wolf scavenge data was not collected in 2001–2002.

Table 1 Species list of scavengers at wolf- and hunter-kills (x indicates presence)

Common name	Scientific name	Wolf	Hunter
American crow[r]	*Corvus brachyrhynchos*	x	
Bald eagle[c]	*Haliaeetus leucocephalus*	x	x
Black bear[c]	*Ursus americanus*	x	
Common raven[c]	*Corvus corax*	x	x
Clark's nutcracker[r]	*Nucifraga columbiana*	x	
Coyote[c]	*Canis latrans*	x	
Golden eagle[c]	*Aquila chrysaetos*	x	x
Grey jay[r]	*Perisoreus canadensis*	x	
Grizzly bear[c]	*Ursus arctus*	x	
Magpie[c]	*Pica pica*	x	x
Red fox[r]	*Vulpes vulpes*	x	
Turkey vulture[r]	*Cathartes aura*	x	

c, common; r, rare.

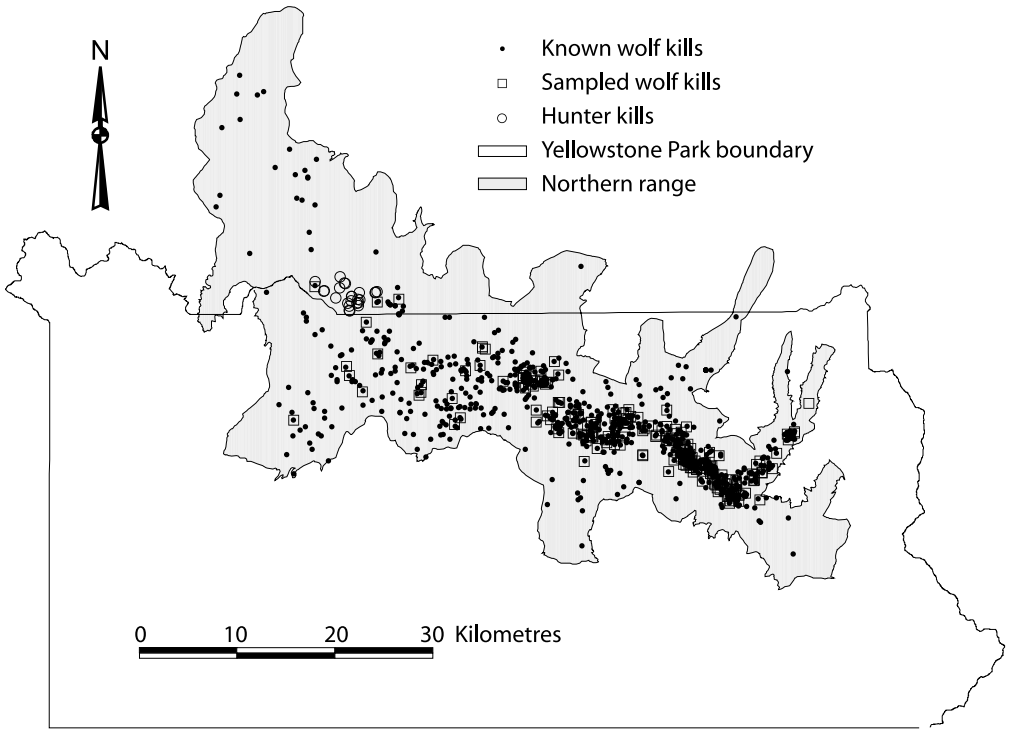

Figure 2 Spatial locations of known wolf kills and hunter kills during the study period. Wolf kills that were sampled for scavenger data are boxed. Hunter kills are aggregated in space because hunters are confined to designated hunting areas. In comparison, wolf kills are more scattered (Wilcoxon rank sum test, $P < 0.001$) as wolf packs are spread out over the landscape.

with that of wolves. Bald eagles, golden eagles, ravens, magpies and coyotes were common at wolf kills during the winter period whereas coyotes were absent at hunter-kills. Mammal tracks were not located at any hunter gut piles with the exception of one fox track that was located in the vicinity of the gut piles but not at any one of them in particular. Grizzly bears began to emerge from hibernation and feed on wolf kills at the very end of the sample period.

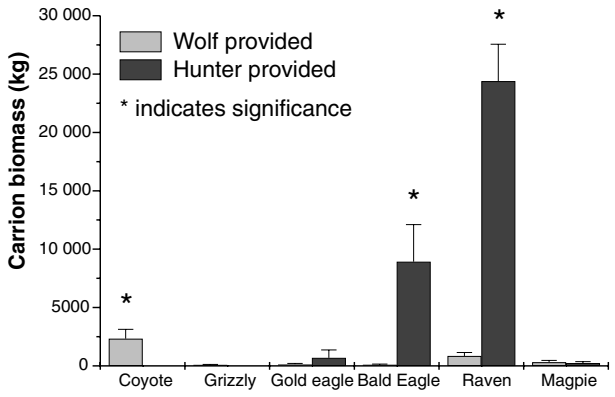

Figure 3 Estimated total carrion biomass to scavengers from wolf- and hunter-killed elk.

Comparison with hunter gut piles is not appropriate, however, because the majority of gut piles from the Gardiner Late Hunt are fully consumed by the time of grizzly den emergence. Ravens and bald eagles consumed significantly more carrion at hunter-kills than at wolf kills (Fig. 3, $P < 0.05$). Consumption by magpies and golden eagles did not differ significantly between hunter and wolf kills ($P > 0.05$). The average of the maximum number of ravens and bald eagles was higher at hunter kills whereas the opposite pattern was found for magpies and golden eagles (Table 2). Average numbers of scavengers at wolf kills did not change during the human hunting period.

Table 2 Summary statistics for the maximum number of each species found at each carcass

	Wolf kills			Hunter kills		
Species	Mean	SE	Range	Mean	SE	Range
Bald eagle	1.46	0.18	0–13	10.07	2.24	0–49
Coyote	4.96	0.39	0–16	0	0	0
Golden eagle	1.26	0.19	0–13	0.31	0.14	0–3
Magpie	8.91	0.75	0–32	3.52	0.92	0–23
Raven	36.05	2.19	1–163	78.17	13.22	3–347

DISCUSSION

We have shown that grey wolves and human hunters alike provide an enormous resource subsidy to Greater Yellowstone's scavengers. In a landscape with limited options for food, carrion is likely to lead to increased winter survival and reproduction for many of these species (Houston 1978; Newton *et al.* 1982; Swenson *et al.* 1986; Blanchard 1987; Dhindsa & Boag 1990; Crabtree & Sheldon 1999b). Hunter provided carrion arrives as a large pulse in mid-winter and is more plentiful than wolf provided carrion which arrives consistently over the course of the entire winter. Which temporal resource regime is more beneficial to scavengers will depend on a trade off between an ability to assimilate and/or cache large amounts of resource quickly and/or tracking that resource over time.

As expected, under-dispersed and super abundant resources (hunter kills) were best tracked by consumers with higher foraging radii (i.e. ravens and bald eagles). Conversely, highly dispersed carrion was best tracked by competitively dominant species (e.g. coyotes). Because of the high temporal and spatial overlap of carrion at hunter kills, scavengers from the local area surrounding the gut piles are super-saturated with resource, leading consumers to recruit from larger and larger areas. Such super-saturation reduces competition and allows far ranging species to gather in high numbers. As wolf kills are spread out over time and space, carrion is under-saturating, leading the competitively dominant coyotes to dominate the resource over other scavengers. The complete absence of coyotes at hunter kills was unexpected as coyote packs are known to occur in the area. This was likely an artefact of exclusion because of the indiscriminate killing of coyotes by humans in the study area outside of YNP. If hunters did not exclude coyotes, our expectation is that they would consume an equivalent or slightly greater amount of carrion than they do at wolf kills, but would not be able to dominate this highly abundant resource. To do so would require that they recruit to the area in numbers that are larger than coyotes are capable of because they have smaller feeding radii and may be constrained by territoriality. Although coyotes would likely reduce the total amount of carrion intake by bald eagles and ravens, we expect that these two species would still consume the bulk of the resource.

The dispersion of wolf- and hunter-killed carcasses represent opposite ends of the spatio-temporal resource spectrum, allowing us to make predictions about the consumption of resources with different spatial and temporal properties (Fig. 4). Wolf kills are distributed regionally across the northern range as they are highly dispersed in time and space, and are consumed primarily by nearby animals. As such, local dynamics such as competition determines access to and consumption of carcasses (Fig. 4, panel 3). Conversely, hunter-kills have a local distribution as they are highly aggregated in time and space. Here, regional dynamics such as recruitment ability, determine the species that consume the bulk of the carrion (Fig. 4, panel 2). In panels 1 and 4, we predict that competition would determine dominance of resources because in neither case would carrion be super-saturated.

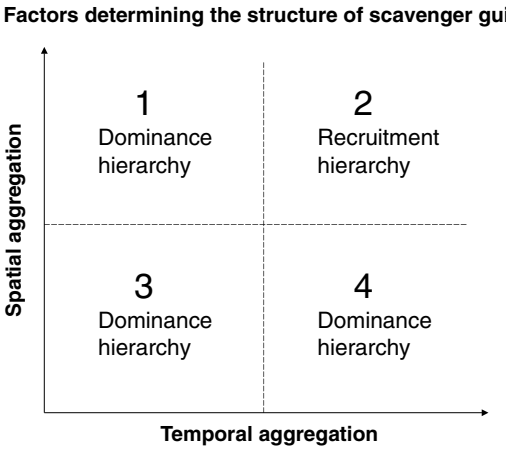

Figure 4 Predictions for the structure of the scavenger guild at a carcass given different spatial and temporal dispersion in resources. In panels 1, 3 and 4 resources are likely to be ephemeral and are thus dominated by competitively superior species in the local scavenger pool. In panel 4, conversely, resources are likely to be saturating and are thus dominated by species with superior recruitment abilities. Resource regimes characterized by recruitment hierarchies are likely to have more pronounced effects on local food chains as consumers switch to alternative prey once the primary resource is consumed (see Discussion).

Species diversity was found to be higher at wolf kills than at hunter kills (Table 1). This was attributable to a combination of factors: the timing of hunter kills precludes hibernating or migratory species, hunter presence may exclude species wary of being shot, and larger sampling effort at wolf kills made it more likely to detect rare species. Of the common species listed in Table 1 that were not present at hunter kills, it is likely that coyotes were excluded by hunters, while grizzly bears and black bears were in hibernation at the time of the highly aggregated late hunt. Hunts at times of the year when bears are not hibernating, however, may result in their scavenging at gut piles. We did not observe any of the rare species listed in Table 1 at hunter kills so it is not possible to say whether this is merely a result of more observation minutes at wolf kills or some biological process.

The evenness of carrion consumption among species was higher at wolf kills than at hunter kills, while the abundance of consumers was higher at hunter kills than at

wolf kills. These two regimes will have different implications on local community dynamics. Once all the carrion is consumed in an area, scavengers may switch to feeding on alternative prey and thus become predators (as long as they are not obligate scavengers as is the case with many vulture species in Africa). In the neighborhood of wolf kills, the trophic effects of prey switching are likely to be relatively small in magnitude and wide in the number of species participating. At hunter-kills, in contrast, the effect is likely to be strong because of the high number of ravens and bald eagles, but narrow because these two species will be doing the bulk of the predation. Food chain effects are thus likely to be stronger at highly aggregated pulses, and to be influenced by species with large feeding radii, compared with highly dispersed and short-lived resources where competitively dominant species are likely to impact the food chain.

This has important implications for conservation and management. If the alternative prey of a highly mobile species is endangered or valued for its economic worth, then conservationists and/or managers should try to avoid creating situations where resources are highly aggregated in time and space. Ravens, for instance, are a predator of the endangered sage grouse (*Centrocercus urophasianus*) (Autenrieth 1981). Managers should take care then not to have highly aggregated hunts in sage grouse habitat because this will likely attract high raven numbers, which may then suppress sage grouse populations. On the other hand, aggregation of resources benefits bald eagles which are also a species of conservation concern. The greater diversity of the scavenger community associated with wolf kills compared with human hunter kills reveals the importance of having natural ecological processes occurring in intact ecosystems. This study reveals a significant component to ongoing comprehensive research on trophic cascades in the GYE because of wolf restoration (Smith *et al.* 2003).

The differential success of scavenger species to resources with varying spatial and temporal dynamics suggests an underlying cause for the evolutionary history of these respective species. Bald eagles and ravens may have developed sociality as a means to expand their foraging radii. By roosting communally, these birds are able to find out about the location of resources from conspecifics and thus more efficiently track distant resources that are highly aggregated in time and space.

From managing hunting to controlling the flow of rivers, humans have ever increasing control over the spatial and temporal dispersion of resources. If we are to properly manage these resources, knowledge of how different pulse regimes affect community composition is crucial. Previous research has shown that generalist species are the most adaptable to tracking resources pulses. Here, we add a spatial component to resource pulse dynamics and demonstrate that species-specific feeding radii (which is a function of movement capabilities and access to knowledge about food resources) influence an animals ability to track resource pulses.

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