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Effect of raven *Corvus corax* scavenging on the kill rates of wolf *Canis lupus* packs

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During late winter 1991 and 1992, we investigated the influence of raven *Corvus corax* scavenging on the predation rate by different-sized wolf *Canis lupus* packs on moose *Alces alces* in the Yukon Territory, Canada. To assess the magnitude of scavenging, we presented 10 ungulate carcasses, pre-warmed to simulate the flesh temperature of freshly-killed prey, to scavengers and measured their daily consumption. Ravens were by far the main scavengers and on average, we counted 18.5 ± 12.7 (SD) ravens and documented removal of 14.1 ± 1.3 (SE) kg biomass each day (N = 53 observation days). However, assuming a daily scavenging rate of 14 kg by ravens fails to explain the almost equally short handling times for moose carcasses of small, medium and large packs. Only when raven consumption rate varies with pack size can we match the observed pattern. Assuming complete consumption, daily raven scavenging has to be 43 kg for ravens feeding on the kills of small wolf packs, 21 kg for ravens feeding on the kills of medium packs and close to zero for ravens feeding on the kills of large packs. Thus raven-wolf competition is highest for small packs, where ravens manage to remove up to 75% of the edible biomass and very low for large packs where ravens hardly manage to remove any edible biomass. Large packs seem to leave less opportunity for ravens to feed on carcasses, possibly because some wolves are always present at the kill and either actively chase away ravens or inhibit access to the carcass.

Key words: Canis lupus, Corvus corax, predation rate, raven, scavengers, wolf, Yukon

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The kill rate by wolves *Canis lupus* on moose *Alces alces* depends foremost on wolf pack size (Thurber & Peterson 1993, Hayes et al. 1991, Hayes et al. 2000). Although large packs kill more individual moose than smaller packs do in winter, the apparent consumption rates are much higher for individual wolves in small packs (2-3 wolves). In southern Yukon, small packs killed 17.2 kg of ungulates/wolf/day and medium packs (4-7 wolves) killed 7.2 kg/wolf/day (Hayes et al. 1991). In central Yukon, kill rates followed a similar trend. Small packs killed 12.7 kg/wolf/day, medium packs 7.6 kg, and large packs (> 7 wolves) 4.6 kg (Hayes et al. 2000). However, in neither of these studies did wolves differ in body condition or body size (R. Hayes, unpubl. data), therefore the observed difference in apparent consumption rate can not be real. The high kill rates by small wolf packs could be caused by wolves abandoning their prey before food is depleted, or by small packs losing proportionally more kill biomass to scavengers than larger packs, as first suggested by Promberger (1992).

Ravens *Corvus corax*, red foxes *Vulpes vulpes*, coyotes *Canis latrans* and wolverines *Gulo gulo* are known to scavenge from ungulate kills made by gray wolves (Mech 1970, Paquet 1992, Peterson et al. 1994, Peterson 1995, Ballard et al. 1997, Hayes et al. 2000, Stahler et al. 2002). Although the daily food requirement of a raven in winter is only about 415 g of meat/day (Heinrich 1994), mutual recruitment of juvenile ravens (Heinrich 1989, Heinrich et al. 1993, Marzluff et al. 1996) and food caching behaviour (Heinrich 1994, Heinrich 1999) make them powerful competitors of carnivores for large mammal carcasses. Following wolves helps ravens to be present at wolf kills within minutes of the actual killing. The presence of wolves at the carcass even seems to help them overcome their innate fear of new food sources (Stahler et al. 2002). Thus, ravens can start feeding immediately on wolf kills, sometimes together with the wolves (R. Hayes, pers. obs.).

So how important are wolf kills to wild ravens, and what effect do ravens have on wolf predation rates? Peterson (1977) concluded that in winter, ravens are almost entirely dependent on food indirectly provided by wolves. Earlier studies recognised that scavengers reduced the amount of prey mass available to wolves (Kolenosky 1972, Ballard et al. 1987, Carbyn 1983), but there have been few studies on carcass use by different scavengers (Heinrich 1989, 1999).

Based on a literature review Milton (1986) speculated that scavenger competition should increase wolf predation rates by removing substantial amounts of food that would otherwise be eaten by wolves. In the Yukon, a preliminary raven-wolf model (Promberger 1992) estimated that scavenging by ravens reduced the food consumption for wolves in small packs more than for wolves in larger packs. Hayes et al. (2000) used raven scavenging data from Promberger (1992) to estimate that small packs lost 50% of consumable biomass from moose kills, medium packs 33% and large packs 10%. The model was based on results of seven field trials that measured the daily mass (in kg) removed by scavengers from baits in late winter 1991, and kill and consumption rate studies of wolves conducted in the same area at the same time (Hayes et al. 2000). We improve the model of Promberger (1992) by adding additional field data from 1992, and we recalculate effects of scavenging on wolf kill and consumption rates with a new model for estimating moose handling period.

Our expectations were:

1) In the Yukon, ravens are the most important scavengers of large ungulate carcasses in late winter. Ravens are highly efficient in finding kills and will remove the bulk of biomass relative to other scavengers.
2) Raven scavenging can explain the almost equal handling time of moose kills by small, medium and large wolf packs.

Study area

We conducted bait trials from January to March during 1991 and 1992 near Finlayson Lake in the east-central Yukon (62°N, 128°W; Fig. 1). Sites were in forested u-shaped valleys above 1,000 m a.s.l., bordered by higher tableland mountains, rolling upland plateaus and hills. Lowland areas are mainly vegetated by mixed boreal forests of black spruce *Picea mariana*, white spruce *Picea glauca*, lodgepole pine *Pinus contorta*, aspen *Populus tremuloides*, and black poplar *Populus balsamifera* (Oswald & Senyk 1977). Paper birch *Betula papyrifera* is scattered throughout the lowlands and northern aspects. The tree-line begins at 1,350-1,500 m. Mean January temperatures range from -27°C to -35°C. Average annual precipitation is 250-300 mm.

During our study wolf, moose and caribou *Rangifer tarandus* populations were rapidly increasing after a reduction in wolf numbers during the 1980s. From 1990 through 1992 wolf density was 3.0-5.6 wolves/1,000 km^2 (Hayes & Harestad 2000), and moose density was 323-382 moose/1,000 km^2 (Hayes et al. 2000). Moose winter throughout the lowland forests in the study area, and they are the most important prey of wolves, followed by caribou (Hayes et al. 2000). The

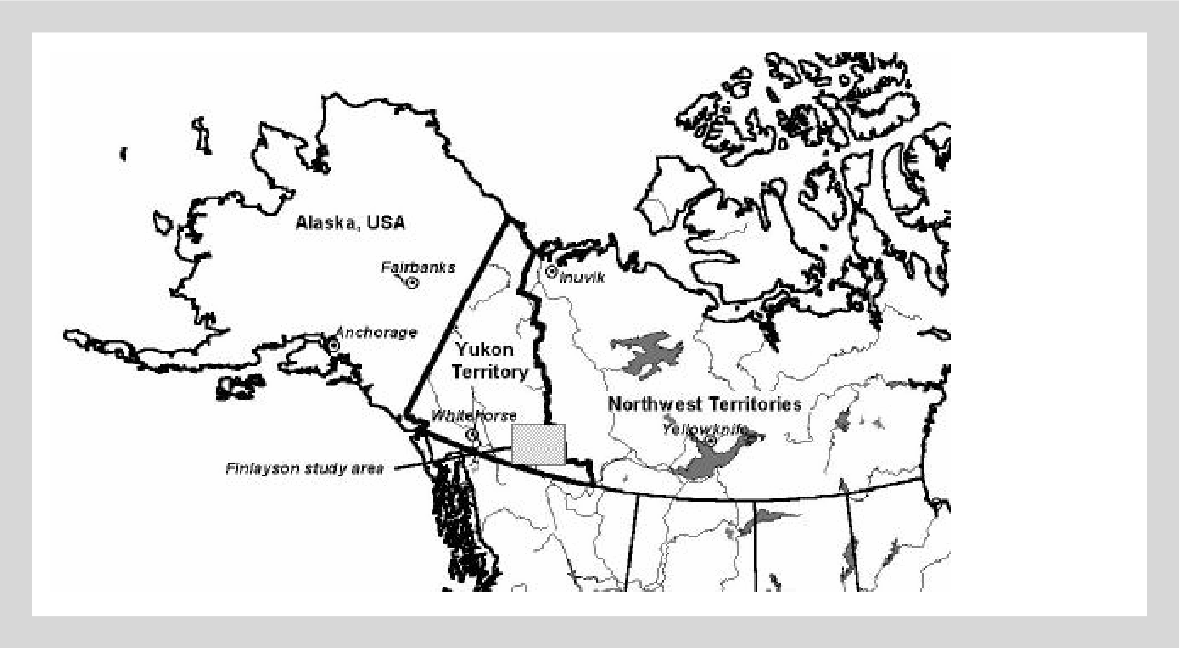

Figure 1. Location of the Finlayson Lake study area in the east-central Yukon during 1990-1994.

Finlayson Lake caribou herd numbered about 6,000 animals in March 1990 (R. Farnell, Yukon Fish and Wildlife Branch, unpubl. data). Most of the herd travels through, or winters near, Finlayson Lake. A small number of mule deer *Odocoileus hemionus* live on the open slopes along the Pelly River. Snowshoe hare *Lepus americanus* were abundant during 1990 and 1991, but numbers crashed during the winter of 1991/92 (Boutin et al. 1995).

Various mammalian scavengers are present in winter including coyote, wolverine, red fox, lynx *Lynx canadensis*, marten *Martes americana*, river otter *Lutra canadensis*, mink *Mustela vison* and weasels *Mustela erminea* and *M. nivalis*. Avian scavengers include raven, gray jay *Perisoreus canadensis*, magpie *Pica pica*, and various small wintering passerine birds. Dene people from Ross River and Watson Lake hunt moose and caribou from the Robert Campbell Highway between January and April. Hunters usually left small remains including intestines, rumen, lower legs and pieces of hide that scavengers could use.

Methods

Raven use of the remains of hunter-killed ungulates

We recorded the number of scavengers at the remains of 24 hunter-killed moose and nine caribou between January and March, 1991, to determine the scavenger community and the relative importance of ravens as scavengers in the Yukon in winter. We revisited hunter kill sites at irregular intervals for up to eight days to document scavenger use (mean = 2.31 days; 17 × 1 observation day, 4 × 2 observation days, 5 × 3 observation days, 2 × 4 observation days and 2 × 8 observation days for a total of 74 observation days). Carcass remains largely consisted of a gut pile with the head, the hide and the lower legs next to it. We used tracks in the snow and direct observations to identify the species of scavenger.

Simulation of wolf kills

We collected carcasses of accidentally killed moose, caribou and mule deer, cut them into quarters to allow handling, and pre-warmed them to 35-40°C to simulate flesh temperature of freshly killed prey. We placed the baits in open areas at dawn before most ravens were active and prepared baits as if wolves had made a kill. We spread hair, bones and flesh around the site, spilling blood (or red dye) and walking trails to feeding sites. Each morning we attempted to attract ravens by using wolf howls (Harrington 1978). To further simulate a wolf kill we cut the hide of carcasses to expose flesh to scavengers as if wolves had been feeding. Subsequent sites were placed about 20 km apart and each site was used only once to avoid conditioning of ravens to baited areas. We monitored seven bait sites in January through March 1991 and three sites in 1992.

We weighed carcass portions each morning (07:00-11:00) and evening (18:00-22:00). We used 100 kg scales supported by a pole and weighed to the nearest half kg. Before each weighing session the area was searched for tracks of terrestrial scavengers, which were brushed off afterwards. Simulations were stopped at the latest after six days, or when all edible portions had been removed. We counted ravens opportunistically 1-3 times per day during daylight hours from vehicle or aircraft and subsequently used the maximum number of ravens seen at any one day to describe raven presence at baits (average maximum).

To test for temperature effects on mass removal rates we recorded the daily high and low temperatures to the nearest °C. We compared the daily rates of mass removal against raven frequency (log of raven numbers), daily low and daily high temperatures using a general linear model (GLM) with alpha set at 0.05.

Comparing raven use of baits and wolf kills

Hayes et al. (2000) studied kill rate by wolves in the Finlayson Lake area at the same time as our study. Observers in fixed-wing aircraft visited kill sites once each day, recording the number of ravens on 161 occasions at 83 different kill sites between February 1990 and March 1994. The daily number of ravens at kill sites was compared to our baits by a T-test, with alpha set to 0.05. If there were multiple observations of ravens at baits in a day, we randomly selected one observation for the comparison of ravens counted at baits versus those counted at real wolf kills.

Modelling wolf-raven competition

To model raven-wolf competition we had to make some assumptions about prey size, edible proportions of kills and daily wolf consumption rates. Franzmann et al. (1978) and Schwartz et al. (1987) found that Alaska moose weights fluctuated by season, area, sex and age, making it difficult to estimate the live weights of killed animals. For our wolf-raven competition model, we used live weights of 400 kg for an adult moose, 250 kg for yearling moose and 150 kg for moose calves. Hayes et al. (2000) found no difference in kill handling periods (number of days spent at kill) for adult moose and calves among small, medium and large wolf packs (range: 2.0-3.3 days). We simplified our model by estimating the mean live biomass of an average moose to be 297 kg, given that kill composition was 52% adults, 17% yearlings and 31% calves (see Hayes et al. 2000). To compare the expected number of moose killed by different-sized packs and the observed number of kills, we standardised the number of moose killed per pack during the observation period by dividing the total mass of prey (Hayes et al. 2000: 59 and Table A2) by 297 kg. For the edible mass of a moose carcass we used the value of 65% calculated by Hayes et al. (2000), which is supported by recent findings from Poland (Jedrzejewski et al. 2002). Thus in our model the average moose provides 193.05 kg of edible biomass.

We estimated the daily consumption rate by wolves from the literature and data from Hayes et al. (2000). Based on basic metabolic rates, Peterson & Cucci (2003) calculated the average daily food requirement of a 35 kg wolf at 3.25 kg per day. Although no data on the average weight of wolves from the Finlayson area were available, 35 kg seems a reasonable assumption. In the southwestern Yukon the average weight of wolves was 37.5 kg (Hayes et al. 1991). In the wolf-moose system in the Yukon, the average kill interval for small packs was larger than for medium and large-sized packs and averaged 6.70 days (Hayes et al. 2000). Thus the average food requirement for a wolf in a small pack is 21.78 kg/wolf of any given moose kill (6.70 days × 3.25 kg). With an average handing period of 3.30 (± 0.19) days each wolf needs to consume 6.6 kg when on a kill (21.78 kg/3.30 days) to fulfill its basic metabolic requirements. For our model we used the slightly higher value of 7.0 kg/wolf for the carcass handling period.

For the total daily consumption rate of ravens we used the average daily mass removal derived from our wolf kill simulations. We then calculated the expected number of handling days in the following way:

$$\text{expected handling days} = \frac{193.05\ \text{kg}}{\text{mean size of pack} \times 7.0\ \text{kg} + \text{measured daily raven consumption}}$$

and compared our results with the handling days reported by Hayes et al. (2000) for small (2.1 ± 0.1 (SE)), medium (5.9 ± 0.4) and large (12.1 ± 0.8) wolf packs.

Results

Raven and other scavenger presence at carcasses

Ravens were the most numerous scavengers among 12 species using hunter kills (Table 1). Red foxes and gray jays were the only other species that regularly scavenged, but their numbers were small and their consumption thus relatively unimportant.

Table 1. Scavenger species, percent occurrence and range in number of scavengers seen or tracked at 33 hunter kills during 74 observation days in the Finlayson Lake study area during January-March, 1991-1992.

Scavenger species	Percent occurrence at hunter kills	Range in number of animals seen at anyone time
Raven	89.5	1-49
Gray jay	60.5	1-4
Red fox	26.3	1-2
Coyote	10.5	1-2
Lynx	10.5	1
Lone wolf [a]	7.9	1
Wolverine	5.3	1
Snowshoe hare [b]	5.3	-
Weasel	2.6	1
Otter	2.6	1
Bald eagle	2.6	1-2
Golden eagle	2.6	1

[a] Lone wolf visits were assumed when single tracks were found and the radio-collared territorial pack was known to be far away.

[b] Snowshoe hare chewed on remaining bones and antlers at two hunter kills.

Mass removal by ravens

The 10 baits averaged 149 ± 12 (SE) kg at the beginning of trials and 68 ± 12 kg by the end. Six bait sites lasted for all six days, two for five days, one for four days and one for three days (N = 53 observation days). Baits lost on average 80 ± 8 (SE) kg biomass during the day and only traces (< 0.5 kg) overnight. Tracks and direct observations confirmed that practically all bait was taken by ravens. Raven removed on average 14.1 ± 1.3 (SE) kg each day from baits, but daily averages varied (Fig. 2).

Ravens always initiated feeding in the first or second day, and their numbers remained high for six days when all observations were ended (see Fig. 2). There was no distinct peak in the average maximum number of ravens, with day three being only different compared to days two (Tukey multiple comparison: $P = 0.03$) and five ($P = 0.003$). The average daily number of ravens counted at baits was 18.5 ± 12.6 (SD) birds, and thus was significantly greater than the average of 4.4 ± 5.3 (SD) birds seen at wolf kills from an aircraft (T-test, unequal variances: $P < 0.001$).

There was no real trend in biomass removal rate (see Fig. 2), and the only difference was between day one and day five (Tukey multiple comparison: $P = 0.048$). The rate of biomass loss was only related to the log of the number of ravens observed ($r^2 = 0.128$, $df = 1$, $T = 2.715$, Beta value = 8.620, SE = 3.175; $P = 0.009$), but unrelated to both daily minimum and maximum temperature.

Modelling moose carcass handling days

With a basic metabolic rate of 3.25 kg/day small packs would be expected to kill 6.4 standard moose over the 180-day winter period, medium packs 18.1 and large packs 37.1. However, only large packs killed moose within the expected range, whereas small packs killed almost four times as many moose and medium packs twice as many moose as expected (Fig. 3). Our handling day model assuming a raven consumption of 14 kg/day was close to the results for medium and large wolf packs calculated by Hayes et al. (2000; Fig. 4), but estimated about three more days for small packs. Even by assuming much higher daily raven consumption rates (e.g. 40 kg/day), we were not able to match the observed pattern. Such a high raven consumption rate would reduce the handling days of small packs to the observed values, but medium and large packs would be unable to cover their basic nutritional needs. Thus an average daily raven scavenging rate alone can not explain the high predation rate of small packs. As a consequence we have to assume that small packs either abandon

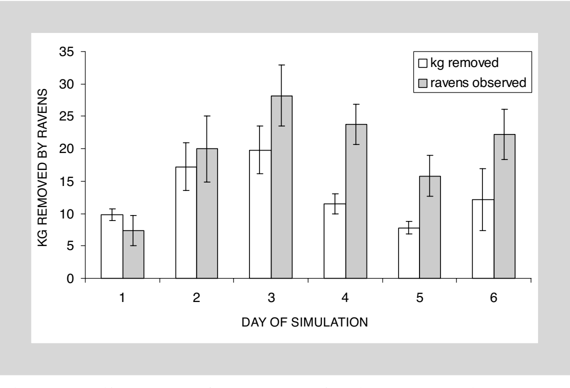

Figure 2. Daily amount of mass removal and average maximum number of ravens counted at 10 baits in the study area during January-March, 1991 and 1992. The error bars indicate the standard error (SE).

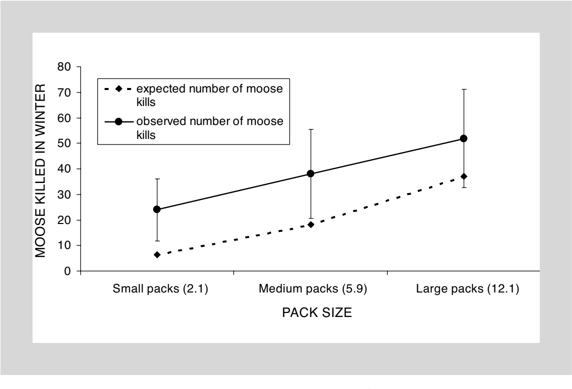

Figure 3. Observed (according to Hayes et al. (2000); error bars indicating the SE) and expected number of standard moose killed by different-sized wolf packs during the 180-day winter season in the Yukon.

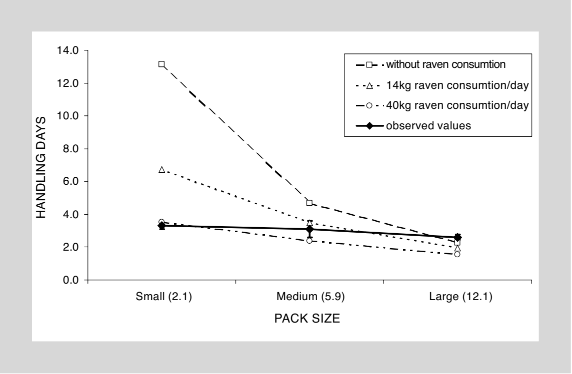

Figure 4. Observed (according to Hayes et al. (2000); error bars indicating the SE) and expected handling days of different-sized wolf packs with and without daily raven consumption.

their kills before depletion, or that the daily rate of raven scavenging varies with pack size. For our handling day model we have to assume a daily raven consumption of 43 kg/day for small packs, 21 kg/day for medium packs and no raven consumption for large packs in order to match the observed pattern in handling days. If this holds true, ravens remove about 75% of the edible biomass from kills of small packs, 34% from kills of medium packs, and close to nothing from kills of large packs.

Discussion

Raven scavenging

Similar to Heinrich (1989), we found large numbers of ravens using our baits, usually in the first day after placing the baits. Ravens are able to quickly build up numbers despite low densities because juvenile birds 'recruit' others to food sources they find by mutually communicating at communal nocturnal roosts (Heinrich 1989) and by calling other ravens in. By recruiting others, juvenile birds increase their access to food bonanzas they otherwise could not get from defending adult raven pairs (Heinrich 1989, 1999). The low frequency of other scavengers at our baits was probably due to the high availability of other food sources. Both coyote and lynx feed mostly on snowshoe hares during all winters in the Yukon, except during cyclic lows (O'Donoghue et al. 1998). During the two winters of our study hares were at peak abundance (Hayes et al. 2000). There was probably low incentive for these predators to scavenge from baits.

At simulated wolf kills an average 19 ravens removed on average 14 kg/day, but we have no information about bird turnover rate or daily variation in bait use. Assuming that on average 19 birds visited a bait site daily, they removed 737 g/bird. This is only 1.8 times the daily food requirement of a raven in winter (Heinrich 1994), and this means that only moderate food caching was going on. This might be an explanation why raven consumption rate seemed to be indifferent of minimum and maximum ambient temperatures.

An average consumption of 14 kg/day by ravens at simulated wolf kills was not enough to explain the nearly equal handling days for moose carcasses of small, medium and large wolf packs. To achieve similar values we had to assume that the daily raven consumption rate can be much higher and in addition varies with pack size. To match the observed pattern ravens would have to remove 43 kg daily at kills of small packs, 21 kg at kills of medium packs and close to nothing at kills of large packs. A removal rate of 43 kg is well within the range described by Heinrich (1994), and we believe such a high mass removal is possible in our study area, given that we did not know the absolute number of birds that used simulated kills each day, and the average number of 19 birds observed is probably an underestimate of the actual number of ravens visiting. The low correlation coefficient of raven numbers and the biomass removed at simulated kills further support that opportunistic counts of ravens at bait sites are insufficient to assess the true number of ravens feeding on the bait.

That the average number of ravens counted at real wolf kills was much lower than at simulated kills is probably an artifact of the different counting methods for simulated and real wolf kills. The small number of ravens observed during aerial counts is most likely due to the difficulty of spotting ravens in the forest (R. Hayes, pers. obs.). Also, single-pass aerial counts will miss ravens that are making caching flights away from carcasses. Also Ballard et al. (1997) only saw an average of 3.7 birds at wolf kills in Alaska, which is similar to our results, and they concluded that the small number of birds did not constitute much competition to wolves. We disagree and believe raven consumption rates are generally underestimated by aerial observers who briefly sample the daily activity at a kill with least rigour.

Wolf-raven competition

The almost equal moose-handling days in small, medium and large wolf packs could be explained with a varying degree of scavenger impact or by small wolf packs simply abandoning kills before depletion of the edible mass. Abandonment could be due to satiated wolves leaving for social reasons or because the meat was freezing. However, there was little evidence that any wolf packs left substantial uneaten portions of moose carcasses during kill rate studies by Hayes et al. (2000). Most carcasses were seen from the air, and the estimated remaining portions were usually inedible lower legs, hide, ribs, head, pelvis and rumen content (R. Hayes, unpubl. data). In addition, five wolf-killed carcasses weighed the day after the wolves departed were completely consumed. One was a bull moose killed by three wolves. Five days later the pack abandoned the kill leaving mainly inedible parts (R. Hayes, unpubl. data).

According to our basic model (consumable biomass of an adult moose of 260 kg; 14 kg raven consumption/day) a pack of three wolves should have stayed for 7.4 days. The shorter handling time and the complete depletion of the kill support our assumption that ravens remove the missing biomass and thus cause the much lower than expected handling days in small packs.

Huggard (1993), Mech et al. (2001) and Jedrzejewski et al. (2002) showed that winter severity can increase wolf predation rates on elk *Cervus elaphus*, and Mech et al. (1998) observed the highest kill rates on caribou during deep snow winters. However, Hayes et al. (2000) found that winter snow conditions were favourable for moose in our study area in all winters, so there was little advantage for wolves to partly consume. Thus we conclude there is reasonable support that scavenging by ravens and not abandonment of the kill before depletion is the driving force for the similar handling periods observed in small, medium and large wolf packs in late winter in the Yukon.

It is logical that ravens remove more edible biomass from kills of small packs than from kills of medium and large packs. Wolves defend carcasses against ravens by chasing them, and dead ravens are occasionally found near wolves and their kills (Peterson 1977, Allan 1979 cited in Stahler et al. 2002). Thus, the more wolves present at and around a kill, the more difficult it is for ravens to gain access to the carcass and remove biomass. The higher scavenging competition seen in small packs is a consequence of 1) few wolves needing more time to eat up a kill, and therefore giving scavengers more time to remove biomass, and 2) the inability of small packs to keep ravens away from the kill.

As a conclusion, raven competition is a sufficient explanation for the fact that small packs kill four times and medium size packs kill twice as many moose in winter than should be expected from their daily food requirements. This has consequences for wolf management, as managers have to be aware that a reduction in wolf numbers will not necessarily result in a lower predation pressure by wolves because fewer wolves in smaller packs have to compensate for raven scavenging by a higher predation rate.

Because raven scavenging is linked to the ability of ravens to quickly find wolf kills and build up in large numbers, raven competition can be expected to be highest in settings where wolves prey on large ungulates in open habitats. In forested ranges where wolves largely prey on medium-sized prey, which is the case in most areas of central Europe (Jedrzejewski et al. 2000, Jedrzejewski et al. 2002), scavenging by ravens can be expected to be of only minor importance for predicting predation rates.

In summary, we have shown that 1) wild ravens are the main scavenger during winter in the Yukon, 2) mass removal from wolf kills must be considerably higher than previously assumed and varies with pack size, and 3) ravens had substantial effects on the modelled kill rate of wolves, especially of those in small packs.

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