Common ravens, *Corvus corax*, preferentially associate with grey wolves, *Canis lupus*, as a foraging strategy in winter

DANIEL STAHLER*†, BERND HEINRICH* & DOUGLAS SMITH†

*Department of Biology, University of Vermont

†Yellowstone Center for Resources, Yellowstone National Park

One foraging strategy that scavengers can employ to discover unpredictable food sources is to associate directly with predators who inadvertently provide food. The common raven, a well known feeding generalist, is also a prominent scavenger of wolves' kills and is found to be in close association with this predator. We tested the hypothesis that ravens preferentially associate with wolves in winter as a kleptoparasitic foraging strategy. The presence, absence and behaviour of ravens was documented during winter observations of wolves, coyotes, *Canis latrans*, and elk, *Cervus elaphus*, as well as the landscape in the absence of these three species. Ravens were found to be in close association with wolves when they were travelling, resting and hunting prey. In comparison, ravens showed no significant association with coyotes, elk or areas on the landscape in the absence of wolves. We also compared ravens' discovery success of wolf-killed and nonwolf-killed carcasses and their behavioural response upon discovery. Ravens found all wolf kills almost immediately and remained at the carcass to feed alongside wolves after the death of the prey. In contrast, ravens were less successful discovering experimentally placed carcasses in the same study region, and did not land or feed despite the availability of fresh, exposed meat. Our results show that ravens' association with wolves is not just an incidental and proximate by-product of the presence of fresh meat. Instead, we show that ravens preferentially associate with wolves in both the presence and absence of food, resulting in the discovery of carcasses and suppression of ravens' innate fear of novel food sources. Through this mode of social foraging, ravens may experience increased foraging efficiency in the use of an otherwise spatially and temporally unpredictable food source.

The ability to gather information from either conspecifics or nonconspecifics on the location and quality of resources has important implications for species dependent upon spatially and temporally unpredictable food sources (Clark & Mangel 1984, 1986; Pulliam & Caraco 1984). Predator-killed ungulate carcasses represent such a food source for scavenger species, and it is presumed that behavioural mechanisms for locating and utilizing carcasses have evolved (Houston 1979; Heinrich 1988a; Marzluff & Heinrich 1991). Although associations between sympatric scavengers and carnivores have been documented (Mech 1966; Kruuk 1972; Schaller 1972; Cooper 1991; Gasaway et al. 1991; Caro 1994), few studies have examined predator–scavenger relationships with respect to the foraging behaviour of scavengers

(Kruuk 1972; Houston 1979; Paquet 1991), with the focus instead on the behavioural ecology of the carnivore that is being kleptoparasitized (Cooper 1991; Fanshawe & FitzGibbon 1993; Caro 1994; Creel & Creel 1996; Carbone et al. 1997).

Interspecific kleptoparasitism, or food stealing, is inherent to predator–scavenger relationships. By employing kleptoparasitism as a foraging strategy, scavengers can improve foraging success by reducing search time, energy expenditure and risks associated with procuring the food themselves, as well as by gaining access to large, high-quality food items (Brockmann & Barnard 1979; Houston 1979; Heinrich 1988b). Behavioural strategies that allow scavengers to gain information on foraging opportunities and kleptoparasitize more efficiently, particularly in ecosystems with high inter- and intraspecific competition, are expected. Examples of such foraging strategies include: travelling the landscape and visually discovering a food source by chance (Houston 1979; Heinrich 1988b), foraging where conspecifics or nonconspecifics are seen to be foraging (Thorpe 1956; Kruuk 1972; Houston

Correspondence: D. R. Stahler, Yellowstone Gray Wolf Restoration Program, Yellowstone Center for Resources, P.O. Box 168, Yellowstone National Park, WY 82190, U.S.A. (email: dan_stahler@nps.gov). B. Heinrich is at the Department of Biology, University of Vermont, Burlington, VT 05405, U.S.A.

1979; Pöysä 1992), responding to vocalizations from other scavengers (Heinrich 1988b; Heinrich & Marzluff 1991), following conspecifics that have previously discovered a food source from nocturnal roost sites (Heinrich 1988b, 1989; Marzluff & Heinrich 1991; Marzluff et al. 1996), and associating with the predators that make carcasses available (Mech 1966; Kruuk 1972; Houston 1979; Cooper 1991; Paquet 1991).

The foraging behaviour of ravens living in highly seasonal northern climates is of particular interest because they feed in large groups and are dependent upon carrion, an unpredictable food source (Bent 1946; Heinrich 1988a, b). In winter, ravens frequently scavenge the kills of large mammalian carnivores (Mech 1966; Peterson 1977; Heinrich 1989) and in some northern areas, ravens are dependent upon wolves to kill and open carcasses (Mech 1970; Peterson 1977; Allen 1979), as they are unable to tear the hide of large mammals (Heinrich 1988b). Wherever wolves persist today, ravens are found feeding at their kills (Mech 1966, 1970; Peterson 1977; Allen 1979; Bjarvall & Isakson 1982; Promberger 1992; Carbyn et al. 1993) and researchers have hypothesized that a unique relationship may exist between these two species (Mech 1966, 1970; Peterson 1977; Allen 1979; Carbyn et al. 1993). Anecdotal evidence suggests that ravens monitor wolf pack activities by either following them directly (Mech 1966, 1970; Peterson 1977; Allen 1979; Bjarvall & Isakson 1982; Carbyn et al. 1993), following their tracks in the snow (Mech 1966), or responding to vocalizations to determine the location of the wolves (Harrington 1978). Although documented, no studies have quantified this predator–scavenger association in detail to sort out possible proximate attraction to prey and carcasses versus attraction to the predator itself.

In this paper, we report the degree of association between ravens and wolves at and away from a food source, making comparisons to raven associations with sympatric coyotes, Canis latrans, elk, Cervus elaphus, and the landscape in the absence of wolves. We hypothesize that ravens preferentially associate with wolves as a kleptoparasitic foraging strategy in winter and predict that ravens follow wolves in the concurrent absence of a food source, resulting in almost immediate discovery of carcasses after a wolf predation event. Furthermore, the degree of raven association is expected to differ depending on wolf activity, as well as between wolf and coyote activity, due to the differential effects these variables have on foraging opportunities for ravens. In addition, we investigated another aspect of social foraging, the reduction of neophobia (Heinrich 1988c) through social facilitation. Ravens are initially fearful of large carcasses when encountered, gradually losing their caution through experience gained either individually or by observing conspecific (Heinrich 1988c; Marzluff & Heinrich 1991; Heinrich et al. 1995) and/or nonconspecific carcass feeders (Heinrich 1999a). By comparing raven discovery success and behavioural response to wolf-killed carcasses versus carcasses not attended by wolves, we tested the hypothesis that ravens experience reduced neophobia through their association with this predator at carcasses, presumably leading to greater foraging success.

STUDY AREA AND METHODS

This study was conducted primarily in the northern portion of Yellowstone National Park (YNP), Wyoming, in an approximate 800-km² area. The elevation of the study site ranges 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 (Houston 1982). Mean annual temperature is 1.8 °C, and mean annual precipitation is 31.7 cm (Houston 1982). The habitat in the study area included forest, mesic meadow, mesic shrub-meadow, riparian grassland, sage grassland and road (Gese et al. 1996).

During winter, elk are the most abundant ungulate species, with the northern range herd estimated at 15 500–17 400 elk (Lemke et al. 1998). Elk carrion available as a result of predation or winter kill provides an important food source for scavengers, including common raven, black-billed magpie, Pica pica, coyote, red fox, Vulpes vulpes, golden eagle, Aquila chrysaetos, bald eagle, Haliaeetus leucocephalus, grizzly bear, Ursus arctos and black bear, U. americanus.

Wolves were reintroduced into YNP in 1995–1996 after an approximate 70-year absence (Bangs & Fritts 1996). The Rose Creek Pack, Druid Peak Pack and Leopold Pack were the three established northern-range wolf packs monitored in this study. Pack sizes ranged between 13–22, 7–11 and 8–14 for Rose Creek, Druid Peak and Leopold packs, respectively, from 1997 to 1999. Some wolves from each pack had previously been radiocollared by the National Park Service and the U. S. Fish and Wildlife Department as part of long-term monitoring and management in compliance with the Endangered Species Act (Bangs & Fritts 1996) and we were granted permission to use radiotelemetry to monitor these individuals. Raven demography is largely unknown in YNP. The winter population estimate for the study area was 60–120 individuals. However, 300–500 ravens live 20 km northwest of the study area near Gardiner, Wyoming, an area outside of YNP's north entrance (T. McEneaney, personal communication, YNP).

Raven Association with Wolves, Coyotes, Landscape, Elk and Carcasses

We collected data on ravens associating with wolves, coyotes, elk and the landscape from October through to April during the winters of 1997–1998, 1998–1999, and the first half of winter in 1999–2000. Direct open-field observations were made of both radiocollared and unmarked wolves that were typically associated as members of resident packs during observations. Visual observations were made from distances of 0.15–4.0 km. Upon visual location of wolves, facilitated by radiotelemetry, known pack movement patterns, and 25–60 × spotting scopes, an all-occurrence sampling period (Altmann 1974) began and we recorded (1) the number of wolves present, (2) the behavioural activity, (3) the duration (recorded within 1 min) of that behaviour bout and (4) raven association.

Wolf activity categories were: (1) travelling: walking, trotting or running, stopping occasionally to scan surroundings; (2) resting: lying down either with head up and alert or with head down and assumed to be resting, and no food source was present; (3) chasing prey: active running pursuit or interacting with ungulate prey species in an attempt to kill; (4) mousing: stalking, searching, orienting, chasing or pouncing on small mammals; and (5) at-kill: feeding on an ungulate carcass or scraps from a carcass within 100 m of that carcass. Because of temporal behaviour patterns and pack cohesion, the above behaviour categories were assigned without ambiguity and when more than half of the individuals in an observed wolf group were performing a particular activity. Activity bouts less than 10 min were not used, except with chasing prey bouts. Because wolf and elk chases frequently ended in a successful kill and were sometimes less than 5 min in duration, the significance in terms of raven association and foraging success warranted that all chasing prey bouts be used for analysis.

To determine the association between wolf activity and ravens, continuous sampling during wolf activity bouts recorded (1) the presence or absence of ravens, (2) the number of ravens, (3) the duration (within 1 min) of raven presence per wolf activity bout and (4) the proximity of ravens to wolves (within 1 m). A raven was considered 'present' when within 250 m of wolves and therefore assumed to be monitoring wolf activity. This value was thought to be a conservative distance for association due to the open landscape and the acuity of ravens' visual perception. Ravens were considered 'at-kill' when feeding on an ungulate carcass or meat scraps within 100 m of that carcass. There were no marked or known individual ravens, and because they frequently flew in and out of the our field of view, counts of individuals at and away from carcasses were probably underestimates of the true number of individuals present.

We collected data on ravens associating with coyotes following the same protocol previously described with wolves. Coyote behaviour categories were (1) travelling, (2) resting and (3) mousing, under the same definitions given for wolf behaviour. During this study, hunting behaviour observed in coyotes was limited to mousing, so prey-chasing bouts were not relevant. At-kill bouts were not recorded because raven and coyote association at carcasses was the result of two scavengers utilizing a wolf kill.

To control for the possibility that the raven and wolf association was simply the result of ubiquitous raven presence on the landscape instead of with wolves per se, we collected data on raven association with fixed points on the landscape. Landscape observation sites were chosen using the following criteria: (1) sites were in the same areas that ravens were observed in association with wolves and (2) sites had distinct landscape features such as boulders, trees, or other topographical distinctions to be used as reference points. Raven presence (<250 m) with respect to fixed landscape points was recorded, along with the number of ravens and duration of their presence.

The fourth sampling method involved observing elk groups in wolf territory and recording raven association. Elk groups ($\bar{X} \pm SE = 80.8 \pm 14.1$ elk, range 4–600, $N=46$) visible from common wolf-viewing areas were selected for observation. Raven presence (<250 m), number of individuals, duration of presence and behaviour were recorded. These data tested the hypothesis that ravens may associate with animals in general, or more specifically, with wolf prey species on the chance that predators will eventually kill an individual prey animal that ravens are monitoring.

Observations of coyotes, elk and fixed points on the landscape were made within a wolf territory when wolves were not present (>2 km away) to assure that raven presence was not due to wolf presence. Assumed independence of wolf, coyote, elk and landscape bouts was maintained by using bouts separated by a night-time period (10–14 h of dark) when ravens are not active and sleeping.

Raven Discovery Time and Subsequent Behaviour at Carcasses

We compared raven discovery of wolf-killed carcasses versus nonwolf-killed carcasses. Discovery times of wolf-killed carcasses were collected by observing predation events and recording the arrival time (within 1 min) of the first raven (<250 m) to a wolf kill after the assumed time of death of the prey species. Data on wolf kills were the result of prey-chasing bouts that ended in the capture of prey. Discovery time of a wolf-killed carcass by ravens was recorded as 0 min if ravens were present during a chasing prey bout that ended in a kill. Following the time of death, maximum raven numbers were recorded at 15-min intervals for the first 60 min of the at-kill bouts and included ravens within 100 m of the carcass. The recorded behaviour of ravens upon discovery was either: (1) land and feed, or (2) leave without feeding. Wolves were either feeding at the carcass or within 20 m of the carcass in all recorded bouts.

To test carcass discovery and behavioural response of ravens to nonwolf-killed carcasses, we conducted 25 experimental trials by placing road-killed ungulate carcasses in wolf territories during the same winter seasons and conditions that wolves were killing prey. We selected carcass placement sites that were located in the same areas of previously observed wolf-killed carcass sites, and conducted a 10-min observation period prior to carcass placement to determine whether ravens were in the vicinity (the trial was aborted if ravens were seen). We placed cut-open carcasses (with unfrozen, exposed red meat) on open, snow-covered areas conspicuous to avian foragers. The snow surrounding the carcass was packed and sprinkled with blood patches to simulate a typical wolf-kill site. Following carcass placement, we conducted a 60-min observation period from a hidden position and recorded the same data as described with wolf-killed carcasses to determine discovery success, discovery time and behavioural response by ravens.

Table 1. Comparison of the bouts recorded for wolf, coyote, elk and landscape showing the percentage of bouts and minutes with ravens present, mean bout length and mean raven presence (min)

Bout type	% Bouts with ravens (number of bouts with ravens/N)	% Time (min) ravens were observed in association*	$\bar{X}\pm SE$ bout length (min)	$\bar{X}\pm SE$ raven presence (min) per bout type
Wolf				
Travelling	89.6 (69/77)	37.7 (1003/2660)	34.6±2.9	14.5±1.4
Resting	81.0 (51/63)	27.5 (1362/4959)	78.7±10.6	26.7±4.2
Chasing prey	87.2 (34/39)	62.9 (393/625)	16.0±2.7	11.6±2.2
Mousing	100 (6/6)	84.7 (166/196)	32.7±9.1	15.8±1.5
Activities combined†	86.5 (160/185)	34.6 (2924/8440)	45.6±4.3	18.3±1.6
At-kill	100 (49/49)	99.7 (5148/5162)	105.4±16.3	105.1±16.3
Coyote				
Travelling	1.7 (1/60)	0.1 (1/1827)	30.5±2.2	N/A
Resting	6.5 (2/31)	0.2 (3/1242)	40.1±3.6	1.5±0.5
Mousing	0 (0/13)	0 (0/456)	35.1±7.8	N/A
Activities combined†	2.9 (3/104)	0.1 (4/3525)	33.9±2.0	1.3±0.3
Landscape	25.7 (19/74)	1.4 (49/3479)	47.0±5.4	2.6±0.8
Elk	6.5 (3/46)	0.1 (2/1680)	36.5±1.0	0.7±0.2

*Produced by the sum of the total number of minutes ravens were present divided by the total number of minutes the category bout was observed.
†All behaviour types excluding at-kill.

Data Analysis

Our sampling unit used to determine raven association was an activity or observation bout. We quantified the proportion of bouts in which at least one raven was present, as well as the proportion of time (in min) during which ravens were present for any given bout type. Behaviour category bouts were combined for wolves (travelling, resting, mousing and chasing prey) and coyotes (travelling, resting and mousing) for pairwise comparisons of raven association with wolves versus coyotes, elk and landscape bouts. At-kill data were excluded from these pairwise comparisons because data on coyotes at kills were not collected. We also made pairwise comparisons between the two canids' travel, rest and mouse bouts, as well as among the wolf behaviour categories (travel, rest, chase, mouse) to determine whether differences existed in the degree of raven attraction.

All pairwise comparisons were performed using the ratio estimation method (Scheaffer et al. 1996), which provided more accurate estimates of proportions based on varying bout lengths and gave more weight to longer bouts. The ratio estimation value was the ratio of the total number of minutes ravens were present for any given bout category to the total number of minutes recorded for that particular bout category. A z test indicated significant differences between the proportions being compared (Ott 1993). We adjusted α level to correct for experimentwise error rate of pairwise comparisons using Bonferroni correction (Sokal & Rohlf 1995) for raven association with wolves compared to coyotes, elk and landscape ($\alpha=0.017$), and for comparison of raven association among various wolf behaviour types ($\alpha=0.005$). The comparison between discovery success of wolf-killed carcasses and nonwolf-killed carcasses was made using a z test comparing two binomial proportions (Ott 1993).

RESULTS

From November 1997 to December 1999, 53 resident wolves were observed from three packs (Leopold, Druid Peak and Rose Creek Packs) for 226.7 h. Wolf group size for activity bouts varied depending on the pack observed and degree of pack cohesion at a given time ($\bar{X} \pm SE=8.6 \pm 0.3$ wolves, range 1–22, $N=234$). Of the 209 wolf activity bouts with ravens present, 56 (26.8%) were collected on at least two of the three packs simultaneously in different parts of the study area by different observers. Individual coyotes and their pack affiliations were not identified, but a minimum of 36 coyotes inhabited a 70-km^2 portion of the Druid Peak Pack's territory (Crabtree & Sheldon 1999) and because observations were made in two other wolf pack territories, at least twice as many individual coyotes could have potentially been observed. Coyote group size varied little ($\bar{X} \pm SE$ coyotes=1.6 ± 0.1, range 1–3, $N=101$), and coyotes were typically solitary or associated in pairs when observed. A total of 58.8, 28.0 and 58.0 h were observed for coyote, elk and landscape bouts, respectively. Activity bout lengths varied widely for each of the four bout categories because changes in behaviour or visibility could not be anticipated and all-occurrence sampling was employed (Table 1).

Preferential Association with Wolves

Ravens were present in the majority of wolf activity bouts observed away from a known carcass, whereas ravens were absent in the majority of coyote, elk and landscape bouts (Table 1). The proportion of time that ravens were observed in association with the four bout categories also varied significantly (Table 1). Ravens spent more time in the presence of wolves than they did with landscape points in the absence of wolves (z test: $z=10.4$,

$P<0.0001$). Ravens spent significantly less time associating with elk, the main prey of the wolf, than with the predators themselves ($z=10.8$, $P<0.0001$). Ravens also showed preferential association with wolves over coyotes away from a carcass ($z=10.3$, $P<0.0001$), even when comparing wolf bouts of comparable group size ($\bar{X} \pm$ SE$=1.7 \pm 0.2$ wolves, range 1–3, $N=23$) to coyote bouts ($z=3.4$, $P<0.001$). Wolves travelling, resting and mousing all attracted ravens more than coyotes engaged in these same activities (travelling: $z=26.9$, $P<0.0001$; resting: $z=19.5$, $P<0.0001$; mousing: $z=10.1$, $P<0.0001$).

The number of ravens in association with wolves away from a carcass ($\bar{X} \pm$ SE$=2.7 \pm 0.2$ ravens, range 1–16, $N=160$) was greater than the number associating with coyotes away from a carcass ($\bar{X} \pm$ SE$=1.3 \pm 0.3$ ravens, range 1–2, $N=3$; Student's t test: $t_3=3.7$, $P<0.05$), elk groups ($\bar{X} \pm$ SE$=1.3 \pm 0.3$ ravens, range 1–2, $N=3$; $t_3=3.7$, $P<0.05$), and points on the landscape ($\bar{X} \pm$ SE$=1.6 \pm 0.2$ ravens, range 1–4, $N=19$; $t_{59}=4.4$, $P<0.0001$). When present, ravens were in closer proximity to wolves ($\bar{X} \pm$ SE$=25.0 \pm 2.2$ m, $N=160$) than to coyotes ($\bar{X} \pm$ SE$=56.7 \pm 23.3$ m, $N=3$), elk groups ($\bar{X} \pm$ SE$=116.7 \pm 44.1$ m, $N=3$), or points on the landscape ($\bar{X} \pm$ SE$=113.7 \pm 14.0$ m, $N=19$).

Association between wolves and ravens was greatest when wolves were at a kill, with 100% ($N=49$) of these bouts having ravens present nearly the entire time, but the proportion of time that ravens were observed in association with each of the behaviour categories varied (Table 1). Ravens spent more time associating with wolves when wolves were chasing prey or mousing compared with when they were travelling (z test: $z=2.7$, $P<0.004$; $z=5.0$, $P<0.0001$) or resting ($z=3.7$, $P<0.0001$; $z=6.0$, $P<0.0001$). Ravens appeared to spend more time associating with wolves when wolves were travelling than when wolves were resting, although the difference did not reach significance following Bonferroni adjustment ($z=1.6$, $P=0.05$).

Discovery Success and Behavioural Response to Wolf-killed and Nonwolf-killed Carcasses

Twenty-nine prey-chasing bouts that ended in the successful predation of an ungulate species (28 elk, one bison, *Bison bison*) were recorded. Discovery success of kills by ravens within the 60-min observation period following the time of death of the prey animal was 100% ($N=29$). Wolf-killed carcasses were discovered almost immediately because some ravens were typically following the wolves prior to the kill. In 24 of the 29 kills (82.8%), ravens (1–13) were present during the chase, within 5–100 m of the wolves, hovering above or perched on boulders nearby, whereas the other five kills were discovered within 4 min of the time of death (Fig. 1; overall $\bar{X} \pm$ SE$=0.5 \pm 0.2$ min, median$=0$ min, range 0–4, $N=29$).

In all wolf kills, arriving ravens responded by landing on the ground or perching on nearby boulders in close proximity to the kill and feeding wolves. In the majority of cases, ravens would approach to within 1 m of the feeding wolves to take advantage of meat scraps made
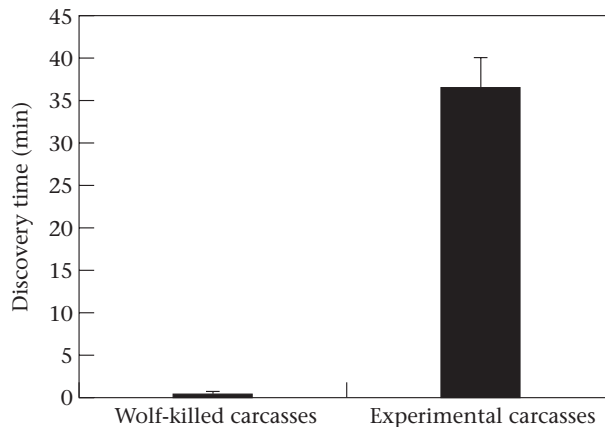

Figure 1. Discovery time of wolf-killed ($N=29$) and experimental ($N=9$) carcasses by ravens. These values represent the arrival time ($\bar{X} \pm$SE) in min of the first raven(s) to approach to within 250 m of the carcasses after the time of prey death (wolf-killed carcass) or placement of carcass (experimental carcass).
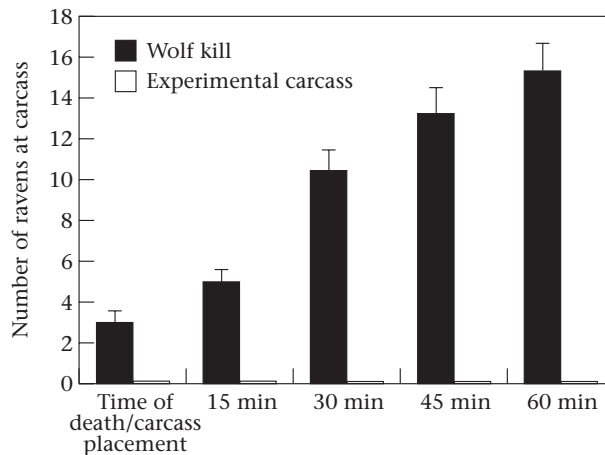

Figure 2. Number of ravens ($\bar{X} \pm$SE) at wolf-killed ($N=29$) and experimental ($N=9$) carcasses at 15-min intervals after initial presence on the landscape for the first 60 min of carcasses' presence. No ravens stayed to feed at experimental carcasses.

available during the evisceration process or peck at blood in the snow. In one kill, one raven landed on the prey animal as it was dying and remained while a wolf began evisceration. The number of ravens increased steadily throughout the first 60 min after the time of death (Fig. 2).

Ravens discovered wolf-killed carcasses with greater success than they did nonwolf-killed carcasses within 60 min of the time of initial carcass presence on the landscape ($z=5.2$, $P<0.0001$). With the experimentally placed carcasses, only nine out of 25 (36%) were discovered within the 60-min observation period following carcass placement. Ravens did not immediately discover these nine experimental carcasses after their initial presence (Fig. 1; $\bar{X} \pm$ SE discovery time$=36.3 \pm 3.7$ min, range 17–52, $N=9$). The initial number of ravens discovering experimental carcasses was either one or two, which was less than initial group size discovering wolf kills ($\bar{X} \pm$ SE experimental carcasses$=1.4 \pm 0.2$ ravens, $N=9$; $\bar{X} \pm$ SE

wolf kills=3.0 ± 0.5 ravens, $N=29$; $t_{34}=3.03$, $P<0.01$). In all of the discovered experimental carcasses, arriving ravens circled above the carcass once or twice before leaving the area for the remainder of the observation period. In contrast to the response towards wolf kills, none of the ravens landed to feed at experimental carcasses (Fig. 2). Magpies discovering these carcasses (in four trials), however, did immediately feed from them.

In determining the number of ravens attending wolf-killed carcasses, we combined data from the 29 observed wolf predation events with data on other wolf-killed carcasses that were discovered after the kill was made. The number of individual ravens attending wolf-killed carcasses at one time ranged between three and 135 ($\bar{X} \pm SE=28.6 \pm 2.1$ ravens, $N=98$), but because ravens were unmarked and frequently coming and going to cache food, these values probably underestimate the actual number of ravens attending wolf kills during our study.

DISCUSSION

In YNP during winter, ungulate carcasses represent a spatially and temporally unpredictable and ephemeral food source for ravens, whether they are the result of predator-caused mortality or other causes. Ravens are the most common and numerous vertebrate scavengers using these carcasses in the winter (Yellowstone Wolf Project, National Park Service, unpublished data), indicating that this resource is an important food source for them. Inter- and intraspecific competition at ungulate carcasses in YNP is high, so foraging strategies employed by scavengers that facilitate discovery of a carcass soon after its initial presence on the landscape presumably lead to greater foraging efficiency and resource intake. Social interaction between ravens and wolves in YNP demonstrates an important scavenger foraging strategy.

Ravens in winter in YNP showed routine daily association with wolves. We observed ravens in close proximity to wolves in the majority of wolf bouts and this presence ranged from 27.5% to 99.7% of the observed minutes for any given behaviour type, serving as estimates for the degree of association in the winter. Ravens preferentially associated with wolves compared to coyotes and elk, and this association could not be explained by ubiquitous raven presence on the landscape.

The infrequent association with coyotes suggests that ravens discriminate between wolves and coyotes based on the differential abilities of these two canids to kill larger prey and thus provide scavenging opportunities for them. Predation on ungulates by coyotes does not occur frequently enough in YNP to provide the scavenging community with carcasses on a regular basis (Gese et al. 1996), although coyotes may benefit ravens by opening nonwolf-killed carcasses. Wolf group size was larger on average than coyote group size, and the activity of a larger canid group size could, arguably, have been more attractive to ravens in the area. Our comparison of similar wolf and coyote group sizes (1–3 individuals), however, suggests that ravens are able to distinguish between these two canids. When ravens were present during coyote

bouts, they flew overhead and then left, suggesting that ravens can make quick assessments on canid identity and/or the potential for food.

The lack of significant raven association with elk groups suggested that ravens are not following elk on the northern range of YNP. Thus, it is probably not advantageous for ravens to follow elk around waiting for one to die. We have observed on several occasions, however, ravens being quick to locate and harass injured elk, apparently drawing the attention of wolves and coyotes through local enhancement.

The almost immediate presence of ravens at wolf-killed carcasses does not itself distinguish whether ravens follow wolves or are attracted to a kill by the activity of the chase when they see it from a distance. However, the frequent presence of ravens with wolves in the absence of a carcass supported the hypothesis that some ravens were following wolves throughout the day. On days where wolves were in continuous visible range, we frequently observed ravens following wolves throughout continuous activity that changed from resting to travelling to chasing prey, which sometimes led to the wolves making a kill.

The differences in the degree of raven association when wolves were resting, travelling, chasing prey, mousing or at a kill coincided with the differential potential for each of these behaviours to provide food for foraging ravens. The trend for ravens to spend more time associating with travelling wolves than resting wolves probably reflects the fact that resting wolves are less likely to kill a prey animal, whereas travelling wolves could potentially encounter prey and have the opportunity to kill. Ravens were present for the majority of minutes we observed wolves chasing prey, presumably because this activity held the greatest potential for foraging success. When wolves were mousing, ravens were on the ground hopping behind the wolves, sometimes less than 1 m away, whereas no ravens were ever seen in the presence of a mousing coyote. Small mammals are an important part of a coyote's diet during winter in YNP (Gese et al. 1996) and any rodent captured is immediately consumed. In contrast, mousing wolves appeared less intent on consuming captured rodents than playing with them, giving associating ravens a better opportunity to steal from a wolf (as occurred in one occasion). Our results suggest that ravens may be making decisions on how much time to spend following wolves based on their activity type and the potential for food acquisition.

The discovery of wolf-killed carcasses by ravens led to greater opportunity for them to obtain meat compared with nonwolf-killed carcasses. Not only did it take longer for ravens to locate nonwolf-killed carcasses, but they also did not utilize the carcasses upon discovery or within the 60-min observation time, despite the availability of red meat. In contrast, ravens discovering wolf kills attempted to obtain meat soon after carcass discovery, often moving to within 1 m of feeding wolves. Apparent fear response to large carcasses by ravens (neophobia) has been shown elsewhere and is characterized by a cautious approach to a carcass and retreating without feeding (Heinrich 1988c). Fear of large carcasses upon first encounter is an innate response (Heinrich 1988c; Heinrich et al. 1995) that is

reduced through experience (Heinrich et al. 1995) or social facilitation (Marzluff & Heinrich 1991). Our results suggest neophobia in ravens upon discovering carcasses unattended by wolves, whereas discovery of wolf-killed carcasses attended by wolves resulted in an apparent suppression of this fear response. Thus, wolves appeared to be a primary stimulus for ravens to start feeding. Heinrich (1999b) found similar feeding responses by ravens in Nova Scotia, Canada, at carcasses in the presence and absence of captive wolves in a fenced enclosure.

Wolves defend carcasses against ravens by chasing them, and dead ravens are occasionally found near wolves and their kills (Peterson 1977; Allen 1979; J. Ryan, personal communication; T. Brooks, personal communication), suggesting that feeding next to wolves is not risk free. Therefore, if foraging next to wolves is strictly a reflection of ravens' opportunism to feed on fresh meat, then they should prefer to feed on meat that is unattended by wolves, or feed equally at meat attended and unattended by wolves. Our findings of ravens preferentially feeding with wolves at carcasses suggest that the ravens received socially facilitated benefits, such as reduced neophobia, which outweighed potential risks associated with feeding next to wolves. Frequent behavioural interactions between these two species were observed at and away from kill sites, such as ravens pulling wolves' tails, ravens interacting with wolf pups at den sites, and playful chasing between them (Stahler 2000). Such interactions may serve to 'educate' ravens on the responses and intent of potentially dangerous, large carnivores, as has been suggested (Heinrich 1989, 1999a), ultimately benefiting ravens when feeding among wolves at carcasses.

We could not determine whether the same ravens were following wolves on different days, or the age and social status of those ravens. Both adult territorial ravens with known nests and nonterritorial foraging groups were found in wolf pack territories. We also found ravens travelling between wolf kills belonging to two different packs, showing that some ravens did not just associate with one pack, and thus probably monitor the activities of several packs when foraging. The fact that we observed different ravens in a variety of group sizes (1–16) associating with different wolf packs simultaneously suggests that more than just a few members of the raven population have adopted this foraging strategy. Our results may also apply to the association between ravens and wolves seen in other ecosystems (Mech 1966; Peterson 1977; Bjarvall & Isakson 1982; Promberger 1992; Carbyn et al. 1993).

Considerably more ravens showed up to feed at wolf kills compared with the number of ravens associating with wolves in the absence of food. We believe this rapid arrival of additional ravens was due to the enhancement of kill-site locations from the activity of birds already present. Local enhancement, or the attraction to individuals already feeding (Thorpe 1956; Turner 1964), is an important component of the foraging strategy of species that use spatially and temporally unpredictable foods in open habitats (Schaller 1972; Houston 1979; Pöysä 1992). In YNP, local enhancement may be influential in directing the attention of other ravens to a kill site on the landscape, and subsequently serving to attract other kleptoparasites such as coyotes, magpies and eagles. Nonbreeding juvenile ravens may also be actively recruiting other vagrant nonbreeders and overpowering territorial adults at carcasses, as has been seen elsewhere (Heinrich 1988b; Marzluff & Heinrich 1991), although we did not record recruitment vocalizations (Heinrich 1988b) because our distance to carcasses was frequently out of audible range. Larger raven aggregations at carcasses may also distract wolves and other scavenger species, which may increase food intake for individual ravens present (Marzluff & Heinrich 1991).

Our results showing ravens following a nonconspecific forager to gain access to food is similar to the symbiotic relationship of the African ratel, *Mellivora capensis*, and human honey hunters following the honeyguide, *Indicator indicator* (Isack & Reyer 1989), coyotes following wolves (Paquet 1991), hyaenas, *Crocuta crocuta*, following wild dogs, *Lycaon pictus*, lions, *Panthera leo* and cheetahs, *Acinonyx jubatus* (Kruuk 1972; Cooper 1991; Caro 1994), and birds following monkeys (Terborgh 1983; Zhang & Wang 2000). As with all scavenger–predator relationships, however, the raven–wolf association reported here demonstrates a kleptoparasitic form of social symbiosis, in that ravens are the primary beneficiaries by stealing food that would otherwise benefit the wolves.

It is significant that ravens associated strongly with wolves in YNP immediately following the 1995–1996 reintroduction of this predator after a 70-year absence in the ecosystem (Bangs & Fritts 1996). Although our data did not distinguish the behavioural mechanisms underlying ravens' preferential association with wolves, we believe that both innate and learned behavioural responses towards wolves are involved; suggesting that the raven–wolf relationship is an ancient evolved one. Regardless of the mechanism, our results are the first to show that ravens actively seek wolves' company to find and gain access to large carcasses and to overcome their apparent fear of them. In addition, we show that some ravens follow wolves despite the concurrent absence of food, demonstrating a kleptoparasitic foraging strategy for scavenger species dependent on spatially and temporally unpredictable food sources.

Acknowledgments

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