Factors affecting carcass use by a guild of scavengers in European temperate woodland

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Abstract: Although facultative scavenging is very common, little is known about the factors governing carrion acquisition by vertebrates. We examined the influence of carcass characteristics, carcass state, and weather conditions on carrion use by main scavengers. Carcasses (N = 214, mainly ungulates) of various origins (predation, natural deaths, harvest) were monitored by systematic inspections (N = 1784) in Białowieża Forest (Poland). Common raven (*Corvus corax* L., 1758), red fox (*Vulpes vulpes* (L., 1758)), and European pine marten (*Martes martes* (L., 1758)) mainly used the prey remains of gray wolves (*Canis lupus* L., 1758). The kills of predators were the preferred carrion, rather than dead ungulates. Common ravens, common buzzards (*Buteo buteo* (L., 1758)), white-tailed eagles (*Haliaeetus albicilla* (L., 1758)), and domestic dogs scavenged more frequently on carcasses in open habitats. Carcasses located in the forest were the most available to European pine martens, jays (*Garrulus glandarius* (L., 1758)), and wild boar (*Sus scrofa* L., 1758). The common tendency was to increase scavenging when temperature decreased, except for raccoon dogs (*Nyctereutes procyonoides* (Gray 1834)). As snow depth increased, jays and great tits (*Parus major* L., 1758) increased scavenging. We suggest that carrion use by scavengers is not random, but a complex process mediated by extrinsic factors and by behavioural adaptations of scavengers.

Résumé : Bien que l'utilisation facultative des charognes soit très commune chez les vertébrés, on connaît peu les facteurs qui régissent l'acquisition des cadavres. Nous avons examiné l'influence des caractéristiques et de l'état des carcasses ainsi que des conditions climatiques sur l'utilisation des charognes par les principaux charognards. Nous avons suivi par inspections systématiques (N = 1784) des carcasses (N = 214, surtout d'ongulés) d'origines diverses (prédation, mort naturelle, récolte) dans la forêt de Białowieża (Pologne). Les grands corbeaux (*Corvus corax* L., 1758), les renards roux (*Vulpes vulpes* (L., 1758)) et les martres des pins d'Europe (*Martes martes* (L., 1758)) utilisent surtout les restes des proies des loups communs (*Canis lupus* L., 1758). Les proies tuées par les prédateurs sont les charognes de prédilection, préférées aux ongulés morts. Les corbeaux, les buses variables (*Buteo buteo* (L., 1758)), les pigargues à queue blanche (*Haliaeetus albicilla* (L., 1758)) et les chiens domestiques se nourrissent plus souvent de carcasses dans les habitats ouverts. Les carcasses dans les forêts sont surtout disponibles aux martres des pins d'Europe, aux geais des chênes (*Garrulus glandarius* (L., 1758)) et aux sangliers d'Eurasie (*Sus scrofa* L., 1758) sauvages. La tendance commune est d'augmenter l'utilisation des charognes lorsque la température décroît, excepté chez les chiens viverrins (*Nyctereutes procyonoides* (Gray, 1834)). Avec l'augmentation de la couche de neige, les geais et les mésanges charbonnières (*Parus major* L., 1758) accroissent leur utilisation des charognes. Nous croyons que l'utilisation des charognes par les charognards n'est pas aléatoire, mais qu'elle est un processus complexe sous l'influence de facteurs extrinsèques et des adaptations comportementales des charognards.

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Introduction

Facultative scavenging is common among vertebrates and it has recently been suggested as being a key ecological process (DeVault et al. 2003; Selva 2004*a*). Scavengers accelerate the return of nutrients, disseminate such nutrients over a wide area, and contribute to dilution of potentially infective

foci (Putman 1978*a*, 1978*b*; Schlatter et al. 1978; DeVault et al. 2003; Wilkinson et al. 2005). On the other hand, carcasses may have important effects on ecosystem diversity and on population dynamics of consumers (Rose and Polis 1998; Towne 2000; Roth 2003; Melis et al. 2004). Additionally, carrion is a supplemental trophic resource during food shortages (Jędrzejewska and Jędrzejewski 1998; Selva 2004*a*). Thus, scavenging may represent "weak links" in food webs, which are essential for the stability and persistence of ecosystems (DeVault et al. 2003). However, relatively little is currently known about the role and fate of carrion in terrestrial ecosystems, specifically the costs and benefits of carcass use by facultative scavengers and the factors governing the decision to scavenge.

Scavenging studies have traditionally focused on the role of competitive or social factors on carcass exploitation by scavengers (e.g., Wallace and Temple 1987; Heinrich 1988; Travaini et al. 1998). Recently, however, a few studies have investigated the proportion of carcasses consumed by a guild

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of scavengers or a certain species, as well as the environmental factors affecting the use of carrion (Bumann and Stauffer 2002; DeVault and Rhodes 2002; Selva et al. 2003; DeVault et al. 2004). Those studies have emphasized the role of habitat in segregating scavengers, or of ambient temperature as the main factor mediating competition among vertebrate scavengers and decomposers. In general, facultative scavenging by vertebrates is viewed as a mere opportunistic behaviour (see review in DeVault et al. 2003). An opportunistic scavenger would use all carcasses proportionally to their abundance in those patches where the scavenger forages (sensu Jaksić 1989). However, foraging decisions are likely a hierarchical process (Kaspari and Joern 1993). First, not all carcasses may be available to a given scavenger; then, the available carcasses may be subject to scavenger choice. According to optimal foraging theory, the choice may be related to energy maximization, especially in the highly seasonal environments of temperate and northern latitudes where winters are periods of hard conditions and prey scarcity and where carrion represents a key food resource (Jędrzejewska and Jędrzejewski 1998; Selva 2004*a*).

In undisturbed temperate forests, ungulates constitute the bulk of the carrion supply (Selva 2004*a*). Three main mortality factors make them available to scavengers. First, large predators subsidize scavengers constantly with the remains of their kills. Secondly, natural deaths supply scavengers with intact corpses in big pulses, usually at the end of the winter. Thirdly, human-caused mortality, mainly hunting, is nowadays an important carcass supplier in many areas (Wilmers et al. 2003*a*, 2003*b*; Selva 2004*a*). Not only the source of mortality but also the richness of the ungulate community contributes to the presence of several carcass types with distinct features.

We hypothesized that facultative scavenging is not a random process. Instead, we expected a differential use of the carcass types by some scavengers, depending on their foraging behaviour, habitat use, and the associated potential risks and benefits. Once a carcass type was potentially available, climatic conditions and carcass state may have governed its rate of use. Our main objective was to determine the extrinsic factors that affected the acquisition of carrion by vertebrate scavengers in a well-preserved temperate woodland (Białowieża Primeval Forest, eastern Poland), characterized by a rich community of vertebrates that include five ungulate and two large predator species. The specific goals were to (*i*) quantify carcass use by facultative scavengers, (*ii*) determine the influence of carcass features (species, origin, location) on carcass selection by scavengers, and (*iii*) assess the effects of environmental variables on carcass use.

Study area

Białowieża Primeval Forest (BPF, 1450 km^2) is located in the Polish–Belarussian borderland. It represents the best preserved woodland of its size, typical for the European lowland temperate forests. The study was conducted in the Polish part of BPF (600 km^2; 52°30′N–53°00′N, 23°30′E–24°15′E), which includes a protected area, the Białowieża National Park (100 km^2), and the commercially exploited forest (Fig. 1). The area is fairly flat (135–202 m above sea level), with small hills and shallow depressions, and is sparsely populated (2–3 people/km^2) (Jędrzejewska and

Jędrzejewski 1998). The most characteristic association is the oak–lime–hornbeam forest (*Quercus robur* L. – *Tilia cordata* Mill. – *Carpinus betulus* L., respectively). Norway spruce (*Picea abies* (L.) H. Karst) and Scots pine (*Pinus sylvestris* L.) dominate the coniferous forests, whereas European alder (*Alnus glutinosa* (L.) Gaertn.) and European ash (*Fraxinus excelsior* (L.)) cover wet areas. The open areas (about 5% of the Polish part of BPF) include river valleys, small clearings in the forest, and village glades (Fig. 1). Detailed information on the vegetation is given by Faliński (1986).

BPF is inhabited by a rich animal community. Ungulates are represented by five species: European bison (*Bison bonasus* (L., 1758)), moose (*Alces alces* (L., 1758)), red deer (*Cervus elaphus* L., 1758), western roe deer (*Capreolus capreolus* (L., 1758)), and wild boar (*Sus scrofa* L., 1758) (Jędrzejewska and Jędrzejewski 1998). Red deer, western roe deer, and boars are commercially hunted in the managed forest. The European bison population is kept stable by yearly culling in winter; some of the culled bison are exposed to scavengers. Forty species of raptors and carnivores, including the gray wolf (*Canis lupus* L., 1758) and the Eurasian lynx (*Lynx lynx* (L., 1758)), have been reported in BPF. Not all the predators are resident or active year round. Raccoon dogs (*Nyctereutes procyonoides* (Gray, 1834)), an exotic species, have long periods of inactivity in the cold season. Part of the common buzzard (*Buteo buteo* (L., 1758)) population migrate during winter, whereas white-tailed eagles (*Haliaeetus albicilla* (L., 1758)) are present in the forest exclusively in winter (Jędrzejewska and Jędrzejewski 1998).

The climate of BPF is transitional between continental and Atlantic types, although continental features prevail. The mean January and July temperatures during the study period (1997–2002) were –1.4 and 19.7 °C, respectively. The minimum recorded daily temperature was –21 °C and the maximum was 29 °C. Mean annual precipitation amounted to 578 mm. Snow cover persisted from 60 to 96 days, with an average of 74 days, and the maximum depth ranged 13–37 cm.
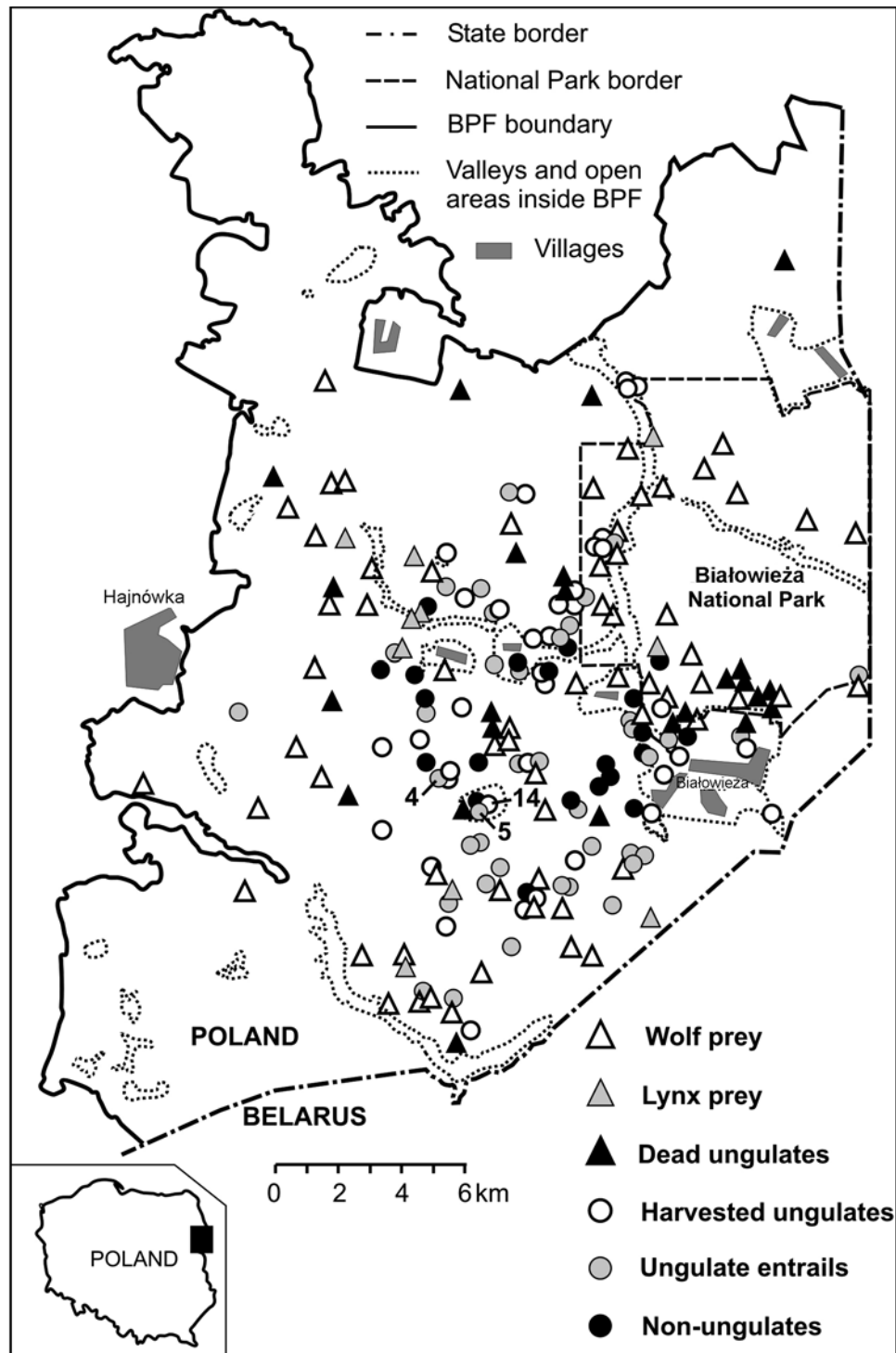
Material and methods

Monitoring of carcasses in the field

Fieldwork was conducted from December 1997 to April 2002. Information on ungulate carcasses was obtained from various sources. A parallel radiotracking study on gray wolves (Jędrzejewski et al. 2002) and snowtracking of gray wolves and Eurasian lynx provided most kills of large predators. Information on (potential) carcass locations was also obtained from foresters, hunters, rangers, local people, and scientific personnel working in BPF. Some carcasses of shot animals, or their entrails, were obtained from hunters and then they were exposed by us. When a carcass was located, we recorded the species, cause of death, time elapsed since death or exposition (days), and habitat characteristics.

A total of 214 carcasses (193 ungulate and 21 non-ungulates) were monitored during 1784 inspections (Fig. 1). Eighty percent of the carcasses were recovered within 3 days from the time of death or exposition. On average, each carcass was inspected 8 times, with a maximum of 47 inspec-

Fig. 1. Location of the study area and distribution of the monitored carcasses in 1997–2002. Numbers close to the symbols indicate the total number of carcasses monitored in approximately the same area if more than one.

tions of long-lasting carcasses and a minimum of 1 visit to quickly depleting carcasses. The mean (±SD) time interval between consecutive visits was 4.6 ± 7.9 days. Carcasses were more frequently inspected at the early stages of carcass depletion (daily or every 2nd day), whereas visits to old carcasses were repeated at longer time intervals. We tried to keep the time spent at carcasses short to minimize possible disturbance. During each inspection, we recorded the species

of bird and mammal that had visited the carcass on the basis of direct observations, tracks in the snow, and other signs such as scats, pellets, feathers, and droppings. The species present at carcasses were considered to have been scavenging on them. We collected all droppings of scavengers, and brushed the snow surface to clean up the tracks. In the snow-free periods, soil around the carcass was raked and sand, mud, or European bison faeces were spread around the car-

Table 1. Number of ungulate carcasses from various sources that were monitored during the study in the Białowieża Primeval Forest (BPF).

	Gray wolf kills	Eurasian lynx kills	Dead	Harvested	Total
Red deer, *Cervus elaphus*	59	4	2	10	75
Western roe deer, *Capreolus capreolus*	—	6	—	1	7
Moose, *Alces alces*	2	—	—	1	3
Wild boar, *Sus scrofa*	2	—	15	25	42
European bison, *Bison bonasus*	—	—	7	10	17
Livestock	—	—	—	3	3

Note: Entrails of ungulates and non-ungulate carcasses excluded.

cass to obtain the prints of the scavengers. We calculated the proportion of the carcass consumed based on the carcass mass measured during inspections, additional visual estimations, and reference body masses of ungulates (Jędrzejewska and Jędrzejewski 1998; Selva et al. 2003; Selva 2004*a*).

Monitored carcasses were divided into six categories according to their origin and type: (1) gray wolf kills, (2) Eurasian lynx kills, (3) dead ungulates, (4) harvested ungulates, (5) entrails of ungulates, and (6) non-ungulates. Gray wolf and Eurasian lynx kills referred to fresh kills from both predators, which usually consisted of remains. Gray wolf prey are large animals, mostly red deer (Table 1). Their remains are well visible in the snow, as they are spread around and the ground is often covered in blood. Gray wolves often revisit their old prey (Jędrzejewski et al. 2002; Selva 2004*a*). In contrast, Eurasian lynx feed on a kill for a few days, and they often guard and camouflage their prey against scavengers (Jędrzejewski et al. 1993*a*). Dead ungulates included intact carcasses of animals (mainly wild boar; Table 1) that had died from disease, starvation, or cold usually at concealed locations. Harvested animals included culled and hunted ungulates, which were subsequently abandoned or deliberately exposed. Most often they were whole-bodied, but usually not intact carcasses. The main hunting season in BPF is autumn and winter. In this category, we also included a few poached and drowned ungulates and road casualties. They were often exposed in small glades as bait for hunting purposes. The leftovers of hunted or culled animals were classified as entrails of ungulates. Non-ungulates refer mainly to dead carnivores. This group included seven raccoon dogs, six red foxes (*Vulpes vulpes* (L., 1758)), four domestic dogs, one Eurasian badger (*Meles meles* (L., 1758)), one gray wolf, one European hare (*Lepus europaeus* Pallas, 1778), and one domestic chicken.

The sample of monitored ungulate carcasses included 147 whole-bodied ungulates (i.e., excluding the entrails; Table 1). Only the most common species among carcasses (European bison, red deer, and wild boar; total $N = 134$) were used to test the effect of the ungulate species on scavenging frequencies. The habitat of the carcass locations was classified as open area or forest. Sixty-nine carcasses were located in open areas (glades, valleys, and clearcuts), whereas 145 were located in the forest.

Meteorological data were obtained from the Białowieża meteorological station, and included mean daily temperature (°C), mean daily snow cover (cm), and daily precipitation (mm) registered on the date of the inspections.

Analysis of carcass use

Two measures were employed to characterize the use of carcasses by scavengers: (1) the percentage of carcasses visited by a given scavenger species and (2) the scavenging frequency, defined as the mean percentage of positive inspections of carcasses (percentage of all inspections at a carcass with a given scavenger species recorded, averaged for all carcasses). The latter reflects how frequently the scavenger used the carcass in relation to the time that the carcass was potentially available (indirectly measured as the number of inspections by observers). Species that visited more than 10% of the monitored carcasses were considered the main scavengers. Gray wolf visits to their own kills were excluded from the analysis.

We used log-linear models (Quinn and Keough 2002; Manly et al. 2002) to analyse the effects of carcass characteristics (origin, species, and location) on the presence of the main scavengers at carcasses. Log-linear analysis is recommended over the logistic regression when all predictors are categorical (Quinn and Keough 2002). Because the influence of the ungulate species could be analysed only in a subset of the monitored carcasses (excluding ungulate entrails and non-ungulates), and because of the small sample size of some combined categories, we tested the effects of the carcass type (six categories), carcass location (two categories), and ungulate species (three categories) separately. We tested the significance of each effect by comparing the maximum-likelihood χ^2 value of the saturated model with that of the model without the interaction term. If the observed significance level for the change of the χ^2 value (partial χ^2) was small, then the hypothesis that the interaction term was zero was rejected, as this indicated that the model without the interaction did not fit well (Quinn and Keough 2002). The standardized residuals were checked for assessing the selection of categories. We did not apply the Bonferroni correction because it is considered unnecessarily conservative for an initial screening or exploration of potential relationships (Moran 2003; Roback and Askins 2005). The significance level α was set at 0.05.

The use of carcasses by scavengers might have varied throughout the process of carcass exploitation in relation to carcass state and environmental factors. We used generalized linear mixed models (GLMMs) to test the effects of weather conditions and the percentage of the carcass consumed on the presence of a scavenger species at a carcass (McCullagh and Nelder 1989). As several monitoring inspections were conducted for every carcass, the carcass number was fitted

Table 2. Carcass use by the main scavenger species recorded in BPF in 1997–2002.

Scavenger species	Percentage of carcasses scavenged upon ($N = 214$)	Scavenging frequency	
		Mean	SE
Common raven, *Corvus corax*	80.8	52.2	2.38
Red fox, *Vulpes vulpes*	71.0	32.5	2.02
Raccoon dog, *Nyctereutes procyonoides*	46.7	17.5	1.77
Jay, *Garrulus glandarius*	44.4	17.9	1.85
Common buzzard, *Buteo buteo*	38.8	12.5	1.43
Wild boar, *Sus scrofa*	37.4	9.1	1.19
Gray wolf, *Canis lupus**	33.3	10.1	1.43
European pine marten, *Martes martes*	27.6	9.0	1.25
White-tailed eagle, *Haliaeetus albicilla*	27.1	9.3	1.32
Great tit, *Parus major*	14.0	2.7	0.63
Domestic dog	11.7	3.3	0.77

Note: N is the number of monitored carcasses during the study and scavenging frequency was measured as the mean percentage of inspections with a scavenger recorded.

*Gray wolf visits to their own kills were excluded from the data ($N = 151$).

as a random factor in the GLMM. In this way, we controlled for a potentially important effect of the carcass on the presence of a given scavenger. Analyses were performed for each scavenger species and included only those carcasses that were visited at least once by that scavenger to avoid the inclusion of carcasses unavailable to the species as a result of their location or the time of the year. The presence of each scavenger species at a carcass was investigated using binomial errors and the logit link as a function of the percentage of the carcass consumed (rescaled in 10 categories from 0 to 9), mean daily temperature, snow cover, and precipitation (fixed effects). The statistical analyses were carried out using the macro GLIMMIX for SAS® version 8.02 (SAS Institute Inc. 1990).

Results

Scavenger species

All monitored carcasses were visited by scavengers. At least 36 species, including 22 birds and 14 mammals, were recorded using carcasses during the study. Table 2 ranks the main scavenger species according to the proportion of carcasses visited and their scavenging frequencies. Common ravens (*Corvus corax* L., 1758) and red foxes were the ultimate scavengers, present in more than 70% of the carcasses. Frequent scavengers (30%–70% of the carcasses scavenged upon) were the raccoon dog and the jay (*Garrulus glandarius* (L., 1758)), both with similar scavenging frequencies. The less frequent avian and mammalian scavengers (10%–30% carcasses scavenged upon) were the great tits (*Parus major* L., 1758) and domestic free-ranging dogs, respectively (Table 2).

Minor scavengers, which visited 1%–10% of the carcasses, included micro-mammals (mice and shrews), black-billed magpie (*Pica pica* (L., 1758)), Eurasian badger, northern goshawk (*Accipiter gentilis* (L., 1758)), Eurasian lynx, European polecat (*Mustela putorius* L., 1758), hooded crow (*Corvus corone* L., 1758), golden eagle (*Aquila chrysaetos* (L., 1758)), and least weasel (*Mustela nivalis* L., 1766). Sporadic scavengers, present at less than 1% of the monitored carcasses, included Eurasian red squirrels (*Sciurus*

vulgaris L., 1758), sparrowhawks (*Accipiter nisus* (L., 1758)), ermine (*Mustela erminea* L., 1758), lesser-spotted eagles (*Aquila pomarina* Brehm, 1831), great-spotted woodpeckers (*Dendrocopos major* (L., 1758)), and several species of small passerines, mainly tits (Paridae). Because of a lack of snow and (or) unclear signs, we were not able to accurately identify the species in 2% of the inspections.

Use of carcass types by main scavengers

Carcass characteristics were an important factor affecting scavenging by most species, and the proportion of carcasses visited by the main scavengers varied in relation to carcass features (Table 3). Carcass origin (killed by predators, dead, or harvested) significantly affected the scavenging of six species (Table 4). Red foxes most often used gray wolf kills and European pine martens (*Martes martes* (L., 1758)) selected kills of large predators (Table 3). The effect of the carcass origin was also significant for common ravens, which most frequently scavenged on gray wolf kills but rarely on dead ungulates. The common buzzard and white-tailed eagle scavenged often on harvested ungulates but rarely visited dead ungulates. Although non-significant, domestic dogs avoided gray wolf kills, and together with great tits, tended to be more frequent at harvested carrion. In general, dead ungulates were used by all scavengers less often than other carcasses. Gray wolves avoided entrails and non-ungulate carcasses. All mammalian scavengers, with the exception of the raccoon dog, avoided non-ungulate carcasses (Table 3).

The interaction between the habitat of carcass location and the presence of scavenger species was highly significant for European pine martens, wild boar, domestic dogs, common ravens, jays, and the two raptor species (Table 4). The European pine marten, jay, and wild boar avoided carcasses located in open areas, whereas common buzzards, white-tailed eagles, common ravens, and domestic dogs showed an opposite pattern (Table 3). The ungulate species had the least important influence on the carcass use by scavengers. It significantly affected only gray wolves and wild boar (Table 4). The wild boar strongly avoided scavenging on

Table 3. Percentage of carcasses from each category visited by the main scavenger species in BPF.

Scavenger species	Carcass origin				Entrails of ungulates	Non-ungulate	Carcass location		Carcass species		
	Gray wolf kills	Eurasian lynx kills	Dead	Harvested			Open	Forest	European bison	Red deer	Wild boar
Common raven	90.5	70.0	62.5	86.0	73.9	81.0	91.3	75.9	88.2	88.0	78.6
Jay	39.7	80.0	33.3	44.0	50.0	42.9	31.9	50.3	29.4	48.0	38.1
Common buzzard	33.3	30.0	20.8	60.0	28.3	52.4	65.2	26.2	58.8	36.0	38.1
White-tailed eagle	25.4	30.0	8.3	46.0	19.6	23.8	47.8	17.2	52.9	30.7	26.2
Great tit	11.1	20.0	12.5	26.0	4.3	14.3	11.6	15.2	23.5	16.0	14.3
Red fox	87.3	60.0	83.3	80.0	54.3	28.6	73.9	69.7	76.5	88.0	85.7
Raccoon dog	41.3	60.0	37.5	60.0	37.0	57.1	40.6	49.7	41.2	44.0	54.8
European pine marten	41.3	50.0	25.0	26.0	13.0	14.3	2.9	39.3	17.6	41.3	26.2
Wild boar	42.9	60.0	25.0	42.0	30.4	28.6	26.1	42.8	58.8	50.7	16.7
Gray wolf	—	20.0	45.8	54.0	17.4	9.5	38.3	29.7	94.1	40.0	32.5
Domestic dog	6.3	20.0	12.5	22.0	10.9	0	23.2	6.2	23.5	8.0	16.7
Number of carcasses	63	10	24	50	46	21	69 (60)	145 (91)	17 (17)	75 (15)	42 (20)

Note: Number of carcasses scavenged by gray wolves (i.e., their own kills excluded) are in parentheses.

conspecifics, whereas gray wolves showed a strong preference for carcasses of European bison (Table 3).

Influence of weather conditions and carcass consumption

GLMM analyses showed a significant random effect of the carcass on the presence of all scavengers ($p < 0.03$ for all species). After having controlled for this effect, we showed a number of fixed effects that significantly influenced carcass attendance by some scavengers (Table 5). The mean daily temperature was the most important climatic factor influencing the use of carcasses. It significantly affected the scavenging of five species: common raven, jay, red fox, raccoon dog, and European pine marten (Table 5). The general tendency was to increase scavenging at lower temperatures, especially by red fox, European pine marten, and jay (Table 5, Fig. 2). Carcass use by common ravens peaked at temperatures around 0 °C (Fig. 2). The opposite pattern was found in raccoon dogs, which visited carcasses more often on warm days.

The effect of snow cover on the probability of scavenging was significant for the three passerine species (common ravens, jays, tits) and the raccoon dog (Table 5). As the snow cover deepened, jays and great tits increased their feeding frequency on carcasses (Table 5, Fig. 3). However, scavenging by common ravens and buzzards was less frequent at the deepest snow cover. The raccoon dog was the only species that scavenged most in the absence of snow (Fig. 3). The proportion of the carcass consumed significantly affected scavenging by all the species, except for the jay, great tit, and common buzzard. Common ravens and white-tailed eagles were more likely to be present at a carcass when only a few parts had been removed, whereas all mammalian scavengers tended to visit carcasses that had been already more consumed. Precipitation significantly affected the European pine marten and wild boar. Both species decreased their scavenging when it was raining or snowing (Table 5).

Discussion

Environmental factors

In a well-preserved, temperate forest of Europe, the guild of vertebrates using carcasses appeared very rich in species, which supports the prevalence of facultative scavenging. Previous diet studies also have shown that ungulate carcasses constituted an important food resource to some predators during the cold season (Jędrzejewska and Jędrzejewski 1998). Furthermore, the consumption of carcasses in BPF increased as winter progressed and other food resources became scarcer (Selva et al. 2003). As evidenced by our study, other factors also mediate the use of carcasses by facultative scavengers. The availability of carrion to vertebrate scavengers in northern climates was affected by carcass characteristics and weather conditions, and some scavengers were selective towards those factors. Vertebrates used carcasses mainly during the cold season, thus supporting the view that temperature is a main factor regulating carrion acquisition between scavengers and decomposers (DeVault et al. 2004).

Weather conditions affected scavenging by birds and mammals via the changes in their energetic requirements, availability of other food resources, and availability of carcasses. At cold temperatures, European pine martens, which

Table 4. Effects of carcass characteristics (origin, location, species) on carcass use by the main scavengers shown by log-linear analyses (see Table 3 for descriptions of carcass origin, location, and species).

Scavenger species	Carcass origin		Carcass location		Carcass species	
	Partial χ^2 (df = 5)	p	Partial χ^2 (df = 1)	p	Partial χ^2 (df = 2)	p
Common raven	11.84	0.037	7.56	0.006	1.88	—
Jay	7.22	—	6.46	0.011	2.33	—
Common buzzard	17.07	0.004	29.59	<0.001	2.97	—
White-tailed eagle	14.24	0.014	21.15	<0.001	3.90	—
Great tit	9.95	0.077	0.42	—	0.86	—
Red fox	35.09	<0.001	0.38	—	1.61	—
Raccoon dog	8.31	—	1.53	—	1.48	—
European pine marten	14.93	0.011	37.91	<0.001	4.74	0.093
Wild boar	6.37	—	5.58	0.018	16.10	<0.001
Gray wolf*	22.59	<0.001	1.22	—	20.02	<0.001
Domestic dog	9.96	0.076	12.10	<0.001	4.02	0.134

Note: Dashes represent p values >0.1, which are absent from the table.

*Gray wolf visits to their own kills were excluded from the analyses. The df value is 4 for the effect of carcass origin on gray wolf scavenging.

Table 5. Effects of weather conditions (i.e., mean daily temperature (°C), snow cover (cm), and precipitation (mm)) and the portion of carcass consumed on the presence of the main scavenger species at carcasses.

Scavenger species	N*	Fixed effect	Parameter estimate	SE	Type III tests	
					χ^2	p
Common raven	1589	Intercept	1.489	0.161		
		Mean temperature	−0.044	0.011	17.39	<0.0001
		Snow cover	−0.047	0.013	12.50	0.0004
		Precipitation	−0.017	0.023	0.51	—
		Portion of carcass consumed	−0.126	0.021	37.82	<0.0001
Jay	1008	Intercept	−0.967	0.196		
		Mean temperature	−0.030	0.015	3.90	0.048
		Snow cover	0.064	0.015	18.75	<0.0001
		Precipitation	0.009	0.033	0.07	—
		Portion of carcass consumed	0.004	0.026	0.03	—
Common buzzard	944	Intercept	−1.057	0.196		
		Mean temperature	−0.009	0.015	0.31	—
		Snow cover	−0.034	0.019	3.26	0.071
		Precipitation	0.010	0.034	0.08	—
		Portion of carcass consumed	0.024	0.028	0.75	—
White-tailed eagle	746	Intercept	−0.146	0.209		
		Mean temperature	0.007	0.018	0.15	—
		Snow cover	−0.006	0.018	0.12	—
		Precipitation	−0.087	0.047	3.50	0.061
		Portion of carcass consumed	−0.142	0.031	21.12	<0.0001
Great tit	542	Intercept	−2.322	0.337		
		Mean temperature	0.025	0.020	1.49	—
		Snow cover	0.115	0.024	23.53	<0.0001
		Precipitation	−0.042	0.048	0.77	—
		Portion of carcass consumed	0.075	0.044	2.87	0.09
Red fox	1515	Intercept	−0.682	0.139		
		Mean temperature	−0.062	0.010	37.46	<0.0001
		Snow cover	−0.006	0.013	0.23	—
		Precipitation	−0.023	0.024	0.93	—
		Portion of carcass consumed	0.082	0.020	17.38	<0.0001

Table 5 (*concluded*).

Scavenger species	N*	Fixed effect	Parameter estimate	SE	Type III tests χ^2	Type III tests p
Raccoon dog	1067	Intercept	−1.079	0.196		
		Mean temperature	0.047	0.013	12.22	0.0005
		Snow cover	−0.099	0.020	25.53	<0.0001
		Precipitation	−0.045	0.030	2.23	—
		Portion of carcass consumed	0.103	0.026	15.55	<0.0001
European pine marten	671	Intercept	−1.991	0.273		
		Mean temperature	−0.084	0.017	23.92	<0.0001
		Snow cover	0.010	0.020	0.26	—
		Precipitation	−0.116	0.049	5.54	0.019
		Portion of carcass consumed	0.201	0.037	29.57	<0.0001
Wild boar	955	Intercept	−2.525	0.260		
		Mean temperature	0.016	0.016	1.08	—
		Snow cover	0.024	0.021	1.29	—
		Precipitation	−0.159	0.059	7.35	0.007
		Portion of carcass consumed	0.172	0.036	22.73	<0.0001
Gray wolf	718	Intercept	−2.286	0.281		
		Mean temperature	−0.016	0.017	0.85	—
		Snow cover	−0.024	0.022	1.11	—
		Precipitation	−0.062	0.043	2.13	—
		Portion of carcass consumed	0.231	0.039	35.78	<0.0001
Domestic dog	326	Intercept	−1.891	0.407		
		Mean temperature	0.005	0.028	0.03	—
		Snow cover	0.060	0.031	3.81	0.051
		Precipitation	−0.172	0.100	2.96	0.085
		Portion of carcass consumed	0.132	0.059	4.98	0.026

Note: Generalized linear mixed models were fitted using a binomial error distribution and a logit-link function. Dashes represent p values >0.1, which are absent from the table. Type III tests df = 1.

*The number of inspections to carcasses that were visited by a given scavenger at least once.

suffer from thermal stress, reduce their activity and stay in well-insulated sites, close to an ungulate carcass where they can frequently feed (Zalewski 1997, 2000). The long inactivity of raccoon dogs during the cold season explains their low frequency of visits to carcasses at low temperatures. However, in their short active periods during winter, they rely nearly exclusively on ungulate carcasses as shown in other diet studies (Jędrzejewska and Jędrzejewski 1998). In contrast to raccoon dogs, the red fox increased scavenging at lower temperatures, probably because of a higher activity during cold weather (Ables 1969). Coyotes (*Canis latrans* Say, 1823) in Yellowstone also spent more time feeding on carcasses as the minimum temperature decreased (Gese et al. 1996). Avian scavengers may switch to meat, a more energetically rewarding food, at low temperatures as did the jays in our study.

During the deepest snow cover large birds decreased scavenging, but the smaller species increased their use of carcasses. This may be partly explained by better access to carcasses by small birds in the absence of larger dominant species, and the difficulties in remembering the exact place of the covered carcass remains. Jays were the only species recorded recovering carcass parts under very deep snow. Scavenging by carnivores may be influenced by the energetic cost of moving in deep snow as shown for European pine martens (Zalewski et al. 1995), coyotes (Gese et al. 1996), and gray wolves (Huggard 1993). Finally, snow cover may affect scavenging in relation to the availability of other

food resources such as rodents (Sonerud 1986; Gese et al. 1996) or seeds.

Habitat type was a main factor determining the availability of carcasses to scavengers, and scavengers used more frequently those carcasses located in their foraging habitat. For instance, it is well known that European pine martens avoid clearcuts and open areas (e.g., Brainerd and Rolstad 2002), so they could potentially scavenge only on carcasses located in the forest. Free-ranging domestic dogs tended to scavenge in open habitats, which are more associated with human presence (e.g., villages and hunting glades). In other areas, the habitat type segregated sympatric species of scavengers, such as vultures or bears (Houston 1988; Lemon 1991; Green et al. 1997). In BPF, common raven flocks were more frequent at European bison carcasses located in open areas, whereas carcasses in the forest were exclusively exploited by territorial pairs (Selva et al. 2003). This may explain the higher frequency of common ravens observed in openings. Some species, which are habitat generalists, can scavenge more intensively in certain habitat types as shown for red foxes and coyotes (Jędrzejewski and Jędrzejewska 1992; Gese et al. 1996).

Adaptations and behavioural mechanisms of scavengers

The adaptations and abilities of scavengers to locate and exploit carrion may also determine the availability and subsequent use of carcass types by scavengers; specifically, (*i*) their capacity to break into carcasses, (*ii*) their visual and

Fig. 2. Frequency of visits by scavengers to carcasses in relation to the mean daily temperature for the scavengers significantly affected (see Table 5). N is the number of monitoring inspections conducted within each temperature class.
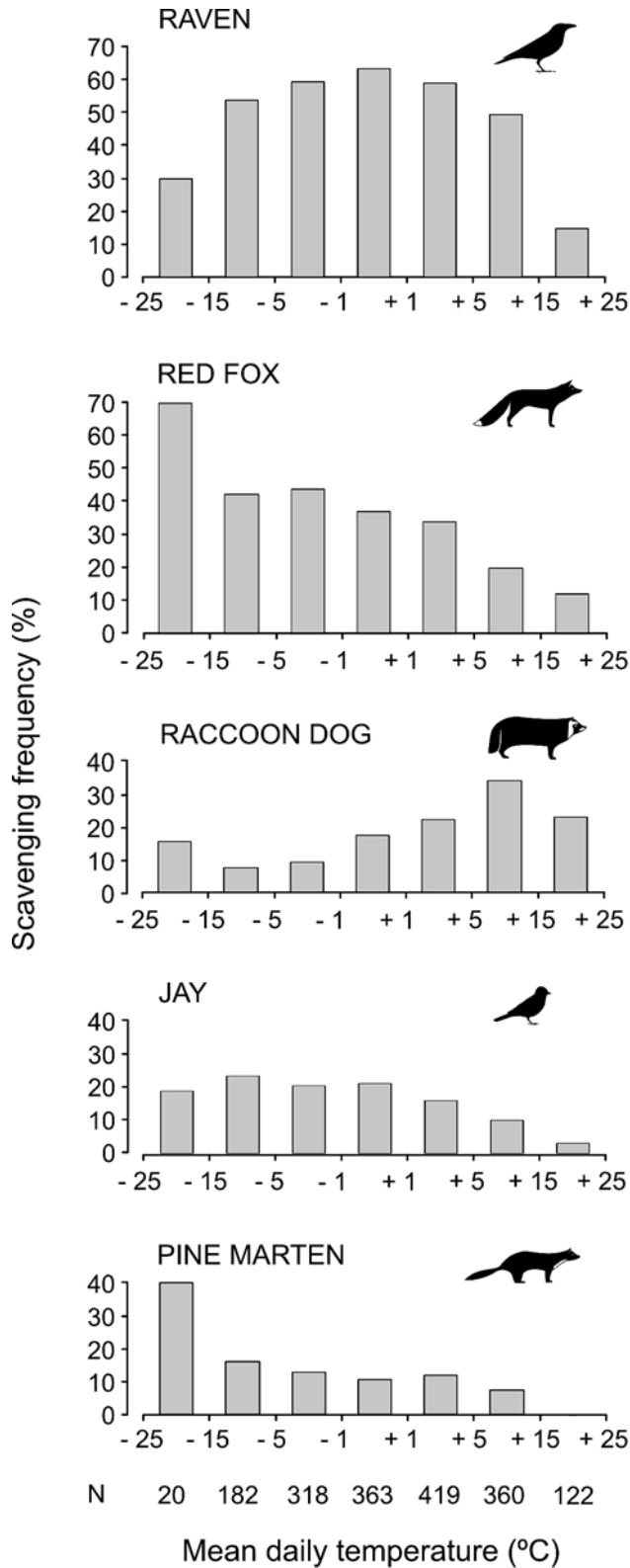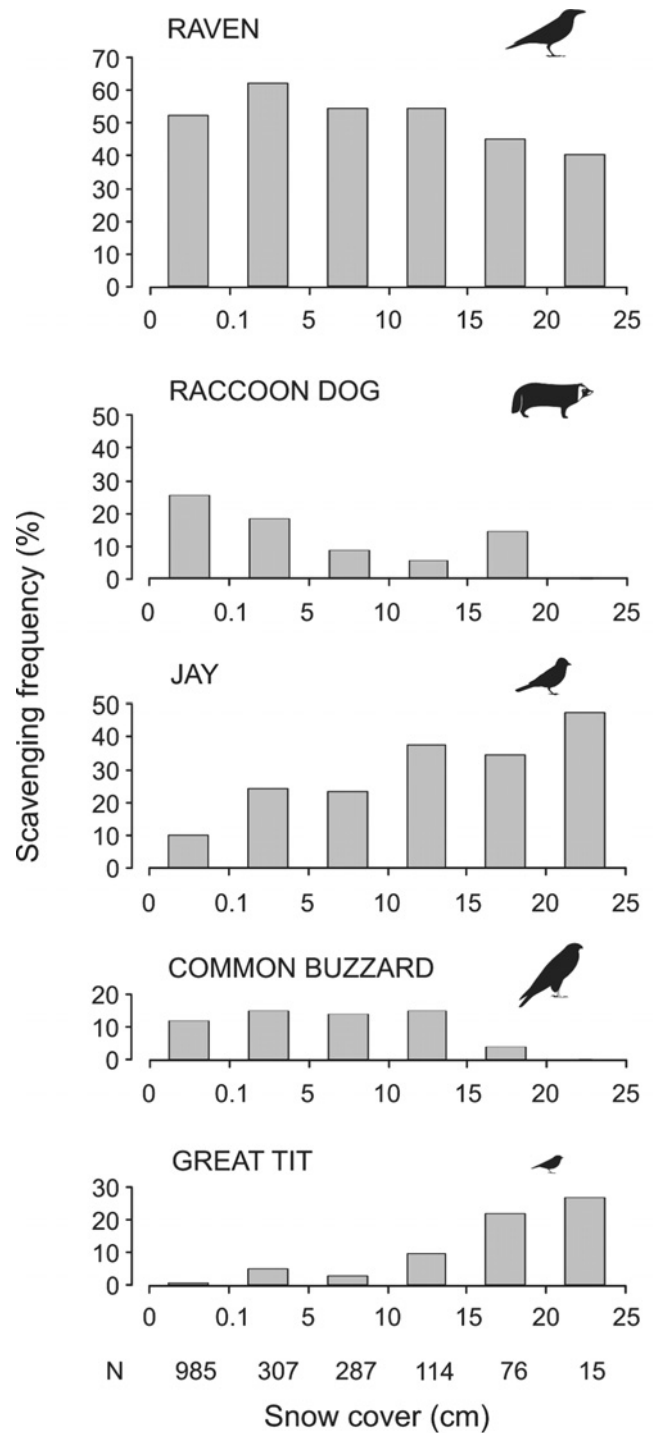
Fig. 3. Frequency of visits by scavengers in relation to snow cover for the scavengers significantly affected (see Table 5). N is the number of monitoring inspections conducted within each snow-cover class.

olfactory abilities, and (*iii*) their foraging behaviour. Opposite to the kills of predators, the corpses of dead ungulates must be first opened, and some scavenger species may be unable to break into intact carcasses, especially when they are deeply frozen. In BPF, gray wolves were the only species able to open dead European bison, thus facilitating access to the carcass by the other members of the scavenging guild (Selva et al. 2003). Olfactory signals may play a great role in carcass discovery, especially at warmer temperatures (Houston 1986; DeVault and Rhodes 2002). All mammalian scavengers, guided mainly by olfactory cues, were more frequent at older and more depleted carcasses in BPF.

Avian scavengers are better adapted than mammals to locate carrion (Houston 1979; Ruxton and Houston 2004). Common ravens are extremely efficient in locating carcasses (Stahler et al. 2002; Selva 2004*a*, 2004*b*). Common ravens and white-tailed eagles, relying on eye-sight when searching for food, were more likely to be present at fresh carcasses and at carcasses located in openings, which are more visible. In Yellowstone, common ravens and eagles were the main consumers of hunter kills (Wilmers et al. 2003*a*). Hunter kills were more aggregated in time and space than predator kills, and could be more quickly located by species with large foraging areas. Also in BPF, raptors were most frequent at the carcasses of harvested animals, which were often placed at hunting glades (Selva et al. 2003).

Scavengers selected carcasses according to their origin, mainly in relation to the risks of disease transmission and predation. Dead ungulates were generally avoided, as scavenging on them may be an important means of acquiring infectious diseases (Ragg et al. 2000). This explains why wild boar, often suffering from illness, avoided feeding on conspecifics, and most mammals rejected non-ungulate (mainly carnivore) carcasses. The raccoon dog was an exception, and its cannibalism also occurred in other areas (Kauhala et al. 1993). In Norway, scavengers were documented rejecting a diseased reindeer calf, but scavenging intensively on a "healthy" carcass nearby (Mysterud et al. 1993). The kills of predators were the most attractive carcass type despite the associated risk from the host predator. Therefore, our study confirmed the important role of large predators in subsidizing scavengers, which has been suggested in other studies (Wilmers et al. 2003*b*). Domestic dogs and raccoon dogs are the guild members more frequently killed by gray wolves (Jędrzejewska and Jędrzejewski 1998; N. Selva, personal observations). However, predation risk may be lower at gray wolf prey, which tend to be left unattended once the pack is satiated. Thus, gray wolf kills were preferred by more species. In contrast, Eurasian lynxes, which often guard their prey, sometimes will kill red foxes and European pine martens (Jędrzejewska and Jędrzejewski 1998; Linnell et al. 1998; Palomares and Caro 1999). Therefore, red foxes used Eurasian lynx prey only after the Eurasian lynx had abandoned it (Jobin et al. 2000). European pine martens, which can escape arboreally, dared to use Eurasian lynx kills with certain frequency. Previous studies in BPF have also found that European pine martens preferred to feed on the remains of gray wolf and Eurasian lynx prey (Jędrzejewski et al. 1993*b*).

The observed scavenging patterns may also be a consequence of the spatiotemporal availability of different carcass types. Kills of large predators are a constant resource, so behavioural mechanisms to locate and optimally use that food could have evolved in some facultative scavengers. On the contrary, in highly seasonal northern climates, the unpredictability and pulsed nature of the natural deaths would have prevented the appearance of evolutionary adaptations to exploit efficiently this resource. Our data support this hypothesis; none of the species were associated with dead animals, whereas several species selected the kills of large predators. Scavengers have often been reported to follow large predators (Kruuk 1972; Paquet 1992); in particular common ravens, which strongly associate with gray wolves as a winter foraging strategy (Stahler et al. 2002). Red foxes actively follow gray wolf trails, but also inspect wild boar lairs where sick or starving animals may perish (Jędrzejewski and Jędrzejewska 1992). The lower utilization of dead ungulates in relation to other carcass types might also be related to the fact that scavengers cannot cope with the sudden surplus of carcasses at a particular time (Houston 1978; Selva 2004*a*).

In conclusion, carcass use by facultative scavengers in a natural temperate forest was not random. It was a prevalent and complex process determined by both extrinsic factors, as also shown by other studies (Bumann and Stauffer 2002; DeVault et al. 2004), and behavioural adaptations of the scavengers. The traditional concept of facultative scavenging as sheer opportunism may be misleading. Under the hard conditions of cold climates, scavenging might be the only opportunity for a species to survive. This study represents a first contribution to elucidate whether facultative scavenging is just an opportunistic behaviour or an optimal foraging strategy in a variable environment. Further research is needed on this topic to advance our understanding of the role of carrion in northern ecosystems and the underlying mechanisms for its exploitation.

Acknowledgements

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