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# Scavenging on European bison carcasses in Bialowieza Primeval Forest (eastern Poland)[1]

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*Abstract*: We investigated the utilization of European bison, *Bison bonasus*, carcasses by the scavenging guild in Bialowieza Primeval Forest (eastern Poland) during 1997-2001. Twelve carcasses were monitored in systematic visits till total depletion ($N$=303). Thirteen species of birds and mammals utilized bison carcasses. Most frequent scavengers and their mean scavenging frequencies (mean percentage of visits to each carcass with a given scavenger species recorded) were raven, *Corvus corax*, 72%; red fox, *Vulpes vulpes*, 41%; wolf, *Canis lupus*, 29%; common buzzard, *Buteo buteo*, 23%; raccoon dog, *Nyctereutes procyonoides*, 20%; and white-tailed eagle, *Haliaeetus albicilla*, 16%. Ravens and white-tailed eagles were observed significantly more often at carcasses placed in clearings than at those exposed in the forest. The opposite was recorded for raccoon dogs. Manifest habitat segregation was also found for flocks of immature ravens and territorial pairs. Wolves had an important facilitation effect for other species and triggered their scavenging activity. Bison carcasses were utilized for an average of 106 ± 61 days (mean ± SD), to over 80% of live weight consumed. The estimated mean daily consumption by all scavengers was 3 kg day$^{-1}$ (range 0-68), being highest during the first 2 weeks (6.8 ± 6.2 kg day$^{-1}$). The utilization time of bison carcasses depended on the index of carcass openness, the number of wolf feeding visits to the carcass, the date of carcass exposure, and the habitat type (forest versus open clearings). Ambient temperature had a significant effect on the rate of carcass depletion, while the effects of snow cover and precipitation were negligible.
*Keywords*: bison carcasses, *Canis lupus*, carcass utilization, carrion consumption, *Corvus corax,* habitat segregation, scavengers, temperate forests.

*Résumé* : Nous avons étudié l'utilisation des carcasses du bison européen *Bison bonasus* par les animaux charognards à la Forêt Vierge de Bialowieza, en Pologne de l'Est, de 1997 à 2001. Nous avons suivi 12 carcasses jusqu'à ce qu'elles soient complètement consommées au cours de visites systématiques ($N$=303). Treize espèces d'oiseaux et de mammifères ont utilisé les carcasses de bison. Parmi celles-ci, les plus fréquentes étaient (ainsi que le pourcentage moyen de visites à chaque carcasse selon l'espèce) : le corbeau *Corvus corax* (72 %), le renard roux *Vulpes vulpes* (41 %), le loup *Canis lupus* (29 %), la buse variable *Buteo buteo* (23 %), le chien viverrin *Nyctereutes procyonoides* (20 %) et le pygargue à queue blanche *Haliaeetus albicilla* (16 %). Les corbeaux et les pygargues à queue blanche ont été observés plus souvent aux carcasses placées dans les clairières qu'à celles situées dans les forêts. Le contraire a été observé chez les chiens viverrins. Nous avons également remarqué une ségrégation des habitats chez les corbeaux, entre les individus immatures et les couples territoriaux. Les loups ont un rôle important en facilitant le travail des autres espèces nécrophages et en incitant ces dernières à entreprendre leurs activités de charognards. Les carcasses de bison étaient utilisées en moyenne pendant 106 ± 61 jours (moyenne ± écart type) pour plus de 80 % du poids de l'animal vivant consommé. En moyenne, chaque jour, les charognards consommaient 3 kg (de 0 à 68 kg) de nourriture sur les carcasses. C'est pendant les deux premières semaines que cette consommation était la plus élevée (6,8 ± 6,2 kg jour$^{-1}$). Le temps d'utilisation des carcasses de bison dépendait du degré d'ouverture de la carcasse, du nombre de visites de loups se nourrissant des carcasses, de la date d'exposition de la carcasse et du type d'habitat (forêt ou clairière). La température ambiante a eu un effet significatif sur le taux de consommation des carcasses. Le couvert nival et les précipitations ont eu des effets négligeables.
*Mots-clés* : *Canis lupus*, carcasses de bison, charognards (nécrophages), consommation de charogne, *Corvus corax,* forêts tempérées, ségrégation des habitats, utilisation de carcasses.

*Nomenclature*: Honacki, Kinman & Koeppl, 1982; Mirek *et al.*, 1995, Mielczarek & Cichocki, 1999.

## Introduction

Although scavenging is a widespread phenomenon in vertebrate animal communities and indeed almost all predators are scavengers to a certain extent, this process has received comparatively little attention in the temperate zone. Most studies were carried out in Africa (Attwell, 1963; Kruuk, 1967; 1972; Schaller, 1972; Houston, 1974; 1975; Anderson & Horwitz, 1979; Richardson, 1980), Southern Europe (Alvarez, Arias de Reyna & Hiraldo, 1976; Hiraldo, Blanco & Bustamante, 1991), and Central and South America (Hernández *et al.,* 1987; Wallace & Temple, 1987; Houston, 1988; Gómez *et al.,* 1994; Travaini *et al.,* 1998), where obligate scavenger species and specialized scavenging guilds exist. Most investigations were focused on avian scavengers or dealt with scavenging as yet another aspect of the ecology of a mammalian predator species.

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In the temperate regions of the Northern Hemisphere, the scavenging guild is less specialized and there are no obligate scavengers, although numerous birds and mammals rely on carcasses during critical periods, *e.g.,* pine marten, *Martes martes* (Jedrzejewski, Zalewski & Jedrzejewska, 1993; Zalewski, 2000), red fox, *Vulpes vulpes* (Cederlund & Lindström, 1983; Jedrzejewski & Jedrzejewska, 1992), raccoon dog, *Nyctereutes procyonoides* (Jedrzejewska & Jedrzejewski, 1998), rough-legged hawk, *Buteo lagopus* (Watson, 1986), raven, *Corvus corax* (Newton, Davis & Davis, 1982; Ratcliffe, 1997), and bears, *Ursus arctos* (Green, Mattson & Peek, 1997). In those cold climate regions, ungulate carcasses are essential as an alternative food supply when the basic prey is unavailable (Houston, 1978; Jedrzejewska & Jedrzejewski, 1998; Sidorovich *et al.,* 2000). Carcass availability can increase the breeding density of scavenging animals (Angerbjörn *et al.,* 1991; Watson, Rae & Stillman, 1992), improve their survival rate (Tannerfeldt, Angerbjörn & ArvidSon, 1994; Helander, 1985), and ensure a stable adult population (Terrasse, 1985; Brown, 1990).

Scavenging assemblages have been described for different types of carcasses: rabbits, *Oryctolagus cuniculus* (Hewson, 1981), hares, *Lepus europaeus* (Travaini *et al.,* 1998), wintering geese, *Anser anser* (Hiraldo, Blanco & Bustamante, 1991), and spawning salmon, *Salmo salar*, and *Oncorhyncus* spp. (Skagen, Knight & Orians, 1991; Hewson, 1995). A few studies have dealt with scavenging guilds on large ungulate carcasses: moose, *Alces alces*, and caribou, *Rangifer tarandus* (Magoun, 1976), livestock (Wallace & Temple, 1987), and several African ungulate species (Kruuk, 1967; Schaller, 1972).

This paper presents a part of a general study on scavenging in Bialowieza Primeval Forest (eastern Poland), one of the last remnants of lowland temperate forests in Europe. The main suppliers of carcasses in such forests had been ungulates, ranging in size from roe deer, *Capreolus capreolus*, to the continent's largest terrestrial mammal, the European bison, *Bison bonasus*. The general study is focused on quantifying the supply of carcasses of different origin (wolf and lynx kills, dead animals) and the pattern of their use by various species of vertebrates. The aim of this project was to investigate the utilization of bison carcasses by scavengers and, in particular, to *i*) determine the main scavenger species of birds and mammals, *ii*) assess the rate of carcass consumption by scavengers, and *iii*) quantify the factors affecting variation in the carcass utilization rates.

## Methods

### STUDY AREA

Bialowieza Primeval Forest (BPF, *ca* 1,450 km$^2$), located in the Polish-Belarussian borderland, is one of the best preserved forest ecosystems in lowland temperate Europe. The study was conducted in the Polish part of BPF (52° 30´- 53° N, 23° 30´- 24°15´ E, *ca* 600 km$^2$), which includes Bialowieza National Park (100 km$^2$) and the commercial, exploited forest. Tree stands of BPF are dominated by oak, *Quercus robur*; hornbeam, *Carpinus betulus*; black alder, *Alnus glutinosa*; spruce, *Picea abies*; and pine, *Pinus silvestris*. Open areas (glades and meadows) cover 4% of the Polish part of BPF. Detailed information on vegetation is given by Falinski (1986).

The climate of BPF is transitional between continental and Atlantic types, with clearly marked cold (1 November-31 March) and warm seasons. The mean January and July temperatures during the study period (winter 1997/98 to spring 2001) were -1.2°C and 19.7°C, respectively. The minimum recorded daily temperature was -21°C and the maximum was 28.8°C. Mean annual precipitation amounted to 578 mm. Snow cover persisted from 60 to 96 days, on average 77 days, with a maximal depth of 23 cm.

The ungulate community in BPF consists of European bison; moose; red deer, *Cervus elaphus*; roe deer; and wild boar, *Sus scrofa*. Large predators include the lynx, *Lynx lynx*, and the wolf, *Canis lupus*. More information on the vertebrate communities is provided by Jedrzejewska and Jedrzejewski (1998). Currently the Polish part of BPF harbours 250-310 free-living bison (density 0.4-0.5 individuals km$^{-2}$), and the population is kept stable by yearly culling. Bison culling (about 10% of the population) takes place in winter when they gather at the supplementary feeding places, where hay is provided (Krasinska & Krasinski, 2000). Every year, some of the culled bison are exposed by rangers, usually in the same places. The history of protection, extinction, and restitution of European bison in BPF is described by Pucek (1991). The natural mortality of free-living bison is low, on average 3% (Krasinski, Krasinska & Bunevich, 1999). European bison fall prey to wolves only in exceptionally rare cases (Krasinski, Bunevich & Krasinska, 1994; Okarma *et al.,* 1995; Jedrzejewski *et al.,* 2002).

### MONITORING OF BISON CARCASSES

From winter 1997/98 to spring 2001, the utilization of 12 bison carcasses by scavengers was monitored. The monitoring was conducted mainly during the cold season, when most bison carcasses ($N=11$) were available (Table I). Half of the monitored carcasses were of culled and deliberately exposed bison, 4 bison had died from natural causes (probably disease), one was a road casualty, and one was a victim of poaching. The monitoring was done by systematic visits to each carcass. A total of 303 visits to bison carcasses were conducted. The mean time interval between consecutive visits, which continued until carcasses were more than 80% consumed, was 3.7 ± 4.6 days (mean ± SD). Carcasses were more frequently monitored at the early stages of carcass depletion. Researchers' visits to carcasses were short (about 10 min) to minimize possible disturbance. On average, each carcass was visited 27 times during the cold season, with a maximum of 47 inspections to long-lasting carcasses and a minimum of 5 visits to a carcass monitored in summer.

In each inspection, we recorded the species of birds and mammals that had visited the carcass, based on direct observations, tracks in the snow, and other signs (feathers, scats, pellets, calls). During each visit, an observer collected all droppings of scavengers and smoothed the snow surface or sand around the carcass. A species was considered as present if it was seen or any signs of it were recorded at the carcass. A species was also consid-

TABLE I. Characteristics of monitored carcasses of European bison and their utilization by scavengers to at least 80% of the bison body mass, consumed in Bialowieza Primeval Forest, 1997-2001. M=male, F=female, O=open glades, F=forest. Index of carcass openness represents the total number of the following parts exposed to scavengers: a) neck, b) organs and entrails, c) upper flank, d) back side. An index of 5 indicates a completely skinned animal with all the above listed parts exposed.

| | | | | | | | | Utilization by scavengers to >80% carcass depletion | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Carcass number | Sex | Age (years) | Date of exposure | Habitat | Index of carcass openness | Estimated live body mass of bison (kg) | Mass exposed to scavengers (kg) | Total biomass consumed (kg) | Consumption as percent of the exposed carcass | Time to >80% of biomass consumed (days) |
| 1 | M | 4 | 1997-12-02 | O | 3 | 366 | 331 | 282 | 85 | 149 |
| 2 | M | 8 | 1997-12-21 | O | 5 | 700 | 455 | 407 | 89 | 86 |
| 3 | M | 10 | 1997-12-18 | F | 2 | 634 | 539 | 500 | 93 | 239 |
| 4 | M | 17 | 1998-02-02 | O | 3 | 634 | 558 | 463 | 83 | 77 |
| 5 | M | 3 | 1998-08-10 | F | 2 | 303 | 279 | 249 | 89 | 31 |
| 6 | F | 15 | 1998-12-16 | O | 3 | 424 | 360 | 324 | 90 | 100 |
| 7 | M | 4 | 1999-02-15 | O | 5 | 360 | 299 | 262 | 88 | 22 |
| 8 | M | 11 | 1999-01-27 | F | 2 | 634 | 590 | 495 | 84 | 133 |
| 9 | M | 3 | 1999-11-16 | O | 2 | 303 | 272 | 220 | 81 | 126 |
| 10 | F | 9 | 2000-01-03 | O | 3 | 424 | 394 | 353 | 89 | 43 |
| 11 | M | 19 | 2001-01-08 | F | 2 | 634 | 571 | 504 | 88 | 110 |
| 12 | M | 16 | 2001-02-26 | O | 2 | 634 | 380 | 320 | 84 | 159 |
| Mean | | 12 | | | | 504 | 419 | 365 | 87 | 106 |
| (SD) | | (6) | | | | (153) | (119) | (105) | (3) | (61) |

ered to have been scavenging if evident signs of feeding were recorded. When possible, we assessed the number of scavenging individuals by counting observed birds or, in the case of mammals, estimating the number of individuals by tracks and trails in the snow. The frequency of scavenging was calculated for each species of scavenger detected for each carcass (the number of visits in which the species was recorded as a percentage of all our visits to that carcass). For four carcasses, the monitoring was supplemented with continuous observations of the scavengers from a blind (a total of 67 hours, including 54 during daylight) in order to verify the maximum number of avian scavengers present together at carcasses and describe the parts of the carcass they fed on.

Two of the bison (numbers 8 and 11) died in the forest and were found by us during snowtracking of wolves, which initially opened the carcasses. All carcasses were opened by rangers (to varying degrees) at exposition or after being found, and their heads were taken for the scientific collection. We assessed carcass openness on a scale from 0 to 5 as follows: 0 – intact carcass; 1, 2, 3, or 4 – carcass with 1 to 4 of the following parts opened and exposed: a) head cut and neck section exposed; b) belly cut lengthwise; stomach, intestines and viscera taken out and exposed; c) skin of upper flank removed; flesh of one side exposed; d) upper side of the back part around the hind leg open; flesh of back part and hind leg exposed; 5 – completely skinned carcass with all above listed parts exposed (Table I).

As weighing bison carcasses in the field was not feasible, the proportion of the dead animal consumed by scavengers was visually estimated and the carcass utilization described in detail. In each visit, documentary photos of the carcass were taken. The monitoring was finished when only big bones clean of flesh remained. At that final state of carcass depletion, the remains were weighed. Carcass consumption by scavengers was estimated based on the degree of carcass utilization assessed in the field and checked against the documentary pictures, the weight of remains, and the estimated initial body mass of the bison. Data on sex and age of each monitored carcass was provided by Dr. Z. A. Krasinski, Bialowieza National Park. In two cases, the dead bison were weighed; the body mass of the other 10 bison was estimated, based on Krasinska and Krasinski (2002), as mean body mass for a given age/sex class (Table I).

The rate of carcass depletion by scavengers (kg consumed $day^{-1}$) was calculated for each period of time between consecutive observers' visits by dividing the biomass consumed by the number of days between those inspections. The depletion rate for all days between observers' visits was considered to be the same. Daily consumption rates by scavengers were calculated until complete carcass depletion. Body parts (head, piece of skin, hind leg) taken from the bison carcasses by rangers were excluded from calculations of the depletion rate. Corrections were made in the cases of legs (already cleaned of flesh) carried away by wolves but not completely consumed (data from snowtracking of wolves; N. Selva, B. Jedrzejewska, W. Jedrzejewski & A. Wajrak, unpubl. data).

The date of carcass exposition was known or could be estimated with reasonable accuracy. For multiple regression analysis, November 1 was considered as day 1, coinciding with the beginning of the cold season. Eight bison carcasses, mostly from culling, were exposed in big clearings or glades, and four were left at the place of bison death, under the forest canopy. Two of the clearings were used by hunters every winter to expose carcasses or entrails of shot game. During the study period, one and six bison carcasses were exposed on those two glades, respectively. Such situations, with two or more ungulate carcasses close to each other, are not uncommon in Bialowieza Forest, where carcass availability (natural deaths and large predators' kills) is high (Jedrzejewska & Jedrzejewski, 1998; authors' unpubl. data).

Meteorological data were obtained from the Bialowieza meteorological station and included mean daily temperature (°C), mean daily snow cover (cm), and daily precipitation (mm).

## Results

### SCAVENGING FREQUENCY OF VARIOUS SPECIES

A total of 13 species of birds and mammals were recorded feeding on bison carcasses in Bialowieza Forest. Most frequent scavengers were raven; red fox; wolf; common buzzard, *Buteo buteo*; white-tailed eagle, *Haliaeetus albicilla*; and raccoon dog (Table II). Raven, fox, and wolf visited all carcasses surveyed. Ravens were recorded on nearly 78% of our visits to carcasses, foxes on 41%, and wolves on 29% (Table II). Avian scavengers more frequently visited bison carcasses placed in glades than those located in the forest. White-tailed eagles were never recorded at carcasses in forest habitats. Among mammals, only raccoon dogs more frequently scavenged on carcasses inside the forest. Red foxes and wolves used carcasses in both habitat types with similar frequency (Table II). The scavenging frequency of ravens, white-tailed eagles, and raccoon dogs was significantly different on carcasses placed in glades than on carcasses in the forest (Mann-Whitney *U*-test, *U* from 32 to 28, $n_1=4$, $n_2=8$, $p$ from 0.004 to 0.048). Minor scavengers were jays, *Garrulus glandarius* (mean scavenging frequency ± SD: 7.6% ± 11.9); pine martens (6.2% ± 15.6); great and blue tits, *Parus major* and *P. caeruleus* (11.3% ± 22.9); wild boar (5.7% ± 5.6); goshawks, *Accipiter gentilis* (1.0% ± 1.7); and stray dogs (5.8% ± 11.9).

The most gregarious species at bison carcasses were ravens, with a maximum recorded number of 50 individuals active around a carcass at the same time. The mean (± SD) group size of ravens recorded was 12 ± 13.6 individuals. Flocks of immature ravens (considered as groups of three or more) included 17.9 ± 14 ravens (mean ± SD). There was a manifest difference between the group size of ravens scavenging on carcasses exposed in the forest and in openings (Mann-Whitney *U*-test, $U=1105$, $n_1=10$, $n_2=130$, $p < 0.0005$). Mean (± SE) number of individuals observed at carcasses was 1.5 ± 0.17 in forest and 12.8 ± 1.21 in clearings. Carcasses exposed in clearings, more visible, were mainly consumed by flocks of immatures, while those under the forest canopy were utilized by the territorial pairs of ravens. In open areas, the observed group size of ravens was more variable: 1-2 individuals in 31% of cases, 3-10 individuals in 29% of cases, and >10 ravens in 40% of cases.

Fox and pine marten scavenged solitarily. Raccoon dog usually fed on bison carrion in pairs and revisited carcasses very often. The maximum time interval between consecutive raccoon dog visits to a carcass was on average 3.7 days. Note, however, that researchers' monitoring visits were spaced out in time, and thus the presence of a species might not always have been recorded (depending on weather conditions and scavengers' behaviour). Wolves also usually visited bison carcasses in groups; the biggest group consisted of 5 individuals. The maximum number of other avian scavengers recorded as present (but not feeding together) at bison carcasses was seven jays, four buzzards, three white-tailed eagles, and two tits.

### CARCASS UTILIZATION PROCESS

Bison carcasses were a challenge for scavengers due to their hard and thick skin, especially when the carcasses were frozen. In the cases of two bison that had died in the forest (numbers 8 and 11), no scavengers were able to feed on them until wolves opened the carcass. Even the eyes were not eaten. In one bison, the nose (the only accessible part) was gnawed by a fox. Wolves opened both carcasses at the rump upper side and consumed the flesh from the pelvis and upper hind leg, They gnawed the hip bone and also the head of the femur slightly. Then, the back part of the stomach, not really damaged, showed up (Figure 1a). From that point, in carcasses with

TABLE II. Frequency of scavenging by six species of most important scavengers at European bison carcasses. Numbers are percentages of visits made by observers during which the presence or signs of a given species of scavenger were recorded. F=forest, O=open glades. Bison carcasses as in Table I.

| Carcass number | Habitat | Total *N* visits by observers | Percentage frequency of scavengers' visits | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | Raven | Red fox | Wolf | Buzzard | White-tailed eagle | Raccoon dog |
| 3 | F | 24 | 58.3 | 33.3 | 4.2 | 0 | 0 | 8.3 |
| 5 | F | 5 | 40.0 | 20.0 | 40.0 | 0 | 0 | 80.0 |
| 8 | F | 29 | 58.6 | 37.9 | 44.8 | 24.1 | 0 | 75.9 |
| 11 | F | 19 | 42.1 | 57.9 | 57.9 | 36.8 | 0 | 26.3 |
| Mean for Forest | | | 49.8 | 37.3 | 36.7 | 15.2 | 0 | 47.6 |
| (SD) | | | (10.1) | (15.7) | (23.0) | (18.3) | (0) | (35.8) |
| 1 | O | 47 | 83.0 | 38.3 | 19.1 | 25.5 | 25.5 | 0 |
| 2 | O | 40 | 80.0 | 32.5 | 15.0 | 20.0 | 27.5 | 0 |
| 4 | O | 23 | 82.6 | 60.9 | 34.8 | 60.9 | 21.7 | 0 |
| 6 | O | 26 | 73.1 | 38.5 | 15.4 | 11.5 | 15.4 | 11.5 |
| 7 | O | 14 | 100 | 50.0 | 21.4 | 42.9 | 28.6 | 28.6 |
| 9 | O | 47 | 78.7 | 48.9 | 21.3 | 17.0 | 23.4 | 8.5 |
| 10 | O | 18 | 83.3 | 33.3 | 50.0 | 0 | 44.4 | 0 |
| 12 | O | 11 | 81.8 | 36.4 | 27.3 | 36.4 | 9.1 | 0 |
| Mean for Open | | | 82.8 | 42.4 | 25.5 | 26.8 | 24.5 | 6.1 |
| (SD) | | | (7.7) | (9.9) | (11.8) | (19.3) | (10.4) | (10.2) |
| Total mean | | | 71.8 | 40.7 | 29.3 | 22.9 | 16.3 | 19.9 |
| (SD) | | | (18.2) | (11.7) | (16.2) | (19.0) | (14.6) | (28.9) |

few exposed parts (index of carcass openness 2), the sequence of utilization was similar. During the second stage of carcass consumption, intestines and stomach skin were consumed by various scavengers, with the stomach content spread in and outside the carcass. All back parts (pelvis, femur, and tibia) were cleaned out of flesh, and the lumbar part of the backbone became visible (Figure 1b). In the next stage, the viscera were eaten, the sternum and distal part of ribs were heavily gnawed, and the lumbar and thoracic parts of the spinal column became accessible. The rib cage and all exposed bones were left clean (Figure 1c). From this phase, carcasses were already less heavy and were often dragged by wolves. Later on, the muscular mass from shoulders and fore legs was consumed. The neck (in all carcasses the head had been removed) was cleaned of flesh, and the first cervical vertebrae became visible. Bones started to be heavily utilized: ribs eaten, head of limb bones (mainly femur) gnawed by wolves to take the marrow, and scapula and hip damaged (Figure 1d). In the last stage of utilization, dismemberment of the carcasses started, partly in consequence of repeated dragging by wolves. Some legs were detached from the body and transported away (mainly by wolves). The backbone was often broken into two parts. Sometimes all remaining parts remained connected by the skin, still attached to the palm bones and hooves, which were seldom consumed.

Wolves played an important role in making the bison carcass accessible to other scavengers, not only by opening it initially but also by progressively providing access to other scavengers. In some cases (four carcasses with the flank open and not yet discovered by wolves), the thoracic cage was cleaned of flesh, but the viscera inside could not be consumed, as few scavengers other than wolves were able to break the ribs. Only once did we observe a white-tailed eagle break them. Furthermore, the anus was picked at by birds, but not enlarged enough to enable the scavengers to get inside the bison body. In the early stages of little-opened carcasses (index of carcass openness 2), still not heavily utilized by wolves, the scavengers' strategy was to feed inside the carcass. They created a "tunnel" to get to the body (entrance at upper hind leg, back side of the belly, or between two broken ribs) and consumed it from inside. This scavenging pattern was often recorded, especially among the smaller carnivores such as pine marten and raccoon dog. This "tunnel" was most obvious at carcass 3, which was little opened and rarely visited by wolves. With the arrival of spring, microbial and invertebrate activity "softened" the carcass and utilization and breaking up by scavengers became easier.

Once the wolves discovered a bison carcass, they visited it repeatedly, although they did not always feed on it (64% of wolf visits to bison carcasses finished in feeding bouts). On average, wolves visited the same bison carcass $6.6 \pm 4.0$ times, and the average interval between consecutive wolf visits to a carcass was $11.6 \pm 13.9$ days (mean $\pm$ SD). Foxes, raccoon dogs, ravens, and buzzards were more often recorded during monitoring visits in which wolf feeding occurred. The differences were significant for fox ($G$-test, $G=7.69$, df$=1$, $p < 0.01$) and raccoon

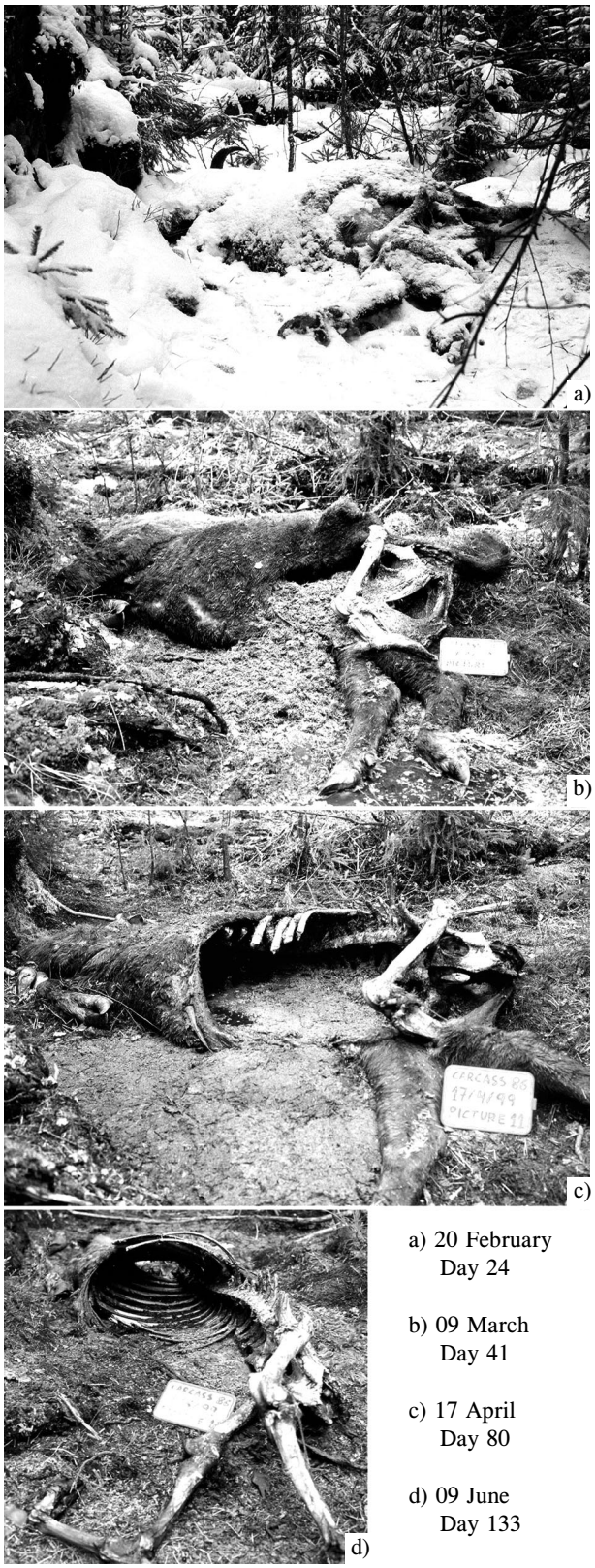


FIGURE 1. Depletion process by scavengers of carcass number 8 during 5 months. This adult bison died in the forest around 27 January 1999. Wolves opened it about 3 weeks later at the upper hind leg and back part. Scavengers first consumed the carcass from inside and later fed on the parts exposed by wolves. In the last stages, the carcass was dragged by wolves and also consumed by invertebrates. Day = days elapsed since bison death.

dog ($G$=6.23, df=1, $p < 0.025$). A typical wolf behaviour was to drag the carcass when feeding on it. If the carcass was still heavy, they moved it slightly and changed its position. Ten out of 12 bison carcasses were dragged by wolves, on average 2.25 ± 1.5 times each (mean ± SD). The total distance they were moved was 27 ± 23.9 m (mean ± SD, maximum 65 m).

Avian scavengers ate mainly intestines, stomach, viscera, and muscles. Medium-size carnivores consumed viscera, muscles, and smaller or softer bones, such as sternum and ribs. Wolves could consume any parts, including the hard skin and big bones. A typical sign of wolf feeding was the head of leg bones, mainly femur and humerus, gnawed to extract the marrow.

### RATE OF CARCASS DEPLETION BY SCAVENGERS

The average time necessary until a dead bison was over 80% consumed by scavengers was 106 ± 61 days (mean ± SD, range 22-239, Table I). Bison carcasses in the forest were consumed for a longer time (mean ± SD: 128 ± 86 days, $N = 4$) than those placed in clearings (mean ± SD: 95 ± 48 days, $N = 8$), though the difference was not significant. Complete carcass depletion took, 126 ± 62 days (mean ± SD). The most important factors affecting the duration of carcass utilization, as revealed by the multiple regression analysis, were the index of carcass openness (OPEN), the number of wolf feeding visits (WOLF), and the date of exposure (DATE; November 1 = day 1). All three factors were negatively correlated with the time of carcass depletion: the time shortened with increasing index of openness, higher frequency of wolf visits, and later dates of carcass exposure (*i.e.,* with the advance of winter season). These three factors explained 77% of the observed variation in the time ($T$) of carcass utilization ($T$ = 308.8 – 40.058 OPEN – 2.027 WOLF – 0.351 DATE; $N$ = 12, $R^2$=0.772, $p$ = 0.006). Semipartial squared correlations ($sr^2$; Tabachnick & Fidell, 1983) were calculated for each independent variable to show its contribution to the total variation explained. Openness of the carcass was most important ($sr^2$ = 0.472), followed by wolf visits ($sr^2$ = 0.233) and date of exposure ($sr^2$ = 0.140). The body mass of the bison and raven scavenging activity (raven scavenging frequency and mean numbers combined) had no effect on how long the carcass depletion process lasted.

The mean (± SD) body mass of bison exposed to scavengers was estimated to be 419 ± 119 kg (Table I). Scavengers consumed, on average, 365 ± 105 kg of carrion (mean ± SD), *i.e.,* 87% of the carcass weight (Table I). At final complete depletion of the bison carcass, 89% ± 4 (mean ± SD) of the whole exposed animal was consumed. The total average rate of carcass consumption by scavengers (kg day$^{-1}$) till complete carcass depletion was 3 ± 0.13 kg day$^{-1}$ (mean ± SE), with a maximum of 68 kg consumed in one day (Figure 2). The depletion process of bison carcass showed a characteristic trend. The daily consumption rates were highest in the beginning of the carcass exploitation (6.8 ± 1.79 kg day$^{-1}$ was the mean ± SE for the first 15-day period, and 3.9 ± 0.90 kg day$^{-1}$, for the second) and declined with time (Figure 2).

We investigated the effect of three weather variables on daily carcass consumption by scavengers: mean daily temperature, snow cover, and precipitation. Only ambient temperature had a significant influence on the rate of carcass depletion. Bison carcasses were mainly utilized by scavengers in the range of temperatures between -15°C and 15°C (Figure 3). The daily consumption of bison carcasses peaked in the range of temperature around 0°C. At spring-summer temperatures (> 5°C) the rate of carcass depletion declined progressively with higher temperatures. At extremely cold temperature (< -15°C), scavengers hardly fed on frozen carcasses (Figure 3). Differences in the daily carcass consumption among the classes of temperature were significant (Kruskall-Wallis $H$=26.496, df=5, $p < 0.0005$). There were no significant effects of snow cover and precipitation on the daily rates of carcass depletion, although the rate of carcass consumption increased slightly with snow, being highest in the range of 15-20 cm snow cover.

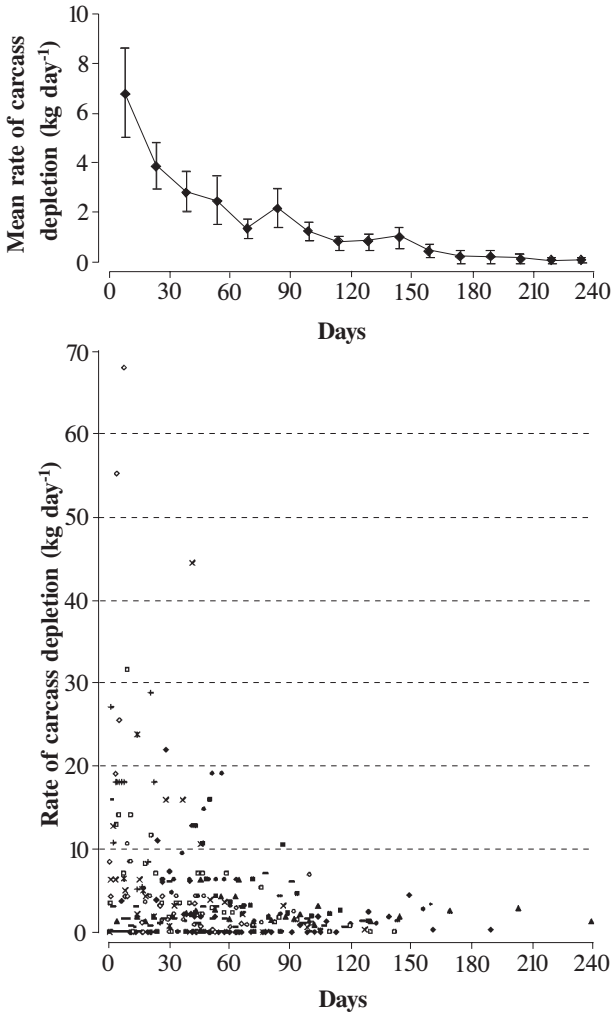


FIGURE 2. Rate of bison carcass depletion (kg consumed by scavengers per day) showed as mean (± SE) of depletion rate of all carcasses per 15-day period (upper graph), and depletion rates of each bison carcass, recorded in the 303 visits during the carcass consumption process (lower graph). Symbols of the same type denote one carcass.

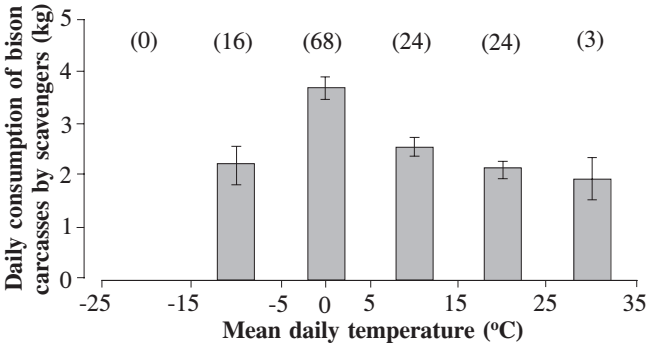


FIGURE 3. Mean (± SE) daily consumption (kg) of bison carcasses by scavengers in relation to mean daily temperature (°C). Maximum values of daily consumption are given in brackets above the bars.

## Discussion

The typical feature of bison carcasses is their large size and long duration. Small carcasses are consumed rapidly by scavengers: 69% of hare carcasses were consumed in the first day (Patagonia; Travaini *et al.,* 1998), and domestic pigs lasted on average 5.4 days (Mexico; Hernández *et al.,* 1987). In African regions, carcasses of large ungulates (a 100-kg yearling wildebeest) were depleted in 30 minutes (Houston, 1974). However, in forests of the northern hemisphere, ungulate carcasses were utilized by non-specialized scavengers for longer periods. Green, Mattson, and Peek (1997) estimated that in Yellowstone, the mean time required to reach 50% depletion of the carcass for adult male American bison, *Bison bison*, was 9.3 days, increasing to 66 days during a severe winter with high carcass availability. In Bialowieza Primeval Forest, even though the winters were mild, European bison carcasses lasted almost the whole cold season. The extinction from BPF of brown bear, a species strongly dependent on long-lasting carcasses (Green, Mattson & Peek, 1997; Mattson, 1997), might contribute to this difference.

The time of carcass depletion did not depend on bison body mass or activity of ravens, but it was affected by carcass openness and wolf visits. Wolf was the only species able to open intact carcasses. Therefore, in the scavengers´ assemblage in BPF, the wolf acted as a keystone species. A similar phenomenon has been documented in other scavenging guilds. In Africa, griffon vultures waited for hyenas to be able to feed on very thick-skinned animals (Houston, 1974); in North America, only bald eagles could open salmon carcasses (Skagen, Knight & Orians, 1991); in Scotland, breaking of sheep carcasses by foxes and badgers assisted scavenging birds (Hewson, 1981; 1984). In northern latitudes, ravens relied on wolves and other carnivores to open large ungulate carcasses (Magoun, 1976; Mech, 1981; Heinrich, 1990; Stahler, Heinrich & Smith, 2002). Furthermore, when the number of accessible parts in the carcass increased, competition among scavengers decreased, thus allowing more individuals to feed together (Alvarez, Arias de Reyna & Hiraldo, 1976). Wolves were the main agent responsible for the dismemberment of the carcasses, and many similarities were found with the utilization pattern described by Haynes (1982) for American bison killed and consumed by wolves. In forested regions with frequent snowfalls, ravens and foxes associate with wolves to feed on their kills or scavenged carcasses (Mech, 1981; Jedrzejewski & Jedrzejewska, 1992; Stahler, Heinrich & Smith, 2002).

The later the carcass was exposed during the cold season, the faster it was consumed by scavengers. Decline of the basic food supply (mainly rodents) during winter forced medium-sized and small predators to feed more often on ungulate carcasses at the end of the cold season. In northern Belarus, during the harshest period of late winter and early spring, all generalist carnivores consumed wild ungulate carrion (Sidorovich *et al.,* 2000). Carcass availability can act as a survival bottleneck that directly influences scavengers´ fitness (Marzluff & Heinrich, 1991), mainly in winter, when food niches of generalist predators become narrower and considerably overlap (Sidorovich *et al.,* 2000). In BPF, the share of rodents in pine marten diet decreased through the winter, and the consumption of ungulate carcasses increased, reaching maximum in February (Jedrzejewski, Zalewski & Jedrzejewska, 1993).

Bison carcasses placed in forest were consumed at slower rates than those exposed in open glades. This result may have been biased, as all carcasses in the forest (natural deaths) were initially little opened. However, differences in utilization time between habitats are also explained by differential use by scavengers. Carcasses in clearings are more easily detected by all avian scavengers, as shown by their higher frequencies in open areas. In the tropical forest of Venezuela, black vultures, *Coragyps attratus*, were found in significantly higher numbers at carcasses in open locations (Houston, 1988). In the case of ravens, forest carcasses were utilized by the territorial pair, while those in glades were consumed by large flocks of immatures, which not only fed actively but may also have been induced to cache food by increased competition between conspecifics (Heinrich & Pepper, 1998). Similar habitat segregation has been described for other avian scavengers foraging in groups (Kirk & Houston, 1995; Donázar *et al.,* 1998). White-tailed eagles may be attracted to carcasses by the high activity of raven crowds, as they were always found together with raven flocks in open areas. It is known from other scavenging assemblages that some species are attracted to the carcasses by decoding the behaviour of others (Kruuk, 1967; 1972; Houston, 1974). By contrast, raccoon dog, a slow, clumsy animal, preferred to scavenge in the forest. In BPF, raccoon dogs often become victims of large predators at carcasses (Jedrzejewska & Jedrzejewski, 1998; authors' pers. observ.). Green, Mattson, and Peek (1997) also found that in Yellowstone the use of carcasses by black bears, *Ursus americanus*, and grizzly bears depended on some habitat features.

At very cold temperatures, scavengers fed very little on carrion due to difficulties in tearing hard-frozen thick-skinned carcasses. On the other hand, on very cold days scavengers may be less active, as Zalewski (2000) documented for pine martens in BPF. In warm climates, maximum temperatures (not lowest ones) were the main abiotic factor governing carcass duration (Hernández *et*

*al.,* 1987). Precise information about rates of carcass consumption by scavengers is still lacking in the literature, and to our knowledge, our study provides the first data of this type.

Diet analysis of over 30 species of predators in BPF also revealed red foxes, raccoon dogs, and common buzzards as important consumers of ungulate carcasses (Jedrzejewska & Jedrzejewski, 1998). This study documented that raven, red fox, and wolf were the most important scavengers of bison carcasses in BPF. Wolves visited the same carcass once every 11.6 days on average. This finding is in agreement with a parallel telemetry study on wolf-kill rates in BPF (Jedrzejewski *et al.,* 2002), which found out that wolves scavenged, on average, once every 12 days.

In conclusion, long-lasting bison carcasses may play an important role in European temperate forests by providing food to many birds and mammals for long periods under severe winter conditions. The scavenging guild, although not so well structured as other more specialized assemblages, cannot be considered completely opportunistic. Wolves act as a keystone species for the rest of the guild, facilitating their scavenging, and noisy crowds of ravens may aid other species in locating carcasses. Habitat preferences of various species may be an important factor structuring the guild of scavengers.

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