Invertebrates outcompete vertebrate facultative scavengers in simulated lynx kills in the Bavarian Forest National Park, Germany

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Abstract

Invertebrates outcompete vertebrate facultative scavengers in simulated lynx kills in the Bavarian Forest National Park, Germany.— Understanding the role of scavengers in ecosystems is important for species conservation and wildlife management. We used road–killed animals, 15 in summer 2003 (June–August) and nine in winter 2003/2004 (from November to January), to test the following hypotheses: (1) vertebrate scavengers such as raven (*Corvus corax*), red fox (*Vulpes vulpes*) and wild boar (*Sus scrofa*) consume a higher proportion of the carcasses than invertebrates; (2) the consumption rate is higher in winter than in summer due to the scarcity of other food resources; and (3) vertebrate scavengers are effective competitors of Eurasian lynx. We monitored 65 animals belonging to eight different mammal and bird species with camera traps. Surprisingly, Eurasian lynx (*Lynx lynx*) was the most important vertebrate scavenger. However, in both seasons, the consumption of vertebrate scavengers was of minor impact. In summer, the carcasses were completely consumed within 10 days, mostly by invertebrates. In winter, only 5% of the carcasses were consumed within 10 days and 16% within 15 days. We conclude that vertebrates in the Bavarian Forest National Park are not strong competitors for lynx.

Key words: Carrion, *Lynx lynx*, Scavenging, Kleptoparasitism, Decomposers, Food competition.

Resumen

Los invertebrados compiten con los vertebrados necrófagos facultativos por las presas simuladas de lince en el parque nacional del bosque de Baviera, Alemania.— Comprender la función de los necrófagos en los ecosistemas es importante para la conservación de especies y la ordenación de la fauna y la flora silvestres. Utilizamos animales que habían muerto en la carretera, 15 en verano de 2003 (de junio a agosto) y nueve en el invierno 2003/2004 (de noviembre a enero) para analizar las hipótesis siguientes: (1) los vertebrados necrófagos como el cuervo (*Corvus corax*), el zorro (*Vulpes vulpes*) y el jabalí (*Sus scrofa*) consumen una proporción mayor de los cadáveres que los invertebrados; (2) el índice de consumo es más elevado en invierno que en verano debido a la escasez de otras fuentes de alimentos, y (3) los vertebrados necrófagos son competidores reales del lince euroasiático. Seguimos a 65 animales que pertenecían a ocho especies diferentes de mamíferos y aves con cámaras de trampeo. Sorprendentemente, el lince euroasiático (*Lynx lynx*) fue el vertebrado necrófago más importante. No obstante, en ambas estaciones, los efectos del consumo de los vertebrados necrófagos fueron de poca magnitud. En verano, los cadáveres fueron consumidos totalmente en 10 días, en su mayor parte por invertebrados. En invierno, solo el 5% de los cadáveres se consumieron en 10 días y el 16%, en 15 días. Concluimos que los invertebrados del parque nacional del bosque de Baviera no son fuertes competidores del lince.

Palabras clave: Carroña, *Lynx lynx*, Necrofagia, Cleptoparasitismo, Descomponedores, Competencia por el alimento.

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Introduction

The availability of wild ungulate carcasses has been limited throughout the European ecosystems for many years. Ungulate populations are hunted intensively and are usually fed in winter. Therefore, their natural mortality rates are very low, and dead animals are quickly removed from the ecosystem. With the return of large predators —such as wolves (*Canis lupus*) and the Eurasian lynx (*Lynx lynx)*— to parts of Europe in recent years, the amount of carrion in the ecosystem may increase.

Until recently, most studies on scavenging of predator kills have been carried out in areas that are home to specialized scavengers, such as vultures and hyenas, specifically in Africa, South America and southern Europe (Kruuk, 1967, 1972; Houston, 1974, 1975, 1979, 1988; Schaller, 1972; Wallace & Temple, 1987; Hiraldo et al., 1991; Gomez et al., 1993; Travaini et al., 1998). In the last decade studies have also been conducted in the temperate zone (Heinrich, 1989, 1999; Stahler et al., 2002; Wilmers et al., 2003; Selva, 2004; Selva et al., 2005; Krofel et al., 2012). Results obtained indicate that the carcasses of animals, both those killed as prey and those dying from other causes, are mostly consumed by vertebrate scavengers. Selva (2004) observed that up to 36 vertebrate species consume animal carcasses. Such data are of relevance for the ecological community.

In temperate regions, animal carcasses are an important source of nutrition in mid–winter when other resources are unavailable or depleted (Jedrzejewska & Jedrzejewski, 1998; Sidorovich et al., 2000), and they are crucial for survival during severe winters (Angerbjörn et al., 1991; Sidorovich et al., 2000; Selva et al., 2003). Carcasses have an important effect on the population dynamics of scavengers (DeVault et al., 2003; Roth, 2003) and can be highly significant for the stability and persistence of ecosystems (McCann et al., 1998). Turnover and distribution of nutrients from the carcasses is accelerated by scavengers, which thereby play an essential role in the nitrogen cycle (Putman, 1978; Braack, 1987; Towne, 2000). Especially in summer, the availability of animal carcasses increases the species richness, such as the abundance of beetles and the heterogeneity of plant communities. Certain developmental stages of some insect species may even depend on the presence of carcasses (Sikes, 1994; Towne, 2000; Melis et al., 2004).

Vertebrate scavengers have the potential to consume large parts of prey. Ravens (*Corvus corax*) were shown to reduce the consumption rate of a single wolf by 70% and of a large wolf pack by 10% (Promberger, 1992; Hayes et al., 2000; Kaczenzky et al., 2005). In the Dinaric mountains, lynxes lost 15% of their kills to scavenging by other large predators such as brown bears (*Ursus arctos*) (Krofel et al., 2012). As a consequence, if parts of a predator's kill are consumed by scavengers, the predator has to increase its kill rate to obtain enough food, as has been observed for wolves (Vucetich et al., 2004) and lynxes (Krofel et al., 2012).

Like other cat species, lynx are solitary predators and stalk hunters. If a lynx is not disturbed and the carcass does not decay, the lynx will feed on the carcass for three to six days (Jobin et al., 2000). Scavengers therefore have a relatively broad window of time to discover and make use of the kill of lynx. To avoid scavengers, lynx usually cache their kills by dragging them into dense vegetation and covering them with leaves or grass, or even snow or soil (Festetics, 1980; Hucht–Ciorga, 1988; Jedrzejewski et al., 1993). Scavenger species that use their olfactory sense for orientation, such as wild boar (*Sus scrofa)* and red fox (*Vulpes vulpes)*, can find even well–hidden carcasses, though probably less often (Hucht–Ciorga, 1988; Jedrzejewska & Jedrzejewski, 1998; Jobin et al., 2000).

Large predators compete with human hunters for the same prey species. An increase in the predator's kill rate caused by scavengers removing parts of the killed prey (Vucetich et al., 2004; Krofel et al., 2012) could potentially exacerbate the conflicts between humans and large predators. As a result, illegal killings of large predators might increase, with possible consequences for the conservation of small predator populations (Cerveny et al., 2002; Breitenmoser & Breitenmoser–Würsten, 2008). To understand this conflict and protect large predators, more information of the scavenger community and its possible influence on predator kills is needed. Our study in the Bavarian Forest National Park aimed to assess the scavenger community and its consumption of ungulate carcasses in summer and in winter. Our hypotheses were that (1) vertebrate scavengers such as ravens, red foxes and wild boars consume a higher proportion of the carcasses than invertebrates. (2) the consumption rate is higher in winter than in summer, because other food resources are scarce in this season, and (3) vertebrate scavengers are effective competitors of Eurasian lynx. For this purpose we set out road kills of ungulates that were simulated as lynx kills and monitored the scavengers using camera traps during the summer of 2003 and the winter of 2003/2004.

Materials and methods

Study area

The study was performed in the Rachel–Lusen–Area of the Bavarian Forest National Park, which is situated in south–eastern Germany along the border with the Czech Republic (49° 3' 19'' N, 13° 12' 9'' E). The park covers an area of more than 240 km². Together with the Šumava National Park in the Czech Republic (690 km²), the Bavarian Forest Nature Park (3,070 km²) and the Šumava Protected Landscape Area (1,000 km²) it constitutes the Bohemian Forest Ecosystem.

The area is mountainous, with altitudes varying between 600 and 1,453 m a.s.l. and mean annual temperature ranging between 6.5°C in the valleys and 3°C along the ridges and at higher elevations.

The mean annual precipitation is between 830 and 2,230 mm, a considerable amount of which occurs as snowfall. Most of the area is forested (97%), consisting mostly of Norway spruce (*Picea abies*) and European beech (*Fagus sylvatica*) (Heurich & Neufanger, 2005).

Among the objectives of the National Park is the conservation of natural processes, including the promotion of undisturbed dynamics within natural communities. This includes the avoidance of control measures for the wild ungulate population through human intervention. Therefore forest and wildlife management is not allowed in 75% of the area (Heurich et al., 2011).

A small population of Eurasian lynx currently lives in the Bohemian Forest Ecosystem. The population derives from 17 lynx that were reintroduced to the Bohemian Forest in the 1980s. Initially, information on lynx presence indicated an increase in numbers and distribution. However, at the end of the 1990s, the growth of the lynx population stagnated and in recent years the number of individuals even decreased (Wölfl et al., 2001). Records from systematic camera trapping revealed a density of approximately 0.9 lynx per 100 km² in the national parks (Weingarth et al., 2012).

Simulation of lynx–kills

We simulated the carcasses as lynx kills to obtain an idea as to whether lynx could be affected by kleptoparasitism in the Bavarian forest, meaning that scavengers of certain species feed on or take away parts of lynx kills. To determine the influence of scavengers, we monitored all animals that fed on the carcasses.

Roe deer (*Capreolus capreolus)* is the most important lynx prey in our study area, followed by red deer (*Cervus elaphus*) (Podolski et al., 2013). This is similar to other areas occupied by lynx (Breitenmoser & Haller, 1987; Haller, 1992; Hucht–Ciorga, 1988; Okarma et al., 1997; Podolski et al., 2013) and we used road–killed ungulates for the simulations. When road–kills were reported, their bodies were collected within 1.5 h and immediately frozen to prevent decomposition. All of the 24 carcasses (19 roe deer, 4 wild boars, and 1 red deer) were frozen in a cold–storage house to avoid flies. Before the carcasses were placed in the wild they were thawed in a cooling chamber.

We simulated a natural lynx kill by cutting each carcass at the neck or thigh and inflicted additional wounds on the carcasses to simulate natural kills, providing access points for scavenging birds. Human odour was minimised by wearing rubber boots and rubber gloves rubbed in lynx scat.

We positioned the carcasses in the morning, simulating the natural behaviour of the lynx by dragging them along the ground for about 30 m to their final destination to leave a scent trail and covering the carcasses with leaves. We also placed scat collected from lynx kept in an enclosure at the site since lynx often drop scat in the vicinity of their kills (Hucht–Ciorga, 1988).

We usually positioned 1–3 carcasses at a time in summer (June, July, August; n = 15) and 1–3 carcasses at a time in winter (November, December, January) and monitored each of them until total depletion. This lasted 10 days in summer and 16 days (n = 6) or 32 days (n = 3) in winter, resulting in 150 and 192 observation and camera trap–days in summer and in winter, respectively.

We positioned the carcasses at 15 different locations at least 1 km apart, distributed throughout the study area to avoid habituation of the scavengers living close to these sites (fig. 1).

Carcass monitoring

Each day of the observation period, we visually estimated the proportion of carcass remaining (in %) and assigned the level to one of eight classes (table 1). We decided against weighing the carcasses daily as done by Promberger (1992) to avoid disturbing the carcasses in the near–natural simulation experiment and because maggots and other decomposers in the flesh in summer would distort the results.

We monitored the carcasses using camera traps (Camtrakker), consisting of compact analogue cameras equipped with motion sensors. The distance between the camera trap and the carcass varied from site to site, averaging 1–2 m, and motion sensors were set at the shortest interval to record as many movements as possible, with a time interval of 1' between the captures. We checked the camera traps daily and photographed the carcasses and recorded the decrease in the amount of tissue (table 1), changes in carcass position, and evidence of other animals in the immediate vicinity, such as tracks, scat and fur. When an animal moved the carcass, we moved the camera trap accordingly, and did not change the position of the carcass. During this procedure, which lasted no longer than 15', we minimized human odour by wearing rubber boots and gloves and chose the morning (two hours after sunrise) for our visits, because mammalian scavengers did not appear before dusk. We assumed that in the intervening hours, our human scent was reduced to a level that did not deter the animals. We observed no indications of individual species avoiding or preferring the simulation sites, as indicated by tracks in the soil or snow.

In general, one camera trap picture was regarded as an observation, but if an individual was captured in a consecutive series of pictures, these pictures were treated as a single observation. In addition, we used tracks in the soil around the carcasses to support the camera trap observations. If an animal was not photographed by the camera but was definitely present based on the tracks, we counted the tracks as one observation.

Determination of the carcass consumption by scavengers

We compared the amount of animal tissue consumed by the scavengers on each day with that normally consumed by the male lynx and by female lynx with kittens (family group) to assess the percentage of consumption by scavengers feeding on the carcasses, as reported by Jobin et al. (2000), who found an average of 3.2 kg per day consumed by a male lynx and 4.9 kg per day by a family group. The consumable fraction of an ungulate carcass is approximately 75%, including the digestive tract (Messier & Crete, 1985). Our measurements of live–trapped adult roe deer in the study area revealed an average weight of 21 kg. The mean killing rate of

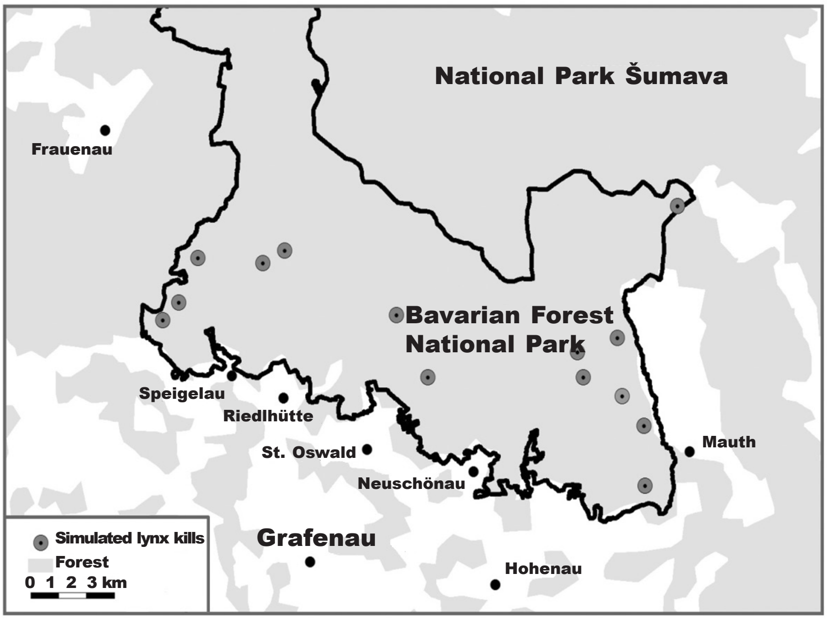

Fig. 1. Map of the Bavarian Forest National Park, showing the placement of the simulated lynx kills.

Fig. 1. Mapa del parque nacional del bosque de Baviera en el que se muestra la ubicación de las presas simuladas de lince.

a lynx in Poland was observed to be one roe deer in 5.4 days (Okarma et al., 1997); in Switzerland, the rate was one every 6.6 days for a male lynx and one every five days for a family group (Breitenmoser & Haller, 1987; Haller, 1992; Jobin et al., 2000). Depending on the size of the prey, we postulated that a lynx can feed 4–10 days on a single kill.

Statistical analysis

To account for the effects of the two different observation periods (summer and winter), the absolute number of observations was converted to the number of observations (individual animals) per camera trap–day (fig. 2, table 2).

We computed a generalized linear mixed model (GLMM, Fahrmeir et al., 2013) using the number of vertebrates as outcome variable to compare the visitation of carcasses by vertebrates both in summer and winter. This mixed quasipoisson model was fitted using a Log–link function, with the observation site as a random intercept, an offset containing the trap days and season as a fixed factor.

We used quasi–poisson regression instead of poisson regression in order to avoid overdispersion.

We conducted a proportional hazards model, also known as the Cox–model (Cox & Oakes, 1984), to compare the time span until the carcasses were detected by vertebrate species in summer and winter. The outcome is the time until the carcass was found, which is a right censored time–to–event variable. It is right censored because some carcasses were not found within the observation time. To account for possible correlation on each observation site, we included a frailty term (Therneau & Grambsch, 2000). In the same way, we compared the time span until the carcasses were found between invertebrate and vertebrate species in summer. We used original incidence data and percentage–based data for the analyses.

All computations were performed in R (R Core Developer Team, 2013), version 2.13.2, using the add–on package mgcv (Wood, 2010) for fitting GLMMs and the package survival for fitting the Cox–model (Therneau, 2014).

Results

Vertebrate species observed at the carcasses

Over the course of the two study periods, June to August 2003 and November 2003 to January 2004, 280 successful observations of eight vertebrate species were recorded. In 45 photographs the species could not be identified (table 2). In summer, red foxes were the most common species observed at the sites (37%), whereas in winter, lynx was the most common species (31%) (fig. 2, table 2). During winter, we also observed three lynxes (female, male, and sex unknown) feeding on the same carcass.

The average rate of observation was one vertebrate every five camera trap–days (fig. 2). GLMM analysis

Table 1. Criteria for classification of the degree of carcass consumption.

Tabla 1. Criterios para clasificar el grado de consumo de los cadáveres.

Class	Remaining tissue (%)	Mean (%)	Characteristics
1	100	100	Carcass complete
2	90–99	95	Carcass with initial signs of consumption
3	70–89	80	Carcass missing one third of the animal tissue
4	50–69	60	More than half of the carcass remaining
5	30–49	40	Less than half of the carcass remaining
6	10–29	20	Carcass with less than one third of the animal tissue remaining
7	1–9	5	Carcass with scattered remains of animal tissue
8	0	0	Carcass with no remaining animal tissue

using a random Intercept for the observation site showed that the number of vertebrates did not significantly vary between seasons (estimate = –0.752, p = 0.17878, SE = 0.541).

Elapsed time until scavengers found the carcasses

The Cox–model with target variable days until detection of the carcass and frailty term for the observation

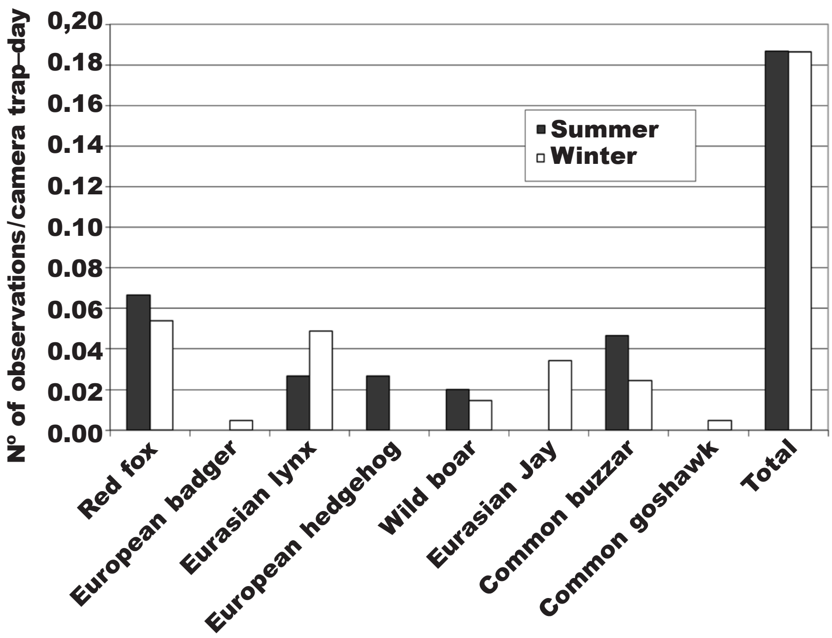

Fig. 2. Observations of different species at the carcasses per camera trap–day. The absolute number of observations was divided by the total number of camera trap–days (in summer and in winter, 150 and 192 respectively).

Fig. 2. Observaciones de diferentes especies en los cadáveres por día de trampeo con cámara. El número absoluto de observaciones se dividió por el total de días de trampeo con cámara (en verano y en invierno, 150 y 192 respectivamente.

Table 2. Observations of various vertebrate species at the carcasses divided in summer and winter. Frequency of observations: percent of carcasses visited by each species, observations/camera trap day: percent of camera–trap days with a species present: Obsv. Frequency of observations; C. Carcasses visited; Obsv/ct Observation / camera trap days.

Tabla 2. Observaciones de varias especies de vertebrados en los cadáveres en verano y en invierno. Frecuencia de las observaciones: porcentaje de cadáveres visitados por cada especie, observaciones por día de trampeo con cámara: porcentaje de días de trampeo con cámara en los que una especie estaba presente: Obsv. Frecuencia de observaciones; C. Cadáveres visitados; Obsv/ct. Observaciones por día de trampeo con cámara.

	Summer			Winter		
Species	Obsv (%)	C (%)	Obsv/ct (%)	Obsv (%)	C (%)	Obsv/ct (%)
Red fox (*Vulpes vulpes*)	37	67	7	23	89	4
Lynx (*Lynx lynx*)	11	20	2	31	122	6
Common buzzard (*Buteo buteo*)	26	47	5	9	33	2
Eurasian jay (*Garrulus glandarius*)	–	–	–	26	100	5
Wild boar (*Sus scrofa*)	11	20	2	6	22	1
Hedgehog (*Erinaceus europaeus*)	15	27	3	–	–	–
Badger (*Meles meles*)	–	–	–	3	11	1
Goshawk (*Accipiter gentilis*)	–	–	–	3	11	1
Total number	27	15	150	35	9	192

site showed that vertebrates found the carcasses more quickly in summer than in winter (estimate –1.16, p = 0.011, fig. 3). Vertebrate species found 67% of the carcasses within 10 days in summer, but only 22% were found within the same time period in winter, when they were frozen and covered with snow. A second Cox–model showed that invertebrates found the carcasses faster than vertebrates in summer (estimate = –1.48, p = 0.058, fig. 3). Within four days in summer, decomposers such as maggots of blowflies and flesh–flies (Calliphoridae, Sarcophagidae*)* were observed on 95% of the deposited carcasses. Lynx, common buzzard, Eurasian jay, and hedgehog found the carcasses within two days. Red fox and wild boar did not arrive until the fourth day.

Consumption of the carcasses

Carcasses were consumed much more quickly in summer than in winter (fig. 4). In summer, all of the carcasses were totally consumed within 10 days. In that period, none of the carcasses was completely consumed in winter. Most of the scavenging in summer was by invertebrates (85% of animal tissue, fig. 5). Vertebrates only played a minor role. Invertebrates reached peak numbers on days 4–6. Red foxes appeared before and after the maggots reached their peak numbers. Red foxes ate mostly internal organs or dragged away parts of the skeleton. Lynx mainly ate muscle tissue, and wild boars and hedgehogs mainly visited the carcasses when the maggots had reached peak numbers. Both species feed mostly on the maggots and less on the carcass tissue and other remains.

Food competition with lynx

Based on our results, if we assume that a male lynx killed a roe deer, competing scavengers would have consumed approximately 19% of the utilizable biomass of the carcass in summer and only 0.7% in winter. If we assume that a lynx family group was feeding on a killed roe deer, the scavengers would have consumed 0.7% of the utilizable biomass of the carcass in summer and 0% in winter.

Discussion

Our study of use and consumption of carcasses provides the first data on the scavenger community in the Bavarian Forest. We observed eight different vertebrate species at the simulated kills, with red foxes being the most frequent visitors. Contrary to other studies (Selva, 2004; Jedrzejewski et al., 1993; Jobin et al., 2000; Kellermann, 2001), we found that invertebrates consumed a much larger proportion of the carcasses than vertebrates and overall carcass consumption was much slower in winter than in summer.

Similar to our study, Selva (2004) identified red fox, common buzzard, Eurasian jay and wild boar

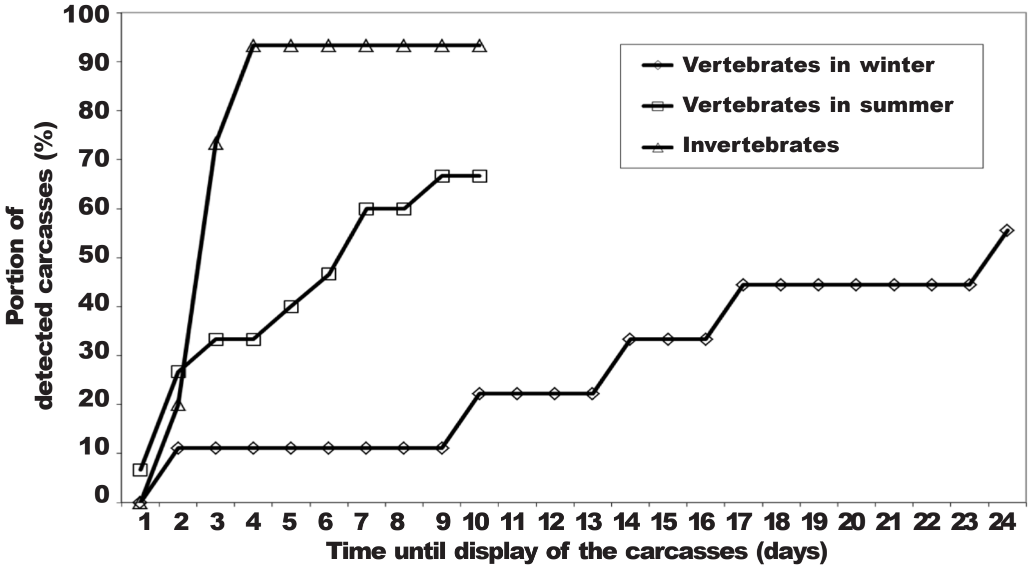

Fig. 3. Observed time until detection of carcasses by invertebrates and vertebrates in summer and winter, respectively. Starting from 0% (unimpaired carcass, no sign of detection) to 100% (completely consumed carcass, detected).

Fig. 3. Tiempo observado hasta la detección de los cadáveres por parte de los invertebrados y los vertebrados en verano y en invierno, respectivamente. Desde 0% (cadáver intacto, ninguna señal detectada) al 100% (cadáver completamente consumido).

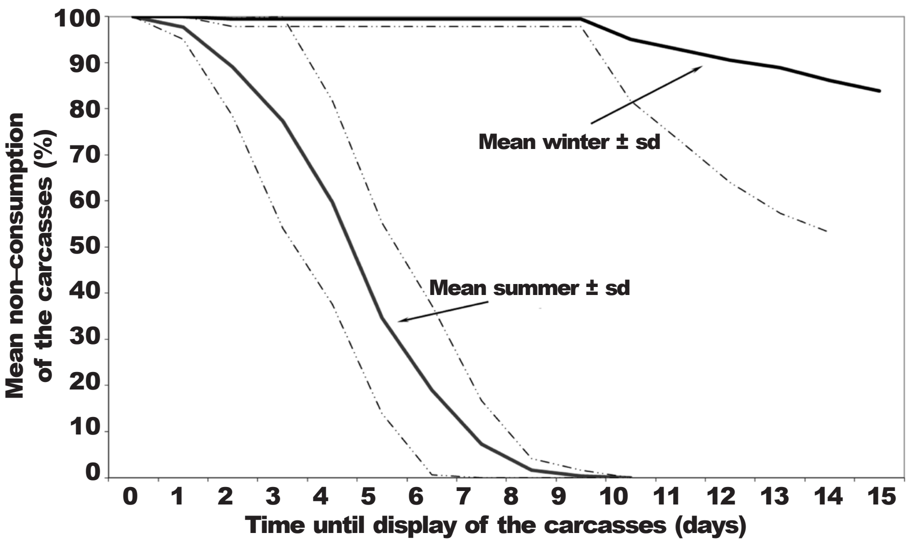

Fig. 4. Observed relative progress of carcass consumption in summer (vertebrates and invertebrates) and winter (vertebrates only), starting from 100% (unimpaired carcass) to 0% (completely consumed). The solid lines indicate the average in each season. The dash–dotted lines on each side of each solid line indicate the standard deviation.

Fig. 4. Progreso relativo observado del consumo de cadáveres en verano (vertebrados e invertebrados) y en invierno (solo vertebrados), desde 100% (cadáver intacto) al 0% (completamente consumido). Las líneas continuas indican el promedio de cada estación. Las líneas discontinuas a cada lado de las líneas continuas indican la desviación estándar.

as the main scavengers in the Białowieża Forest in Poland. However, they only observed lynx sporadically at the carcasses. In the same forest, Jedrzejewski et al. (1993) identified wild boar as the most frequent scavenger species, followed by raven and red fox. In the Swiss Alps and the Carpathian mountains of Romania, red fox was the predominant scavenger (Jobin et al., 2000; Kellermann, 2001). In our study during the summer, invertebrates such as blowflies and flesh–flies were the most efficient carcass finders and scavengers. Vertebrates such as red fox and wild boar usually found the carcass only after four days. Although red fox (Jobin et al., 2000) and wild boar (Jedrzejewska & Jedrzejewski, 1998) have little difficulty locating cached carcasses, days could pass until these scavengers discovered carrion by the scent. In contrast, the common buzzard and Eurasian jay sometimes found the carcass on the first day, but their consumption was very low. Other birds, namely vultures and ravens, are also very effective in locating carrion (Cortes–Avizanda et al., 2012). For example, turkey vultures (*Cathartes aura)* were able to find 96% of the carcasses within three days (Houston, 1986), and vultures can consume a 100 kg carcass within 30 min (Houston, 1974). In contrast to Poland, where ravens found 92% of the carcasses within three days and drew the attention of other species to their finds (Selva, 2004), this species was not observed in our study. In Poland, most of the carcasses, including European bison (*Bison bonasus)*, red deer, and wild boar, were larger than in our study and were mostly found by avian scavengers in open rather than in closed woodland.

The time it takes to locate a carcass is an important factor and depends strongly on the conditions under which a lynx leaves its kill. The risk of lynx kills being discovered by scavengers is probably low, because lynx often move the kill from the killing site and camouflage it. They also keep the immediate area where they consumes their kill tidy, with the bones and hide thoroughly cleaned (Kruuk, 1986; Hucht–Ciorga, 1988; Jedrzejewska & Jedrzejewski, 1998; Breitenmoser & Breitenmoser–Würsten, 2008). In a large area covered by closed forest, it is unlikely that scavenging birds, such as ravens, can easily locate the hidden, relatively small lynx kills. This could explain why ravens, which are common in our study area, were not observed at the carcasses. While lynx are capable of relocating and covering small roe deer kills, they are not able to do so with large red deer carcasses. For this reason, in the study of Jedrzejewska & Jedrzejewski (1998), scavengers were observed at only 28% of the roe deer kills but at 77% of the red deer kills. These authors also noted that scavengers visited 63% of the wolf kills, but only 38% of the lynx kills, which indicates that lynx are able to hide their kills from scavengers effectively. At the peak of maggot development, hedgehogs and wild boar visited the carcasses, eating mainly maggots and consuming little flesh. Besides a large proportion of plant matter, the omnivorous wild boars also consume a broad spectrum of invertebrates and carrion (Niethammer & Krapp, 1986; Briedermann, 1990).

The differences in carcass consumption between summer and winter are probably primarily due to four factors. First, temperature seems to mediate competition between vertebrate scavengers and invertebrate decomposers (DeVault et al., 2004). At temperatures below 0°C, blowflies and flesh–flies become inactive, and as temperatures increase, the rate at which maggots consume a carcass increases (Rognes, 1991; Campobasso et al., 2001). Second, in winter, snow often covers the carcasses, making it difficult for scavengers to detect them, both visually and olfactorily. Third, in contrast, defoliation and snow under a fresh kill increase the visibility of the carcasses from the air, possibly explaining the higher number of observations of European jay and goshawk (*Accipter gentilis)* in winter in our study. Poor visibility could also explain the decrease in scavenging by ravens in spring and summer (Kellermann, 2001). In our study, however, the common buzzard showed less scavenging activity in winter. This can be explained by the fact that buzzards leave their territories and disperse after the first snowfall. And lastly, in winter, food availability decreases and carrion becomes an important alternative trophic resource (Lockie, 1959; Goszczynski, 1974; Festetics, 1980; Pulliainen, 1981; Jedrzejewski & Jedrzejewska, 1992; Labhardt, 1996; Selva, 2004; Cortes–Avizanda et al., 2009). In summer, food is available in abundance, and most scavengers do not make use of carrion. Both our observations and those of Labhardt (1996) on the lower number of scavenging red foxes in spring and summer support these conclusions.

Our observed scavenger consumption rate of 0.7 % in winter was much lower than that observed in winter studies in Poland (15%; Jedrzejewski & Jedrzejewska, 1998) and Romania (18%; Kellermann, 2001), probably because effective scavengers, such as ravens, did not visit the carcasses, and predators with conspicuous kills such as wolves, which occur in Poland and Romania (Selva, 2004), do not occur in our study area. Another explanation could be the lower scavenger densities in the mountainous, snow rich environment of the Bavarian Forest. This conclusion is also supported by the relatively large time span the vertebrate scavengers needed to detect the carcasses. Although, in our study, various vertebrates were observed at the carcasses, their influence was so low that they cannot be considered to be competitors of lynx. Surprisingly, the second most frequently observed scavenger was the lynx. They consumed more flesh than any of the other observed vertebrates. Other studies have rarely recorded lynx consuming carrion other than their own kills (Hucht–Ciorga, 1988; Selva, 2004; Selva et al., 2005). Hucht–Ciorga (1988) documented for the Bavarian forest that lynxes sometimes only took foreign carrion when it was placed next to the lynx kill. One explanation for this behaviour might be the practice of hunters in the area to regularly leave the remains of shot deer, a predictable food supply for lynx. Our observation of three lynx feeding on the same carcass might be explained by the fact that solitary individuals of different sex are more tolerant of each other at breeding time (Schmidt

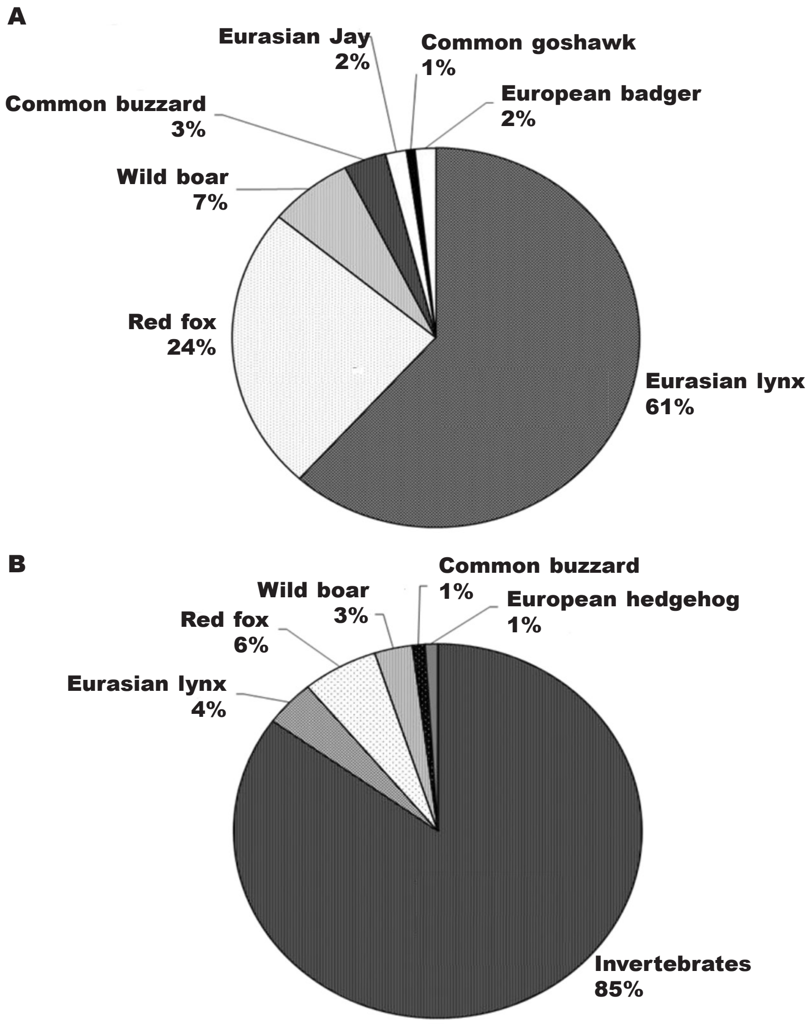

Fig. 5. Carcass consumption by the different species in percent in summer (A) and winter (B), determined with the criteria shown in table 1.

Fig. 5. Consumo de cadáveres por parte de las diferentes especies en verano (A) y en invierno (B), determinado con el criterio mostrado en la tabla 1.

et al., 1997; Breitenmoser & Breitenmoser–Würsten, 2008). Another explanation might be that sub–adults scavenge the kills of a territorial adult when it is not present or is alternately feeding on several simultaneously available kills.

Another interesting observation was two lynx feeding simultaneously on one carcass in winter, leaving their own scat alternating with other animals feeding on the same carcass, including red fox, wild boar and badger. In Switzerland, red foxes visited natural lynx kills only after lynx had abandoned the kill site (Jobin et al., 2000), whereas in Romania, red foxes frequented lynx kills while lynx were still utilising them (Kellermann, 2001).

Despite the small number of simulated kills in this study, our results indicate that the impact of vertebrates on the consumption was low all year. We conclude that other vertebrates in the national park are not strong competitors for lynx and that the impact of invertebrates on carrion decomposition should be given a higher priority in future research. In our study, blowflies and their kin were the most effective scavengers during the summer months. However, in natural lynx kills, lynx feed regularly on the carcass, thereby reducing the ideal nutritional conditions for maggots by not allowing their development to the same extent as in simulated kills (Smith, 1986). A high impact of scavenging maggots on lynx kills would be expected especially under natural conditions when the prey is large, such as a red deer, which takes a single lynx about seven days to completely consume. Nevertheless, invertebrates can out–compete other scavengers, since they are the first to find the carrion. Depending on temperature and season, their development can rapidly increase so that carcasses are mostly consumed when vertebrates arrive.

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