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NOTES AND COMMENTS

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Scavenging and carcass caching behavior by European wildcat (*Felis silvestris*)

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Abstract
While scavenging has been repeatedly reported for several felid species, surprisingly little information is available on scavenging behavior of the European wildcat (*Felis silvestris*). To fill this knowledge gap, we used camera traps to document scavenging behavior at the 48 experimentally set deer carcasses at random locations throughout the year. We recorded European wildcats scavenging on 38% of the eight carcasses set in winter and on none set in the other parts of the year. Wildcats fed on two carcasses for extended periods (up to 22 days) with an average of 3.3 visits per day and 7.8-h interval between the visits. We recorded scavenging throughout the day, but analysis indicated a crepuscular pattern. We also recorded caching behavior on 7% of the visits (n = 105), when wildcats used leaves or snow to partly or completely cover the carcasses. Beside wildcats, 12 other vertebrate species of scavengers were recorded at the carcasses. We recorded agonistic interaction with European badger (*Meles meles*) and despite its smaller size, the wildcat managed to defend the carcass. The extensive feeding, frequent caching behavior and active defense from scavengers indicate that the wildcats recognized the ungulate carcasses as an important food source in winter and that scavenging could be a neglected aspect of the European wildcat ecology. We also suggest that caching behavior could be regularly used by the European wildcat when feeding on larger carcasses, but was likely previously missed due to limited research effort to record scavenging and caching behavior.

KEYWORDS
camera traps, felids, food caching, interference competition, scavengers

1 | INTRODUCTION

Scavenging, where organisms from microbes to vertebrates compete to consume ephemeral carrion, is an important ecological process (Sebastián-González et al., 2019; Wilmers, Stahler, Crabtree, Smith, & Getz, 2003). Scavengers provide functions in ecosystems and to humanity by removing decaying carrion and potentially harmful pathogens, as well as stabilizing food webs (Ćirović, Penezić, & Krofel, 2016; Sebastián-González et al., 2020; Wilson & Wolkovich, 2011). At the same time, carrion is an inexpensive resource that is used as a nutritional supplement in the diet of many facultative scavengers (Allen, Elbroch, Wilmers, & Wittmer, 2015; Inagaki et al., 2020), especially during winter when other food sources are less available (Krofel, 2011; Selva, Jedrzejewska, Jedrzejewski, & Wajrak, 2005; Wilmers et al., 2003). Despite the benefits of feeding on carrion, there are also risks of injury or death, since fresh carcasses often attract several scavengers, which results in increased probability for agonistic inter- or intra-specific interactions (Allen, Wilmers, Elbroch, Golla, & Wittmer, 2016). Many scavengers and predators have developed various behavioral adjustments to reduce the competition, such as caching the carcass in trees, in caves or covering it with various materials (Balme, Miller, Pitman, & Hunter, 2017; Bischoff-Mattson & Mattson, 2009; de Ruiter & Berger, 2001; Krofel, Skrbinšek, & Mohorović, 2019).

Felids are mostly hyper-carnivorous specialized hunters with dentition and other morphological adaptations specialized for hunting (Van Valkenburgh, 1989). However, many felid species readily scavenge when carcasses are available (Hunter, 2015). The proportion of food obtained through scavenging is generally considered to be lower compared to the more generalist carnivores (e.g., hyaenids, ursids, canids and mustelids), but can still be substantial for some felids. Scavenging is frequently reported for the larger felids of the *Panthera* lineage, while much less is known about this behavior among the smaller cats. Scavenging has been reported for several of the smaller felid species (Hunter, 2015), including the African wildcat (*Felis lybica*) (Herbst, 2009), sand cat (*F. margarita*) (Brighten & Burnside, 2019) and black-footed cat (*Felis nigripes*) (Renard, Lavoie, Pitt, & Larivière, 2015; Sliwa, 1994), many of which were also reported caching larger kills or carcasses. It remains unknown whether the lower frequency of reporting is connected with lower frequency of scavenging among smaller felids or is this due to a lack of studies on scavenging behavior of the smaller felids.

Surprisingly little information is available on scavenging behavior of the European wildcat (*Felis silvestris*). European wildcats occur predominantly in forested landscapes of Europe and feed mostly on rodents and other small prey (Hunter, 2015). While about half of the wildcat dietary studies in Europe reported consumption of ungulates, they typically represent less than 2% of diet (see review by Apostolico, Vercillo, La Porta, & Ragni, 2016). Since ungulates are usually too large for a wildcat to kill, it is likely that a large part of this food is obtained through scavenging, but predation cannot be excluded, because such dietary studies rely on analysis of stomach content or scats and are thus not able to distinguish between predation and scavenging. Thus, the scavenging behavior and the ecological role of European wildcats within the scavenging guilds in Europe remains poorly understood. To fill this knowledge gap, we used motion-triggered camera traps deployed at 48 experimentally-set deer carcasses in forest ecosystems in Slovenia and Italy to record scavenging by European wildcats. Our goal was to describe the frequency of scavenging and caching behavior, observe potential interspecific interactions at the carcasses, and to study circadian and seasonal use of the carcasses by the wildcats.

2 | METHODS

Our study was conducted in the forest landscape of Southern Slovenia and Northeastern Italy, where three regions were selected to monitor scavenging activity on experimentally-set ungulate carcasses: Kočevska (45°30′–45°49′N, 14°42′–14°60′E), Notranjska (45°35′–45°58′N, 14°15′–14°30′E) and Primorska-Kras (45°32′–46°04′N, 14°13′–14°50′E). Kočevska and Notranjska are part of the Dinaric forest ecosystem characterized by high cover of mature forests dominated by fir and beech associations. The average annual temperature in these regions ranges from 6 to 9°C and snow cover lasts from 50 days at 500 m and up to several months at higher elevations. Primorska-Kras is located near the Slovenian-Italian border and has stronger Mediterranean influence and lower forest cover with predominant oak, pine and hophornbeam associations. The average annual temperature in this region ranges from 9 to 13°C and snow cover is mostly absent or lasts less than 10 days per year. No reliable estimates of European wildcat densities exist for these regions, but according to personal experiences from the fieldwork in these regions, we assume that densities are higher in Dinaric forests than in the Primorska-Kras region.

We placed camera traps on deer carcasses ($n = 48$) killed through vehicle collisions in the three study areas: 24 carcasses of European roe deer (*Capreolus capreolus*) and one carcass of red deer (*Cervus elaphus*) in Kočevska, six roe deer and two red deer carcasses in Notranjska, and 15 roe deer carcasses in Primorska-Kras (Table 1). Carcasses were placed at randomly-selected locations within the study area and monitored with several types of motion-activated camera traps, including commercial camera traps with black infrared (UOVision UV565GD, Scoutguard Sg580m and U-Way U150X) in Kočevsko and Primorska-Kras, and infrared-sensitive IP camera system set (Mobotix M22M-Sec-Night) with independent infrared light ($n = 7$) or DSLR camera (Canon 350D) with white flash ($n = 1$) in Notranjska. Monitoring of carcasses took place in 2010–2020 through all the seasons. All carcasses were monitored until all muscle tissue was consumed or/and completely decomposed.

We manually checked all the recordings and extracted those with wildcats. For the purpose of analysis, we separated the year into two seasons: winter (December–March) and summer (April–November). We calculated the proportion of carcasses used by the

TABLE 1 Proportion of carcasses scavenged by the European wildcats in each study area and season

Season	Kočevska	Notranjska	Primorska-Kras	All areas
Winter	50% (4)	25% (4)	– (0)	38% (8)
Summer	0% (21)	0% (4)	0% (15)	0% (40)
All year	8% (25)	13% (8)	0% (15)	6% (48)

Note: Sample sizes are provided in the parenthesis. Seasonal differences were statistically significant (Fisher's Exact Test, $df = 1$, $p = .008$).

wildcats in each study area and each season, recorded number of visits to the carcasses and time required for the wildcats to find the carcasses, analyzed circadian activity and noted feeding and carcass-caching behavior, as well as any interspecific interactions taking place around the monitored carcasses. We did not attempt to measure the duration of visits, because in most cases the exact time of departure from the carcass was not recorded. We counted recordings as different visits, when they were more than 30 min apart without any record in-between. Due to difficulties in distinguishing different wildcats from the video recordings, the number of individuals using the carcasses remains unknown. In Notranjska, the only carcass visited by the wildcat was monitored with a DSLR photo-camera with white flash, which resulted in a single photo. Possibly the flash disturbed the wildcat and because no video recordings were available, we were not able to observe behavior in any details. Therefore we used this record only for calculating the proportion of carcasses found by the wildcats and time needed for wildcats to find the carcasses. We used kernel density estimation to determine the activity patterns of wildcat visits to carcasses, by transforming the time each visit started into radians values. We then used the overlap package (Meredith & Ridout, 2017) to fit the data to a circular kernel density and estimated the activity among time periods from the distribution of the kernel density. We used Fisher's Exact Test to tests for significance of seasonal differences in the use of carcasses.

3 | RESULTS

European wildcats were recorded on two (8%) of the monitored carcasses in Kočevska (both were from roe deer), one (13%) of the monitored carcasses in Notranjska (red deer), and none of the carcasses in Primorska-Kras (Table 1). All three instances of wildcat scavenging occurred in winter, and scavenging was significantly more often in winter than in summer (Fisher's Exact Test, $df = 1$, $p = .008$). Carcasses were discovered by the wildcats on average 13.4 days after deployment (on 2nd, 8th and 30th day after deployment). In total, we recorded 106 visits to the carcasses. In Notranjska, the wildcat visited the carcass only once (likely due to disturbance by camera flash), while in Kočevska, wildcats visited carcasses on average 52.5 times per carcass (46 and 59 times for each of the carcasses) with an average return interval between consecutive visits of 6.2 h ($n = 103$) and maximum of 41 h (average for each of the carcasses: 4.4 and 7.8 h). On average, the wildcats visited carcass 3.2-times per day (average for each of the carcasses: 2.7 and 4.2-times). The first carcass in Kočevska was recorded visited for 22 days (visited at least once on every day except the ninth day) and the second carcass was visited for 11 days (visited every day).

We recorded wildcats feeding on these carcasses on 36% of the visits ($n = 105$; 35% for the first carcass and 37% for the first carcass). They were feeding predominantly on the hindquarters and afterwards to a lesser extent on the abdomen, back, chest cavity, shoulders and neck (Supporting Information 1). Caching behavior was observed at both carcasses monitored with video surveillance, when wildcats used leaves, twigs or snow to partly or completely cover the carcass with their front paws (Supporting Information 2). Wildcats were recorded covering the carcass at least on 7% of the visits (n = 105; 5% and 9% for each carcass) and covering was more frequent during the first visits to each of the carcasses (57% of the recorded caching behaviors occurred during the first 2 days after wildcats discovered the carcasses). When returning to the carcasses, wildcats sometimes used front paws to again expose the carcass for feeding. The same behavior was used when snowfall covered the carcasses. In deep snow, wildcats also used carcass for resting by sitting or lying on top of them (Supporting Information 3). We did not observe any urine-spraying or defecating by the wildcats around the carcasses, but claw-marking (another scent-marking behavior) was recorded once (Supporting Information 4). Wildcat visits to the carcasses were recorded throughout the 24-h cycle with a crepuscular pattern and the strongest peak in the early morning (Figure 1). Circadian use was similar for both carcasses (Supporting Information 5, Figure S1).

We recorded a confrontation with an European badger (*Meles meles*), which was aggressively chased from the carcass by the wildcat with raised tail, growling,

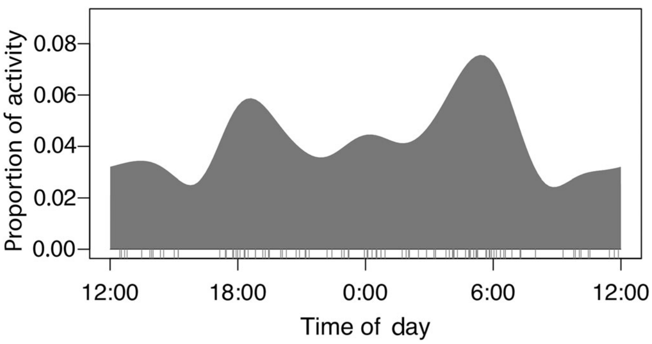

FIGURE 1 Circadian use of roe deer carcasses by the European wildcats in Kočevska, Dinaric Mountains, Slovenia as estimated via kernel density

hissing and snarling (Supporting Information 6). Two other potential interactions were noted, but only the wildcat could be seen on the video, while the other animals were outside of the camera view and could only be heard. Other scavengers recorded at the same carcasses as wildcats, but which we did not observe to interact directly with the wildcats, include (with % of all monitored carcasses that were visited by given species): red fox (*Vulpes vulpes*; 79%), wild boar (*Sus scrofa*; 29%), mouse (*Apodemus* sp.; 2%), common buzzard (*Buteo buteo*; 27%), Ural owl (*Strix uralensis*; 2%) and common raven (*Corvus corax*; 10%). Scavengers at other carcasses during the study included: brown bear (*Ursus arctos*; 42%), golden jackal (*Canis aureus*; 2%), domestic dog (*Canis familiaris*; 2%), beech marten (*Martes foina*; 38%) and great tit (*Parus major*; 2%).

4 | DISCUSSION

We have documented that European wildcats scavenged from 38% of the carcasses we placed during winter, and that they fed on these carcasses for extended periods with several visits per day. The extensive feeding, frequent caching behavior and active defense from other scavengers indicates that the wildcats recognized the carcasses as an important food source. Although the sample size was relatively small (48 carcasses in total and 8 from winter period), this indicates that scavenging could be an important, but neglected aspect of behavioral ecology of European wildcat during the winter period.

Many facultative scavengers use carrion as a supplemental food source (Wilson & Wolkovich, 2011). This is especially true during winter when other food sources may be less available but energetic needs are often higher (Krofel, 2011; Selva et al., 2005; Wilmers et al., 2003). For European wildcats, large ungulate carcasses may be an important source of food during winter because rodent availability could be low because of snow cover (Selva et al., 2005; Sonerud, 1986). Winter is also the period when availability of ungulate carcasses is highest due to increased natural mortality connected with high snow levels, cold temperatures and reduced food availability for herbivores (Selva et al., 2005; Selva, Jedrzejewska, Jedrzejewski, & Wajrak, 2003). More frequent consumption of ungulates during winter by the European wildcats was also suggested by the diet analyses (Apostolico et al., 2016). Absence of wildcats at the monitored carcasses in Primorska-Kras region could be connected to several factors, but is most likely related to the lack of monitored carcasses during winter period in this region.

Many carnivores cache animal carcasses they have killed or scavenged from as a means of food preservation. Caching can be used for long-term storage of surplus food during times of hyperabundance, such as when arctic foxes (*Alopex lagopus*) store waterfowl eggs from nesting season for later consumption (Careau, Giroux, & Berteaux, 2007). But more often, caching is used for short-term food storage, especially for large animal carcasses. For example, bears will cover the carcasses of ungulates or other large prey they kill or scavenge in order to consume over a period of days (Allen, Wittmer, Ingaki, Yamazaki, & Koike, 2020) and similar behavior is used by several felid species, especially for remains of the prey they have killed (Hunter, 2015). There is very limited literature available about the caching behavior of European wildcats, for example, Macdonald (1976) reported probable caching in captive conditions and Ruiz-Villar, López-Bao, and Palomares (2020) recently reported about a wildcat scavenging and caching a road-killed deer. Most of the previously documented incidents actually refer to the African wildcats (L. Hunter, pers. comm.), which were formerly treated as a subspecies of *F. silvestris*, but are now recognized as a distinct species (Kitchener et al., 2017). However, we have shown that European wildcats regularly cached both carcasses they repeatedly scavenged from. They used leaves, twigs and snow to cover the carcass (sometimes completely) in a similar way as observed in felids that frequently consume ungulates, for example, Eurasian lynx (Krofel et al., 2019) and puma (Bischoff-Mattson & Mattson, 2009). This behavior is thought to effectively slow down decomposition and reduce probability of carcass detection by competing invertebrate and vertebrate scavengers (Bischoff-Mattson & Mattson, 2009; Krofel et al., 2019). The observed caching activity, along with the high frequency and prolonged feeding, suggests wildcats are trying to preserve the carcass for as long as possible. We suggest that caching behavior could be regularly performed by European wildcats when using larger carcasses, but was previously likely neglected due to limited research effort to document this behavior. Also during our monitoring, we likely missed some of this behavior, because the moment of departure was often not recorded on the camera and wildcats mostly covered the carcasses before leaving.

New knowledge about the ungulate-caching behavior by European wildcats has implications also for researchers and management activities that use animal signs to detect presence of wildlife species. Field guides for animal tracking in Europe often suggest that caching of ungulate carcasses by covering with leaves, snow and other material is a reliable sign of the lynx or bear presence (e.g., Bang, Dahlstrøm, & Walters, 2001; Krofel & Potočnik, 2016; Molinari, Breitenmoser, & Molinari, 2000). Our observations demonstrate that partly or completely covered ungulate carcass could also be the result of scavenging by a European wildcat. While caching by bears can be typically distinguished by large amount of material used to cover the carcass, caching by the wildcat results in very similar signs to those made by the Eurasian lynx. Besides, the observed feeding pattern of the wildcats (predominant feeding on the hindquarters and gradual proceeding towards the neck) was the same as reported in Eurasian lynx (Krofel et al., 2019). Thus we suggest caution when determining lynx kill sites only based on the signs of covering the carcass, in regions where wildcats are present.

Use of camera-traps also enabled us to observe interspecific interaction between European wildcat and European badger. This was likely connected with the interference competition for the carcass, as badgers were recorded scavenging on this and other carcasses. Although European badger is larger in body size compared to European wildcat, the latter managed to defend the carcass during the encounter we observed. This could reflect higher resource holding potential of the wildcat compared to the badger, similar to other felid species that are known for their higher resource holding potential compared to other carnivores (Allen & Krofel, 2017). Resource holding potential is often not dependent only on body size, but can also be related to other physical features, behavioral traits, motivation and ownership status (Allen & Krofel, 2017).

The advent of camera traps has been already instrumental in documenting cryptic scavenging behaviors of wild felids and other wildlife (e.g., Allen et al., 2015; Krofel & Jerina, 2016; Peers, Majchrzak, Konkolics, Boonstra, & Boutin, 2018). Using an experimental design and monitoring of ungulate carcasses with camera traps have enabled us to study this neglected aspect of European wildcat ecology. In this way we were able to differentiate scavenging from predation, which is often difficult with the use of traditional methods, such as scat or stomach content analysis, used in previous research. The use of other field methods would also make it difficult to document carcass caching by wildcats, which is likely why it has gone largely undetected until now. Therefore we recommend further research using this approach to better understand behavior and ecological processes connected with scavenging by wildcats and other felids, including interspecific interactions.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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