Caching Behavior of Large Prey by Eurasian Lynx: Quantifying the Anti-Scavenging Benefits

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Abstract: Large solitary felids often kill large prey items that can provide multiple meals. However, being able to utilize these multiple meals requires that they can cache the meat in a manner that delays its discovery by vertebrate and invertebrate scavengers. Covering the kill with vegetation and snow is a commonly observed strategy among felids. This study investigates the utility of this strategy using observational data from Eurasian lynx (*Lynx lynx*)-killed roe deer (*Capreolus capreolus*) carcasses, and a set of two experiments focused on vertebrate and invertebrate scavengers, respectively. Lynx-killed roe deer that were covered by snow or vegetation were less likely to have been visited by scavengers. Experimentally-deployed video-monitored roe deer carcasses had significantly longer time prior to discovery by avian scavengers when covered with vegetation. Carcass parts placed in cages that excluded vertebrate scavengers had delayed invertebrate activity when covered with vegetation. All three datasets indicated that covering a kill was a successful caching/anti-scavenger strategy. These results can help explain why lynx functional responses reach plateaus at relatively low kill rates. The success of this anti-scavenging behavior therefore has clear effects on the dynamics of a predator–prey system.

Keywords: caching; *Capreolus capreolus*; carrion; Eurasian lynx; *Lynx lynx*; Norway; predation; roe deer; scavenging

1. Introduction

The impacts of large carnivore predation on wild ungulate populations has received much research focus and considerable effort has been spent on quantifying predation rates as a function of prey density (i.e., functional responses, [1]) as these are regarded as key parameters to model predator impacts [2,3]. While functional responses may be crucial for some solitary species feeding on small prey and for social carnivores where group size allows rapid consumption of even large prey, there may be some predator–prey systems where other predation parameters are equally important. For example, large solitary felids routinely kill large ungulate prey equal to, or several times heavier than, their body weight that can potentially provide food for multiple days [4–7]. For such species handling and consumption time are likely to exceed search and killing time [8,9]. Any factor affecting their ability to consume a kill completely could result in an increased kill rate.

An ungulate carcass represents a very attractive resource to a range of vertebrate and invertebrate scavengers [10–15]. The effect of such scavenging and kleptoparasitic loss of kills is believed to be an important driver of kill rates [16], energetics [17,18], and potentially even sociality [19]. The issue

has been widely explored for group hunting canid species, and has been reported for solitary felid species such as cheetah (*Acinonyx jubatus*) [20] and mountain lion (*Puma concolor*) [21]. Solitary felids are believed to use a range of behaviors, including covering the kill with snow and/or vegetation as an anti-scavenging/anti-kleptoparasitic caching strategy [22,23]. In the Bavarian forest (Germany), invertebrates were the most important scavengers of simulated kills in both summer and winter [13].

Eurasian lynx (*Lynx lynx*) in Central and Northern Europe, in contrast to their congeneric species and Eurasian lynx in Turkey, feeding mostly on smaller prey such as brown hares [24], have the ecology of far larger felids, mainly feeding on roe deer (*Capreolus capreolus*), which are 50–100% heavier than an adult lynx [6]. They normally feed on roe deer kills for periods of 2–7 days [8]. Vegetation and snow are used to cover kills during this period. We aimed to quantify the anti-scavenging effect of this covering behavior through three approaches. Firstly, we present observational data based on investigations of lynx-killed roe deer. Secondly, we present results from deer carcasses that were experimentally placed in the forest and video-monitored to determine the discovery time by vertebrate scavengers. Thirdly, we present the result of an experiment that recorded the rate at which invertebrate scavengers consumed carcass parts that were not accessible to vertebrate scavengers. In all cases, we compared discovery/consumption rates of carcasses that were covered with vegetation in the manner that lynx use, or left uncovered.

2. Materials and Methods

2.1. Study Area

The study was conducted in South-Eastern Norway, in Viken and Innlandet counties (formerly Hedmark, Østfold and Akershus counties). The northern part of the study area is characterized by extensive boreal forest with relatively low human population densities. The habitat in the southern part consists of intensively exploited boreal forest interspersed with agricultural land [25]. At the time of the study, Eurasian lynx were widespread in the landscape and mainly preyed on roe deer [6]. Important potential vertebrate scavengers were pine marten (*Martes martes*), badger (*Meles meles*), red fox (*Vulpes vulpes*), domestic cat (*Felis domesticus*), raven (*Corvus corax*), hooded crow (*Corvus corone cornix*), magpie (*Pica pica*) and Eurasian jay (*Garrulus glandarius*).

2.2. Lynx-Killed Roe Deer

The roe deer kills of very high frequency (VHF) radio-collared and snow-tracked lynx were routinely located in the period 1995–2008 [25,26]. Field procedures are described in Nilsen et al. 2009 [25]. Permissions were granted by the Norwegian Environment Agency and procedures were approved by the Norwegian Committee for Experimental Animal Welfare (permit numbers 08/127430, 07/81885, 07/7883, 2004/48647, 201/01/641.5/FHB, 127/03/641.5/fhb, 1460/99/641.5/FBe, 1081/97/641.5/FBe, and Norwegian Institute for Nature Research (NINA) 1/95). Most of the lynx-killed roe deer carcasses included in this study were found in winter (72 in winter and 7 in summer, Table S1). Kills were checked at various times. When studying predation behavior of collared lynx we only approached kills when the lynx had abandoned the kill. When snow-tracking unmarked lynx or trying to recapture already collared lynx, we would approach a new found kill straight away in order to place traps. When the kills were examined, any signs of the presence of scavengers were recorded (such as scats, footprints, feathers) as well as signs of the kill being covered by the lynx. However, we cannot exclude that some scavengers remained undetected. We knew lynx identity for 53 lynx-killed roe deer carcasses. For this subset of data, we explored individual variation in lynx caching behavior by comparing the proportion of covered carcasses for single individuals vs. females with kittens, and for males vs. females, by means of Chi-square tests. We had information on habitat type for 66 of the lynx-killed roe deer carcasses. For this subset of data, we compared the proportion of covered carcasses in open habitats and forest habitats, by means of Chi-square tests.

We used multivariate logistic regression models to explore which variables better explained the probability of a carcass being scavenged or not. The full model explaining the probability of a carcass being scavenged included number of days after being killed, the treatment (not covered/covered) and their interaction as explanatory variables. The final model was selected by model reduction, where only explanatory variables with significance $p < 0.05$ were retained in the model.

2.3. Experimentally-Deployed Roe Deer Carcasses

From 2002 to 2003, we monitored 26 experimentally-deployed whole roe deer carcasses (obtained as roadkill) as simulated lynx kills for 7 days using time-lapse video equipment (Table S2). The time-lapse video observations were made with a VHS tape recorder (Sanyo TLS 1960P) powered by two 12-volt batteries. This was connected to an infrared light (IR 70, 940 Nm), that was switched on 15 min before dusk and switched off 15 min after dawn, and a lens (Sony CWSHR WVF) with a miniTV cable (20 to 120 m long), so that the batteries and the tape could be changed every 24–72 h without disturbing the carcass site. We recorded 72 h on a 180 min videotape with a time-lapse of 2.5 frames per sec. The lens and IR light were mounted in a tree (2–3 m height) ca. 5 m from the carcass. The carcasses were deployed in forested habitat (in forest, small openings in forest, or forest edges). An equal number of kills were deployed in summer and winter seasons. Fourteen kills were completely covered with grass, moss or snow in the manner similar to lynx, and 12 were left completely exposed. For each kill, we determined the time of first arrival of mammalian and avian scavengers as a measure of time to detection. However, subsequent consumption rate by birds and mammals was not quantified, so detection time might not be directly related to consumption rate, although it is expected that scavengers detect the cues of other scavengers on a site [27]. Within seven days from deployment, four carcasses were not found by any scavengers, three were found only by mammals and five were found only by birds. Linear models were run to explore the factors influencing discovery time separately for birds and mammals, where the full model included treatment (covered/not covered), season (winter/summer) and their interaction as explanatory variables and number of days from deployment to discovery as dependent variable.

## 2.4. Invertebrate Scavenging Experiments

In summer 2003, we deployed two whole roe deer and eight roe deer body parts (obtained as roadkill animals, divided approximately into quarters for each treatment, with skin and hair in place). The five pairs of carcasses/carcass parts were placed in iron mesh cages (size $1 \times 1 \times 0.5$ m, mesh diameter 2.5 cm) in forest habitat to explore the rate of weight loss by invertebrate scavenging and decomposition while excluding all vertebrate scavengers above the size of a small rodent (Table S3). The experiment was designed to permit weighing the cage with only a minimal vertical lift to avoid losing tissue or dislodging parts of the carcass or the covering. A finer mesh (mesh diameter 1.9 cm) was also installed in the base of the cage, to minimize this issue, ensuring that only decomposition fluids and gasses were lost. However, it is important to be aware of the fact that the weight includes the eventual weight of insect eggs and maggots laid on, or feeding on, the carcass. Our scales were accurate to 100 g. We cannot exclude the possibility that small rodents might have removed some minor amounts of tissue. We used a paired experimental design, where one sample was covered with vegetation and another was left uncovered. Each sample was weighed daily (for a few missing days, we averaged the adjacent days) for 3 weeks following deployment. A four-parameter Weibull model, which represents an asymmetric sinusoidal decay [27], was fitted to the linear stretch of each subset of data by non-linear regression [28]. Three parameters were extracted to describe each curve: (1) day of start of decay (minimum value of the second order derivate of the curve); (2) day of inflection (minimum value of the first order derivate of the curve); (3) day of flattening out (maximum value of the second order derivate of the curve). The values for these three stages were compared using Mann–Whitney U tests.

Analyses were done in R [29], where the Weibull models were run with the add-on package drc [30].

3. Results

3.1. Lynx-Killed Roe Deer

We inspected 79 lynx-killed roe deer from one to eleven days after the kill was made. Eighteen of the 79 (23%) carcasses had tracks from one or several scavengers (thirteen, four, and one carcasses had signs of avian, mammalian and unknown scavengers, respectively). Lynx had covered 35 of 79 (44%) of the carcasses partially or totally with snow or a combination of live and dead plant material available at the kill-site. Only 9% of the covered carcasses vs. 28% of the uncovered carcasses were scavenged (Figure 1).
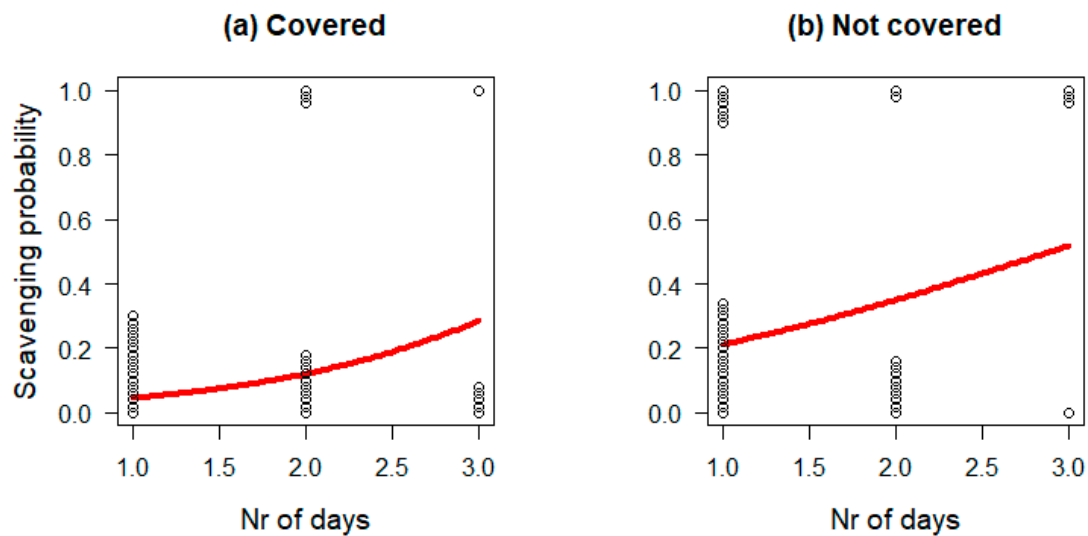
Figure 1. Logistic regression model curves explaining the probability of being scavenged in relation to the number of days since the kill was made for (**a**) covered and (**b**) not covered lynx-killed roe deer carcasses in South-Eastern Norway (*n* = 74).

Each identified lynx individual killed on average 2.21 (±1.35) of the 53 roe deer carcasses for which we had information on lynx identity. We could not detect differences in caching behavior between single individuals compared to family groups (female with kittens) (Chi-square = 1.93, df = 1, *p* = 0.164) or between males compared to females (Chi-square = 1.73, df = 1, *p* = 0.188). Similarly, we could not detect differences in caching behavior in open areas compared to forest (Chi-square = 0.433, df = 1, *p* = 0.5105).

The logistic model explaining the probability of being scavenged selected by model reduction included number of days after the kill and treatment as explanatory variables. The probability of being scavenged increased with number of days since the kill was made, and when the kill was uncovered. The regression equation for covered carcasses was y = 0.03 + 0.69 * Nr of days, whereas the regression equation for not covered carcasses was y = 0.80 + 0.69 * Nr of days (*p* < 0.05 for all terms).

3.2. Experimentally-Deployed Roe Deer Carcasses

For mammalian scavengers, the model reduction ended with a model including only the main effect of season with a positive effect of 'winter', implying a longer time to first discovery in winter (Adjusted R^2 = 0.376, *n* = 26, Table 1a; Figure 1). For avian scavengers, the model reduction included only the main effect of treatment with a negative effect of 'not covered', implying a longer time to first discovery of covered kills (R^2 = 0.446, *n* = 26, Table 1b, Figure 2).

Table 1. Estimates of model (selected by model reduction) explaining discovery time for (a) mammalian and (b) avian scavengers of 26 carcasses with season of placement, treatment (covered vs. not covered (NC)) and their interaction as explanatory variables.

	Estimate	SE	95% CI Lower	95% CI Upper	*p*-Value
(a) Mammals					
Summer	2.81	0.50	1.82	3.80	<0.001
Winter	3.13	0.71	1.73	4.53	<0.001
(b) Avian					
Covered	4.51	0.58	3.37	5.64	<0.001
Not covered	−3.25	0.85	−4.92	−1.57	<0.001
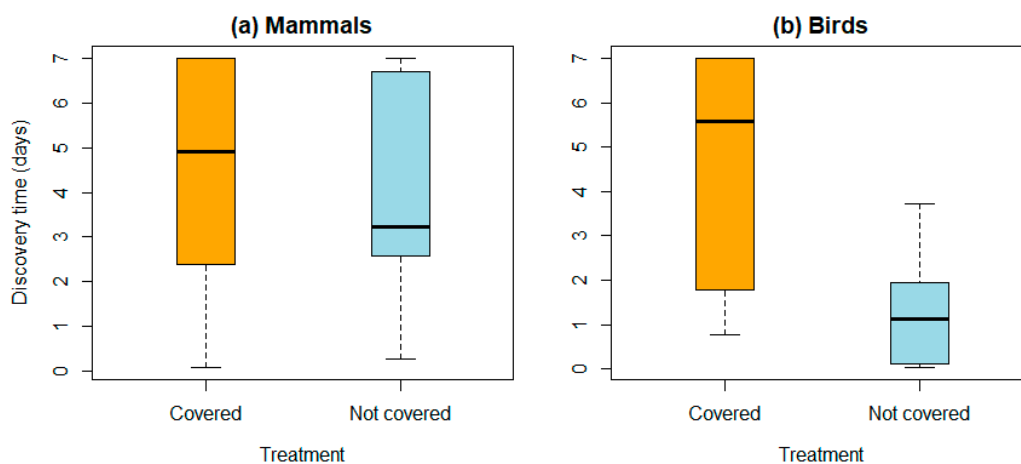
Figure 2. Box plots showing the effect of covering video-monitored experimentally-deployed roe deer carcasses on time to discovery (in days) for (**a**) mammalian, and (**b**) avian scavengers in South-Eastern Norway.

3.3. Insect Scavenging Experiments

Although in most cases the covered carcasses started to decay later than uncovered carcasses (*n* = 5 in each treatment), the difference between median dates of decay initiation of covered versus uncovered carcasses (6.27 vs. 4.27; ns) was not significant. Both the inflection point (8.41 vs. 5.41; *p* = 0.015) and day of flattening out of the decay curve (11.11 vs. 6.41; *p* = 0.0079) occurred significantly later for covered carcasses (Table 2, Figure 3), implying that covering slowed invertebrate consumption/decomposition.

Table 2. Values obtained by fitting a four-parameter Weibull model by non-linear regression to the consecutive weigh of the roe deer carcasses deployed to simulate lynx kills (NC: not covered; C: covered). In parentheses, it is reported the initial weight of the not covered/covered carcasses/carcass parts. Day of start of decay = minimum value of the second order derivate, inflection point = minimum value of the first order derivate and day of flattening out of the decay curve = maximum value of the second order derivate.

	Day of Start of Decay NC	C	Inflection Point NC	C	Day of Flattening Out NC	C
Whole carcass (25/23.2 kg)	5.47	18.05	7.57	20.01	9.59	21.89
August pair 1 (15/4.8 kg)	4.12	0.00	4.79	6.03	5.41	12.22
August pair 2 (3.2/3.3 kg)	4.26	4.07	5.38	6.84	6.48	9.45
September pair 1 (17.4/4 kg)	4.71	8.07	5.58	9.61	6.39	11.13
September pair 2 (3.3/3.2 kg)	4.04	6.28	5.02	8.41	5.94	10.46
Median	4.26	6.28	5.38	8.41	6.39	11.13
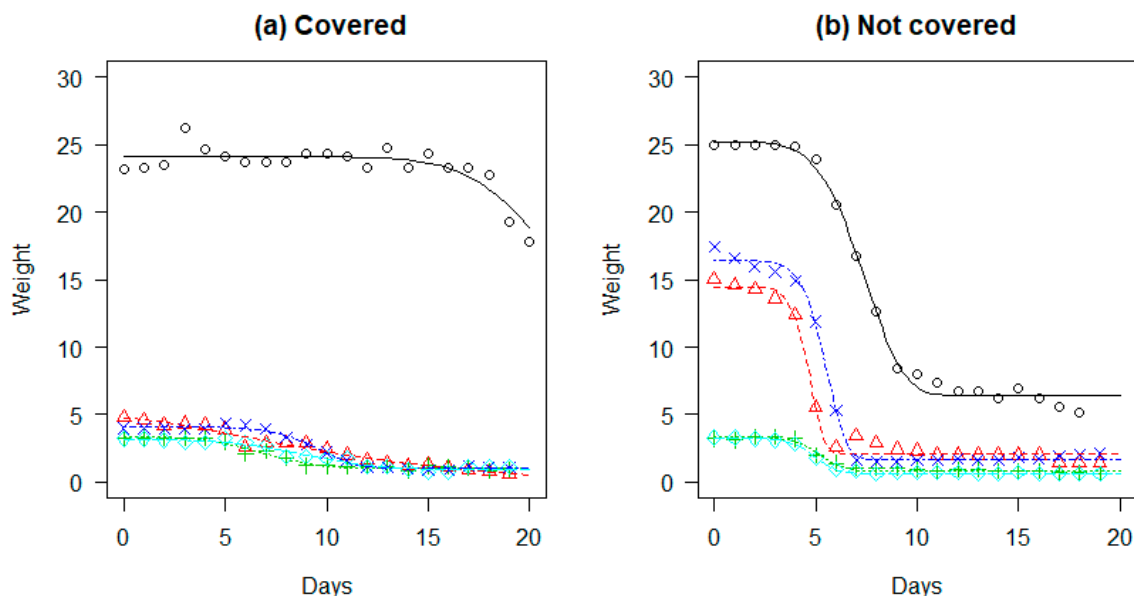
Figure 3. Daily weight variation (kg) and fitted Weibull curves describing the decay process of (**a**) five covered, and (**b**) five uncovered paired roe deer carcass or parts placed in a metal cage to exclude vertebrate scavengers during summer in South-Eastern Norway. The line in black in (**a**,**b**) are whole carcasses; the other lines are parts.

4. Discussion

This study provides clear evidence that the simple act of covering a kill with vegetation or snow delays scavenger arrival and the rate of meat loss. The lynx-killed roe deer that were uncovered were three times more likely to have been found by scavengers than the kills that were covered. Covering the video-monitored experimental carcasses delayed their discovery by avian scavengers by 4–5 days. Covering the carcass parts delayed the rate of consumption by invertebrates by more than five days, although this result should be taken with caution due to the limited sample size for the insect experiment. This implies that covering a carcass constitutes a very effective cache protection measure [13,31] for a large felid preying on ungulates in forested habitats. Our results are consistent with a similar study on mountain lion caching behavior in Arizona, which showed that simulated caching reduced wastage during dry and hot periods [21].

Although most of the lynx-killed roe deer carcasses were from the winter, and only ca. 10% were from the summer, it is likely that caching behavior is similar in the two seasons. In the summer, there is no snow to cover kills with, so lynx can only use vegetation, and there is more competition with invertebrate scavengers, making covering more important (see experiment). However, in the summer there are also more leaves on trees and bushes making visual detection by avian scavengers harder. In the summer, the olfactory cues due to insect and microorganism activity might also increase the probability of a carcass being discovered. These aspects are not likely to affect the overall relative utility of covering kills vs. leaving them uncovered.

Although other authors have described this tendency of large felids to cover their cached kills with vegetation e.g., [5,13,21], this is the first study to actually test the anti-scavenger efficacy of this measure in the field, using both observational data from documented lynx kills and experimental approaches. Combined, these studies are revealing insights into the subtle ways that predator behavior responds to the potential for food loss from both vertebrate and invertebrate scavengers [11].

The results from the video-monitoring suggest that covering was efficient for deterring avian, but not mammal, scavengers. This indicates that the effect is mainly through visual occlusion, rather than by reducing the olfactory signal of the kills. The effect on invertebrate activity is probably through a process of physically obstructing invertebrate access to the kill, although the covering may also shade the kill and reduce decomposition speed by reducing the temperature. In a similar study

conducted in the Bavarian forest in summer, roe deer carcasses simulating lynx kills (covered by vegetation) were completely consumed within 10 days, mostly by invertebrates [13].

Although the main focus of our study was to test the efficacy of caching, it is interesting to note that considerable periods of time, measured in days, went by before scavengers detected the kills. In contrast, studies on cheetahs in savannah ecosystems have shown that scavengers find kills within hours of death [20]. The effect is that many cheetah kills are either lost to kleptoparasites or are so rapidly consumed by scavengers that cheetahs are not able to consume more than one meal per kill. The lynxes in our study area, by comparison, were usually able to completely consume most of the meat on their kills over several days. This allows them to continue being roe deer specialists even when roe deer occur at low density [31], because even though there may be considerable search time expended in finding a prey, once killed it can provide food for many days. In turn, this can help explain why lynx presence has such a clear impact on low-density roe deer populations [32,33]. This efficient use of prey also implies that the energy budget of lynx should be considerably buffered against changes in prey density. The results also provide insight into the ways in which studying predator–prey dynamics needs to consider wider ecosystem processes.

At the time of our study, the area lacked the large scavengers such as wolverine (*Gulo gulo*), brown bear (*Ursus arctos*), wolf (*Canis lupus*) and wild boar (*Sus scrofa*), which could potentially drive a lynx off its kill and appropriate the kill in a single act. However, a study conducted in Sweden found no evidence of kleptoparasitism by wolves on roe deer killed by lynx [34]. The largest scavengers we documented were humans who regularly removed lynx kills [35], not an uncommon practice on a global scale [36]. It is hard to know how the absence of these natural members of the mammalian scavenger guild influences the generality of our results. A study conducted in Slovenia and Croatia found that brown bears were able to discover 32% of lynx prey remains, and 15% of all biomass of large prey killed by lynx was lost to bears [37]. Since this study was conducted, wolves and wild boar have colonized the landscape, opening for future comparative studies. However, the situation does reflect the current reality for lynx throughout much of its present day distribution in Europe [38,39], and the literature does tend to place greatest emphasis on the role of avian scavengers [16,40] for which our results indicate that the anti-scavenging behavior had the greatest effect.

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