Scavenging patterns of generalist predators in forested areas: The potential implications of increase in carrion availability on a threatened capercaillie population

Jorge Tobajas1, Pilar Oliva-Vidal1,2, Josep Piqué3, Ivan Afonso-Jordana4, Diego García-Ferre5, Rubén Moreno-Opo6 & Antoni Margalida1,2

1 Instituto de Investigación en Recursos Cinegéticos (IREC), CSIC-UCLM-JCCM, Ciudad Real, Spain
2 Department of Animal Science, Faculty of Life Sciences and Engineering, University of Lleida, Lleida, Spain
3 TRAGSATEC, Madrid, Spain
4 Consell Generau d’Aran, Vielha, Spain
5 Servei de Fauna i Flora, Generalitat de Catalunya, Barcelona, Spain
6 Ministerio para la Transición Ecológica y el Reto Demográfico. Pza. San Juan de la Cruz s/n, Madrid, Spain

Keywords
biological conservation; facultative scavengers; carrion ecology; food subsidy; predator-prey relationships; grouse; Tetrao urogallus.

Abstract
The increases in ungulate populations and hunting bags throughout Europe and North America have resulted in higher carcass numbers available for mesocarnivore species in temperate and boreal forests. The increase in food resources can sustain denser predator populations, potentially affecting prey species such as the threatened western capercaillie Tetrao urogallus. We investigated the ungulate population trends in recent decades and the carrion use by facultative scavengers in areas of the Pyrenees occupied by capercaillie to assess the potential effects on predation of nests and adult birds, and on its population trend. We found a significant increase in the number of ungulates harvested during the period of sharp capercaillie population decline. Carrion was provided experimentally in forested areas occupied by capercaillie showing that remains were mainly consumed by red fox Vulpes vulpes, followed by wild boar Sus scrofa and marten species (Martes sp.). Season (cold or warm) was the most important factor determining scavenging activity in most species. Main predators of capercaillie nests and adults were martens and red fox, with no predation by wild boar. Our data show that main predators of capercaillie are the same species that mainly consume carrion, especially in winter, and that plentiful carrion resources could maintain higher populations of these species, potentially increasing predation pressure on the capercaillie population. This study shows that managing carrion arising from hunting activity in areas of capercaillie distribution is a necessary management action to reduce the available carrion biomass and so reduce the impact of mesocarnivores on capercaillie conservation.

Introduction
The extirpation of large carnivores and the legal protection of mesocarnivores has triggered increases in mesocarnivore populations in many areas, resulting in increasing predation pressure on mesocarnivore prey species (Ritchie & Johnson, 2009; Jiménez et al. 2019), in some cases affecting prey populations conservation (Kämmерle et al. 2017). The abundance of generalist mesocarnivores generally depends on food availability, the abundance of their main prey being especially relevant (Oaten & Murdoch, 1975; Delibes-Mateos et al. 2008). If their main prey or food resource becomes less abundant, or is drastically reduced, generalist predators shift their diet to other food resources, which can induce spillover predation on alternative prey species (Marcström, Kenward & Engren, 1988).

Carrion is an important, or alternative, resource for generalist predators, which can behave as facultative scavengers according to its availability (DeVault, Rhodes & Shivik, 2003; Mateo-Tomás et al. 2015; Margalida et al. 2017). Carrion is especially important in habitats and at times when the availability of prey or other food resources is low, such as in temperate and alpine ecosystems and in cold weather (Needham et al. 2014; Pereira et al. 2014; Carricondo-Sánchez et al. 2016). Animals in temperate and arctic regions commonly die from starvation during extended periods of cold weather (Wilmers et al. 2003; Selva et al. 2005). Carrion can occur in temporal pulses, or be scattered across...
extensive areas, and can act as a lifesaver for scavengers during the harshest periods. The spatiotemporal availability of carrion will influence the density, distribution, and diversity of scavengers (DeVault et al. 2003; Mateo-Tomás et al. 2015; Jahren et al. 2020), affecting their survival and shifting their diets and feeding behaviour (Selas & Vik, 2006; Newsome et al. 2015). Accidental and intentional supplementary feeding of predators by humans (e.g. discarded hunting remains, supplementary feeding stations) may also increase food availability, leading to functional and numerical responses in predators that can affect alternative prey populations when such supplementary food is scarce (Oro et al. 2013; Newsome et al. 2015; Rees et al. 2020), especially when prey populations are at low levels (Fernández-Ollalla et al. 2012).

Ungulates have expanded their ranges and increased in numbers in Europe and North America in recent decades (Côté et al. 2004; Massei et al. 2015), leading to increased hunting bags (Milner et al. 2006; Margalida, Colomer & Sanuy, 2011; Massei et al. 2015). However, ungulates also die naturally (of disease and/or starvation) resulting in a spatiotemporally pulsed supply of carrion (Wilmers et al. 2003; Selva et al. 2005; Pereira et al. 2014). Death by predation results in a more stable level of carrion throughout the year (Wilmers & Post, 2006; Wikenros et al. 2013), while human-related mortality, mainly due to hunting, usually occurs during late autumn and winter (Wikenros et al. 2013). In the case of carrion resulting from hunting, there is an annual temporal pulse consisting of thousands of tonnes of food that subsidize ecosystems worldwide (Vicente et al. 2011; Oro et al. 2013) which provides supplementary food resources during prey shortages and may have substantial impacts on the population dynamics of both predators and their prey (DeVault et al. 2003; Needham et al. 2014; Rees et al. 2020). Facultative scavengers such as the red fox (*Vulpes vulpes*) or marten species (*Martes spp.*) can profit from this resource during winter, contributing to the maintenance of dense populations (Wikenros et al. 2013; Mateo-Tomás et al. 2015; Carricondo-Sanchez et al. 2016) with subsequent impacts on alternative prey species, such as capercaillie (*Tetrao urogallus*) or other grouse species (Needham et al. 2014; Jahren et al. 2016; Kämmerle et al. 2017) (Fig. 1).

Capercaillie populations have been in progressive decline throughout Europe (Storch, 2007; Jahren et al. 2016; Kämmerle et al. 2017), beginning earlier in the south of their range and especially sharply in the fragmented and threatened populations of the Iberian Peninsula (Storch, 2007; Gil, Gómez-Serrano & López-López, 2020). This decline has been attributed to low reproductive success and recruitment due to variety factors, such as climate change, habitat loss and fragmentation, human disturbance and the impact of generalist predators (Storch, 2007; Moreno-Opo et al. 2015; Jahren et al. 2016, 2020; Kämmerle et al. 2017). It has been suggested that the increase in generalist predator populations, such as the red fox and marten species, has been favoured by the increase in agricultural areas and human settlements, the lack of apex-predators, and especially by the increase in carrion from wild ungulates as well as conservation policies protecting mesocarnivores (Kurki et al. 1998; Selas & Vik, 2006; Jahren et al. 2020). As well as taking adult birds, these species are known nest and chick predators and have been linked to negative impacts on the breeding success of capercaillie (Kahuala & Helle, 2002;
Wegge & Kastdalen, 2007; Kämmerle & Storch, 2019). This relationship has been studied in the boreal regions of northern Europe, but there are no detailed studies of the threatened relict capercaillie populations in southern Europe (Moreno-Opo et al. 2015).

The objectives of this study were to (1) evaluate the scavenger community in temperate forests in the relict fragmented Pyrenean distribution of the capercaillie; (2) assess the factors related to the scavenging efficiency of carrion use by the scavenger community; (3) evaluate the predator species of capercaillie nests and adults in Pyrenean forests; (4) link the scavenger community to capercaillie predators; and (5) examine whether the increase in carrion availability due to increases in ungulate abundance and the numbers killed by hunters in recent decades could have subsidized the predator community during periods of food scarcity. We hypothesized (Fig. 1) (1) that scavenging on carcasses and remains of ungulates killed by hunters constitutes a significant part of the trophic resources of capercaillie predators during late autumn and winter, when other food sources are scarce and (2) that this may contribute to maintaining dense mesocarnivore populations, with subsequent potential predation impacts on the threatened capercaillie populations in the Pyrenees.

Materials and methods

Study areas

The study was carried out in three areas containing relict populations of western capercaillie on the southern slopes of the Catalán Pyrenees, NE Spain (Siall, Virós and Tornafort, Fig. 2). The three study areas are distributed along a latitudinal gradient in the Catalán Pyrenees, from the southernmost population (Siall) to the core population (Virós), and contain a range of low to high density populations of capercaillie (Fig. 2). The two southern areas studied (Siall and Tornafort) have a sub-Mediterranean, mountain climate with habitats dominated by Scots Pine (Pinus sylvestris) with scattered deciduous species on limestone soil, and a shrub understory of mainly Bearberry Arctostaphylos uva-ursi, Boxwood Buxus sempervirens and Common Juniper Juniperus communis (Canut et al. 2006). The northern area studied (Virós) has a continental alpine climate on siliceous soil, dominated by Black Pine Pinus uncinata in the highest areas with a Rhododendron Rhododendron ferrugineum and Bilberry Vaccinium myrtillus scrub understory (Canut et al. 2006).

Capercaillie predation and population monitoring

The capercaillie populations in our study areas have been monitored regularly, but not all leks were surveyed every year. Therefore, the data used correspond to the leks which were actually surveyed between 1986 and 2019 with simultaneous surveys in the same year (n = 6). We used the number of males counted on a lek as a proxy for the population trend in each study area (more details in Supporting Information S3).

Data on adult and nest predation were obtained by tracking 49 adult capercaillie (26 males and 23 females) between 2009 and 2015. Birds were captured using ground nets and metallic mesh traps and then fitted with VHF collar transmitters (Holohil and Biotrack, 21 g weight). Nest predation and its causes were obtained from 45 nests, belonging to tagged females (n = 35), found during summer reproduction censuses (n = 6) or reported by people searching for mushrooms (n = 4). Nests were continuously monitored with camera

Figure 2 Map showing the study areas and the range of western capercaillie (Tetrao urogallus) in the Pyrenees, Spain. Modified from Robles, Ballesteros & Canut, 2006.
traps and temperature data loggers to determine their fate until the eggs were either predated or hatched. In order to determine the trend in nest predation, simple linear regressions between the proportion of nest predated as a response variable and the year of study period were performed.

**Carcass experimental protocol**

We investigated carcass consumption patterns by the vertebrate scavenger community in mountain forests in the three study areas between 2015 and 2018 (Table 1). A total of 37 carcasses from naturally deceased livestock and harvested wild ungulates, consisting of two carcass types, intact \((n = 24)\) or open bodies (body parts or gutted bodies) \((n = 13)\), were randomly placed in the study area throughout the year and left until only parts of the skeleton and skin remained (more details Supporting Information S4). The carcasses were grouped for analysis into three size categories: A \((< 15 \text{ kg}, n = 12)\); B \((15–40 \text{ kg}, n = 15)\); and C \((>40 \text{ kg}, n = 10)\). Carcasses were generally placed inside mature pine forest, between 1200 and 1900 m asl, under dense tree canopies to hide them from vultures.

To document scavenging events, we placed a camera-trap (Moultrie® M-990i Gen 2 and M-999i, Moultrie Feeders, Birmingham, AL, USA) in front of each carcass, fixed to a nearby tree \((5–10 \text{ m away})\). Images from the cameras were analysed to determine the scavenging species, and the date and time of the scavenging events, that were grouped by scavenger species into four groups; red fox, martens, wild boar and corvids (more details Supporting Information S4). For each carcass, we established the scavenger community, a scavenger’s efficiency (understood as the ability to find and exploit carrion; includes carcass detection time, scavenger occurrence and scavenging frequency and activity), and carcass persistence to assess differences among carcass types and sizes, study areas, seasons (cold or warm) and habitat characteristics surrounded carcasses locations (altitude, distance from settlements, proportion of farmland and open areas) (more details Supporting Information S4). The cold season was considered to run from November to March and the warm season from April to October.

Regarding the scavenger communities, we calculated the species richness (number of scavenging species consuming the carcass) and the Shannon–Wiener diversity index.

**Table 1** Occurrence and timing of each scavenger group visiting carcasses provided in the three study areas, as well as species richness and Shannon–Wiener diversity measures (standard errors in brackets). The first scavenger to arrive is also shown.

| Species                      | Siall (n = 12) | Tornafort (n = 13) | Virós (n = 12) | Cold (n = 12) | Warm (n = 25) | Total (n = 37) | 1st arrival |
|------------------------------|---------------|--------------------|---------------|--------------|---------------|---------------|-------------|
| Red fox *Vulpes vulpes*      | 12 (100)      | 13 (100)           | 11 (91.67)    | 12 (100)     | 24 (96.00)    | 36 (97.30)    | 10 (27.0)   |
| Wild boar *Sus scrofa*       | 9 (75)        | 7 (92.31)          | 10 (83.33)    | 9 (75)       | 22 (88.00)    | 31 (83.78)    | 13 (35.1)   |
| Marten *Martes martes*       | 5 (41.67)     | 7 (53.85)          | 9 (75.00)     | 7 (58.33)    | 14 (56.00)    | 21 (56.76)    | 12 (32.4)   |
| Marten *Martes foina*        | 2 (16.67)     | 7 (53.85)          | 9 (75.00)     | 7 (58.33)    | 14 (56.00)    | 21 (56.76)    | 12 (32.4)   |
| Domestic dog *Canis familiaris* | 1 (8.33) | 1 (7.69)          | 1 (8.33)      | 3 (25)       | 4 (16.00)     | 7 (18.92)     | 1 (2.70)    |
| European badger *Meles meles* | 0 (0)       | 0 (0)              | 1 (8.33)      | 0 (0)        | 1 (4.00)      | 3 (8.11)      | 0 (0)       |
| Common genet *Genetta genetta* | 0 (0)       | 0 (0)              | 1 (8.33)      | 0 (0)        | 1 (4.00)      | 1 (2.70)      | 0 (0)       |
| Least weasel *Mustela nivalis* | 0 (0)       | 0 (0)              | 1 (8.33)      | 0 (0)        | 1 (4.00)      | 1 (2.70)      | 0 (0)       |
| Common raven *Corvus corax*  | 4 (33.33)     | 0 (0)              | 1 (8.33)      | 3 (25)       | 2 (8.00)      | 5 (13.51)     | 1 (2.70)    |
| Jay *Garrulus glandarius*    | 1 (8.33)      | 3 (23.08)          | 2 (16.67)     | 3 (25)       | 3 (12.00)     | 6 (16.22)     | 0 (0)       |
| Carrion crow *Corvus cornone*| 0 (0)         | 1 (7.69)           | 0 (0)         | 0 (0)        | 1 (4.00)      | 1 (2.70)      | 0 (0)       |
| Northern goshawk *Accipiter gentilis* | 0 (0) | 1 (7.69)          | 0 (0)         | 0 (0)        | 1 (4.00)      | 1 (2.70)      | 0 (0)       |
| Dormouse *Eliomys quercinus** | 0 (0)         | 0 (0)              | 1 (8.33)      | 0 (0)        | 1 (4.00)      | 1 (2.70)      | 0 (0)       |
| Wood mouse *Apodemus sylvaticus* | 0 (0)      | 2 (15.38)          | 1 (8.33)      | 0 (0)        | 3 (12.00)     | 2 (5.41)      | 0 (0)       |
| Red squirrel *Sciurus vulgaris* | 0 (0)       | 0 (0)              | 1 (8.33)      | 0 (0)        | 1 (4.00)      | 1 (2.70)      | 0 (0)       |
| Mean richness (SE)           | 7 (2.92)      | 9 (3.23)           | 13 (3.17)     | 7 (2.92)     | 15 (3.20)     | 15 (3.11)     |             |
| Mean diversity (SE)          | 0.94 (0.13)   | 0.96 (0.12)        | 1.07 (0.18)   | 0.80 (0.11)  | 1.08 (0.11)   | 0.99 (0.08)   |             |

* Not evaluated in Siall study area.
evaluate scavenging efficiency and carcass persistence, we estimated the carcass detection time (in days between carcass placement and the arrival of the first vertebrate scavenger) and carcass consumption time (in days between carcass placement and its complete consumption) for each carcass. In addition, to determine how each scavenger community utilized the carcass, for each scavenger group (as described below), we calculated: detection time for the first scavenger to arrive; occurrence (percentage of the total carcasses visited by a given scavenger group); scavenging activity (the number of scavenging events divided by the consumption time in days); and the relative scavenging frequency (proportion of scavenging events by a given scavenger group of the total scavenging events at this carcass). The latter reflects how frequently a scavenger group used the carcass in relation to the total use by the scavenger community.

**Trend in ungulate populations**

In order to assess the ungulate population trend and the availability of carrion in the study areas, we compiled the available hunting bag data on a regional scale (Province of Lleida) and on a local scale from the controlled hunting area in the Tornafort study area. The data series used correspond to wild ungulates and red fox removals from 2000 to 2018 whenever data have been available. Hunting statistics were obtained from the official records of the Department of Agriculture, Livestock, Fisheries, and Food of the Generalitat de Catalunya. Linear and exponential functions were fitted to the data for each species to observe if the trends in hunting bags over time fit with some of these functions (Supporting Information S1-S2).

**Statistical analysis**

To investigate the effects of landscape composition, anthropogenic factors, and carcass characteristics on the scavenger community and scavenging efficiency, we used linear models (LMs) and generalized linear models (GLMs) with Gaussian error distributions and identity link functions to describe the factors related to species diversity, carcass detection time (log transformed) and carcass consumption time, and Poisson error distribution and log link functions for species richness. We used altitude, distance from settlements, proportion of farmland, proportion of open areas, carcass size category, carcass type (intact or open body), study area and season (cold or warm) as fixed factors. For the model selection, we constructed a set of models with all possible combinations using the dredge function in the ‘MuMin’ package in R 4.0.0 (R Core Team, 2020). Finally, we selected the best fitting model based on the Akaike information criterion for small sample sizes (AICc) and considered biologically plausible models with ΔAICc < 2 to have similar predictive accuracy (Burnham & Anderson, 2004). When more than one candidate model was obtained (ΔAICc < 2), we calculated the Akaike weights (AICcw) to assess the weight of evidence in favour of each candidate model (Burnham & Anderson, 2004).

LMs and GLMs were used to evaluate the detection time, scavenger activity and frequency. We constructed a set of models following these same procedures. The explanatory factors were altitude, distance from settlements, proportion of farmland, proportion of open areas, carcass size category, carcass type (intact or open body), study area and season (cold or warm), and the response variables were scavenging activity, scavenging frequency and detection time (log transformed) for each scavenger species. Models were constructed using Gaussian error distributions and identity link functions, except for corvid models of scavenging activity and frequency, where a Poisson error distribution with log link was used.

To ascertain whether species differed in their efficiency of carrion use, we fitted LMs and GLMs using occurrence, scavenging activity and detection time (log transformed) as the response variables, with scavenger species as the categorical predictor. We used Gaussian error distributions and identity link functions, with the exception of occurrence for which binomial error and logit link were used. Where significant effects were found, pairwise comparisons were performed using a t-test with Bonferroni correction to determine significant differences (P < 0.05) between species.

All the models were performed using the R packages ‘nlme’ and ‘lme4’ in R 4.0.0 (R Core Team, 2020) and we checked the collinearity, marginal distribution, and heteroscedasticity of residuals using the Shapiro–Wilk normality test and Q–Q plots to meet normality, and visual checks to meet homoscedasticity assumptions.

**Results**

**Predation and population trends of capercaillie**

The maximum number of males counted on leks in the study areas showed a general decrease in the capercaillie population (β = −0.548, F1,19 = 8.142, P = 0.01) (Fig. 3). The southern population (Siall) showed a decrease of 71% since 1986–1987, but in the last survey in 2020, no males were observed and the population was considered extinct. In Tornafort, no males were observed on the three leks monitored during the last survey in 2019 (Supporting Information S3), suggesting that this population maybe also on the brink of extinction. In contrast, the two leks studied in the northern population (Viròs) showed a different trend; one decreased by 33% between 1986 and 2015 and the other had increased by 150% since 2005 (Supporting Information S3).

Mortality data from the 49 radio-tagged adult capercaillie showed that predation was the main cause of death, accounting for 30% (n = 15) of the total number of tagged individuals (Fig. 4). Of these confirmed predation events, carnivores were responsible for 47%, followed by birds of prey with 20%. The predator species or group (mammals or birds of prey) could not be determined for the remaining 33% of predation events.

Data from the 45 monitored capercaillie nests showed a nest predation rate of 42.4% and 6.0% of nests were abandoned (Fig. 4). Nest predation was caused by carnivore...
Species in all cases, with half of the cases attributed to marten species and the other half to red foxes. Nest predation showed a significant trend, with an increasing proportion of nests predated as the study period progressed ($\beta = 0.533$, $F_{1,44} = 12.27$, $P = 0.001$).

**Scavenger community composition and efficiency**

A total of 2,205 independent feeding events were recorded, involving 15 scavenging species (Table 1). The species richness differed between carcasses, ranging from one to seven scavenger species, with more species in the warm season (Table 1). The Shannon–Wiener diversity index varied in a similar way, ranging from 0–2.24, and was also higher in the warm season (Table 1). The most frequently recorded scavengers in the three study areas were red fox, wild boar, marten species, domestic dog Canis familiaris, European badger Meles meles, common raven Corvus corax and Eurasian jay Garrulus glandarius (Table 1).

The analysis of the models indicates that scavenger species diversity increased during the warm season in areas at higher altitude with higher proportions of open habitats and close to human settlements, the two latter habitat variables appearing in the four best-supported models (Table 2). The best scavenger species richness model included the season, proportion of farmland, and carcass characteristics (carcass size and type – richness was higher in large carcasses and open bodies –Table 2). The detection time model had four best-ranked models which included particularly the proportion of open habitats, as well as carcass type, season, altitude, and distance from settlements (Table 2). The models indicate that open body carcasses in areas with a higher proportion of open habitats, at a greater distance from human settlements, at low altitudes, and at warm season were detected more quickly. The consumption time model was related to carcass size, the proportion of open habitats, and the study area (Table 1). The time needed to totally consume a carcass was higher for larger carcasses, in areas with a higher proportion of open habitats, and it was lower in the southern study area (Siall).

**Carrion use by scavenger species**

We found significant differences between the occurrence patterns of the scavenger species ($\chi^2 = 50.3$, df = 3, $P < 0.001$). Red fox and wild boar occurrences were significantly higher than either marten or corvid occurrences ($P < 0.05$), but not between them (Table 1). Marten occurrence was significantly higher than corvid occurrence ($P < 0.05$). Regarding scavenging activity (Fig. 5), significant differences were found between species ($F_{3,140} = 10.18$, $P < 0.001$). Red foxes scavenged carcasses significantly more active than all other groups ($P < 0.05$), followed by wild boar, and then the martens and corvids (Fig. 5).
although the differences between these latter groups were not significant ($P > 0.05$). Finally, carcass detection time did not differ between any of the scavenger groups ($F_{3,99} = 0.521$, $P = 0.669$; Fig. 5).

The models of factors related to scavenging efficiency indicate that season was the factor most related to the scavenging frequency for the red fox, wild boar, and marten species, but differences in study area also played a part for marten species and habitat characteristics in the wild boar (Table 3). The models including season only as the explanatory variable were the best ranked for red fox and the main factor for wild boar. Red foxes scavenged more frequently in the cold season, while wild boar scavenged more frequently in the warm season, at higher altitude and in areas with lower proportion of farmlands and open habitats (Fig. 5). The marten species were more frequent in the cold season in the southern study areas but were more frequent in the warm season in the northern area (Fig. 5). The best-ranked models for corvid scavenging frequency included the proportion of open habitats and farmland and study area (southern study areas) as explanatory factors (Table 3).

In the same way as for scavenging frequency, modelling of scavenging activity showed season as an explanatory factor for all species groups (Table 3). For red fox and wild boar, the season and altitude variables were selected in the best-ranked models (Table 3). Wild boar showed higher scavenging activity in the warm season in all areas, but red foxes showed higher activity during the cold season in the two northern study areas (Virós and Tornafo) (Table 3). Altitude had a positive effect on both red foxes and wild boar, which were more active at carcasses at higher altitudes and also at larger carcasses. The scavenger activity for marten species was related to season, altitude, and also to the distance from settlements (Table 3). Martens scavened more frequently in the cold season, close to human settlements, and at higher altitudes. The scavenging activity by corvids was mainly related to altitude and the proportion of open habitats, with a weaker effect of season in the best-ranked models (Table 3). Scavenging activity by corvids was higher at lower altitudes, in areas with a higher proportion of open habitats, and in the warm season.

The factors determining carcass detection time differed between groups (Table 3). For red foxes, the best-ranked models included the proportion of open habitats, altitude, and the carcass type (Table 3). Detection time was lower in areas with a higher proportion of open habitats, at lower altitude and when carcasses were partially open. For wild boar, the best detection time model included season, elevation, proportion of open habitats, and carcass size as determining factors (Table 3). Detection time was lower when carcasses were larger and when the weather was warm, at higher altitudes and in open areas. The best-ranked detection time models for martens included proportion of open habitats and season. Martens detected carcasses faster both when the proportion of open habitats was larger and during the warm season (Table 3). No factors were observed to affect detection time for corvid species, and the null model was best ranked (Table 3).

### Trends in hunting bags

Although the number of hunting licenses held in Lleida province has decreased by 33% over the last two decades (2000–2018), the data on harvested animals show a continuous increase in most ungulate species (Fig. 6). This increase in harvest has been more pronounced during the last...
10 years, at both regional and local scales, with exponential increases for most of the deer species and also for wild boar (Fig. 6, Supporting Information S1). Similarly, at the regional scale, there has been an increase in red fox hunting during recent years and a slight increase at the local scale (Supporting Information S1-S2).

**Discussion**

Data from carrion use in Pyrenean forests in areas where capercaillie live showed that season, landscape, and carcass characteristics are related to the composition of the scavenger community and their scavenging efficiency (Table 2). Season and landscape characteristics seem to determine scavenger diversity (Moleón et al. 2015; Pardo-Barquin, Mateo-Tomás & Olea, 2019), while scavenger species richness is determined by the proportion of farmlands and carcass characteristics, such as carcass size or whether carcasses are open allowing ease of detection and use by a wider number of species (Moleón et al. 2015; Gomo et al. 2017). The data also showed that the main scavenger species were red foxes and wild boar, which scavenged carcasses more frequently with occurrence rates of 97% and 84% respectively. While red foxes and wild boar were the most active scavenger species, red foxes were significantly more efficient. Although there was variability between species, carcass detection time

![Figure 5](image-url) Data of carrion use by the different scavenger groups (scavenging frequency, scavenging activity, and carcass detection time) in the study areas and seasons. Data are shown as mean ± SE.
was generally lower where the ability of scavenger species to detect carcass odour was higher, such as during the warm season and when carcasses were partially opened (Fig. 5, Tables 2 and 3) (DeVault et al. 2003; Peers et al. 2020). Other factors that influenced carcass detection time were related to species density and habitat use, such as the proportion of open habitats, distance from settlements, and altitude (Kurki et al. 1998; Prigioni et al. 2008; Jahren et al. 2020). In mountainous areas, open landscapes and habitats at lower altitude are more productive and generally maintain a higher abundance of species such as red foxes (Carricondo-Sanchez et al. 2016; Walton et al. 2017; Jahren et al. 2020).

Table 3 AICc-based model selection to assess the effects of factors on the scavenging groups’ efficiency variables

| Response variable | Species | Model | k | AICc | ΔAICc | AICcw |
|-------------------|---------|-------|---|------|-------|-------|
| Scavenging frequency | red fox | season | 1 | 16.36 | 0.00 | 1.00 |
| | | season+farmland | 2 | 18.76 | 2.30 | |
| | marten | season+study area | 3 | 49.14 | 0.00 | 0.477 |
| | | study area | 1 | 50.25 | 1.11 | 0.274 |
| | | season | 1 | 50.43 | 1.29 | 0.250 |
| | | season+type | 2 | 52.77 | 3.63 | |
| | wild boar | season | 1 | 11.09 | 0.00 | 0.390 |
| | | season+altitude | 2 | 11.86 | 0.77 | 0.266 |
| | | season+farmland | 2 | 12.62 | 1.53 | 0.181 |
| | | season+open | 2 | 12.84 | 1.75 | 0.162 |
| | | season+size | 2 | 13.15 | 2.06 | |
| | corvid | open | 1 | 55.23 | 0.00 | 0.494 |
| | | study area | 1 | 56.48 | 1.25 | 0.264 |
| | | farmland | 1 | 56.66 | 1.43 | 0.242 |
| | | open+farmland | 2 | 57.45 | 2.22 | |
| Scavenging activity | red fox | season | 1 | 117.65 | 0.00 | 0.683 |
| | | season+altitude | 2 | 119.18 | 1.53 | 0.317 |
| | | season+altitude+study area | 3 | 119.82 | 2.17 | |
| | marten | season | 1 | 63.23 | 0.00 | 0.339 |
| | | season+altitude | 2 | 63.42 | 0.19 | 0.308 |
| | | season+altitude+distance | 3 | 64.37 | 1.14 | 0.192 |
| | | season+distance | 2 | 64.72 | 1.49 | 0.161 |
| | | season+open | 2 | 65.70 | 2.47 | |
| | wild boar | season+altitude | 2 | 55.37 | 0.00 | 0.451 |
| | | season+altitude+size | 1 | 55.98 | 0.61 | 0.331 |
| | | altitude | 1 | 56.82 | 1.45 | 0.218 |
| | | season | 1 | 57.54 | 2.17 | |
| | corvid | altitude | 1 | 35.95 | 0.00 | 0.355 |
| | | open | 1 | 36.13 | 0.18 | 0.324 |
| | | altitude+open | 2 | 37.52 | 1.57 | 0.162 |
| | | season | 1 | 37.55 | 1.60 | 0.159 |
| | | altitude+season | 2 | 38.02 | 2.07 | |
| Detection time | red fox | open | 1 | 108.94 | 0.00 | 0.444 |
| | | altitude | 1 | 110.35 | 1.41 | 0.216 |
| | | open+altitude | 2 | 110.70 | 1.76 | 0.180 |
| | | open+type | 2 | 110.89 | 1.95 | 0.160 |
| | | study area | 1 | 110.98 | 2.04 | |
| | marten | open | 1 | 63.86 | 0.00 | 0.694 |
| | | open+season | 2 | 65.50 | 1.64 | 0.306 |
| | | open+season+size | 3 | 66.21 | 2.35 | |
| | wild boar | season | 1 | 111.59 | 0.00 | 0.312 |
| | | elevation | 1 | 111.90 | 0.31 | 0.268 |
| | | open | 1 | 111.94 | 0.35 | 0.262 |
| | | size | 1 | 112.94 | 1.35 | 0.159 |
| | | season+size | 2 | 113.73 | 2.14 | |
| | corvid | null | 1 | 85.80 | 0.00 | 1.00 |
| | | open+altitude | 2 | 89.01 | 3.21 | |

The number of estimated parameters (k), AICc values, AICc differences (ΔAICc) for the highest-ranked model, and Akaike weights (AICcw) are shown. Selected models are in bold.
On the other hand, several species tended to avoid areas where humans are present (e.g. red fox), while others, such as the stone marten, could be pushed to use areas near to human settlements (Prigioni et al. 2008).

Carcass consumption time depends on carcass size, scavenger’s abundance, and season (DeVault et al. 2003; Moleón et al. 2015; Morales-Reyes et al. 2017; Peers et al. 2020). It would be expected that larger carcasses take longer to be consumed, and in warm seasons insect and microbial activity hastens carrion depletion (DeVault et al. 2003). However, in our case, the higher carrion use by facultative scavengers during the cold season (mainly by red foxes and martens) seems to result in faster depletion of carcasses compared with the warm season (Selva et al. 2005; Morales-Reyes et al. 2017). This was not the case in the southern study area, where the carcasses were consumed faster in the warm season, probably because higher temperatures there result in higher microbial activity, and because of the greater scavenging activity by red foxes (Fig. 5) due to less food being available for them during the warm, dry season (Moleón et al. 2015).

The importance of carrion in the fox’s diet during the cold season has previously been observed in areas where capercaillies are distributed, such as in temperate forests and alpine areas in central and northern Europe (Jędrezewska & Jędrezewska, 1992; Cagnacci, Lovari & Meriggi, 2003; Selva et al. 2005; Needham et al. 2014). The use of carrion during winter has similarly been observed in mustelids, although it seems to be less important in their diet than for foxes (Selva et al. 2005; Prigioni et al. 2008), which agrees with our results. The differences observed in the use of carrion between foxes and mustelids in our study may be due to a greater abundance of foxes, the availability of other food resources for mustelids and their lower efficiency as facultative scavengers, and/or spatial and trophic segregation (Kurki et al. 1998; Prigioni et al. 2008; Willebrand et al. 2017).

Our observations on capercaillie adult and nest predation are among the first to be published for the Pyrenean population and the first to try to understand the role of scavengers as capercaillie predators. Adult capercaillie and nest predation rates in our study areas reflect the importance of carnivore predation for this small and fragmented population (Fig. 4, Supporting Information S3). Our observations point to red foxes and marten species being responsible for all of the nest failures and most adult predation. It has been suggested that foxes and martens are the main predators of capercaillie in Europe, together with raptors such as the goshawk Accipiter gentilis (Kahuala & Helle, 2002; Wegge & Kastdalen, 2007; Kämmerle et al. 2017; Kämmerle &
Storch, 2019), and also that they are one of the main factors driving declines in capercaillie breeding success and population densities (Marström et al. 1988; Baines, Aebischer & Macleod, 2016; Jahren et al. 2016). Although wild boar was important scavenger in our study areas, they did not pred ate any nests in our study. Wild boar has been described as predators of artificial nests in Mediterranean and Scandinavian habitats, but evidence for capercaillie nest predation by wild boar is still scarce (5.7-9% of nests, Saniga, 2002; Oja et al. 2017).

Several studies have found a relationship between the increased abundance of a predator’s preferred prey (e.g. voles) and reduced predation on grouse species (Marström et al. 1988; Breisjöberget et al. 2018; Ludwig, Roos & Baines, 2020). Although the high availability of carrion could play this role in our study areas (Peers et al. 2020), the temporary nature of the pulse in ungulate carrion availability due to winter mortality and the hunting season means that carrion availability suddenly decreases in spring, just when the capercaillie breeding season begins (March–April). But the predators also start to breed just at this time, increasing their food requirements and probably turning their attention to capercaillie as an alternative food resource (Wikenros et al. 2013; Needham et al. 2014). Our data showed that the primary capercaillie predators are those that take most advantage of carrion during the winter (red fox and marten species), suggesting that the high availability of carrion in winter may allow denser populations of these species at the end of winter (Selas & Vik, 2006; Needham et al. 2014; Morales-Reyes et al. 2017), potentially increasing predator pressure on the capercaillie population (Jahren et al. 2016; Kämmerle et al. 2017). This greater abundance of predator species not only needs a greater amount of food in the spring but also could increase the probability of predator/capercaillie encounters and increase the probability of capercaillie predation (Cortés-Avizanda et al. 2009; Kämmerle & Storch, 2019; Rees et al. 2020).

The population trends of wild ungulates at regional and local scales throughout Europe have shown a very sharp increase in recent decades (Selas & Vik, 2006; Masset et al. 2015). Similarly, the number of harvested animals has increased in the same way (Margalida et al. 2011; Linnell et al. 2020) (Fig. 6, Supporting Information S1-S2). This increase in hunting carrion availability in otherwise unproductive environments provides an abundant and valuable winter food resource for predator species (Wikenros et al. 2013). Altogether, these trends in carrion availability could have led to progressive increases in predator, and probably to increase predation on capercaillie. However, the direct impact should be addressed in an experimental way to ensure this relationship. It is important to appoint that several factors have been observed that may be negatively affecting capercaillie populations such as climate change, habitat loss and fragmentation, human disturbance, and the mentioned impact of generalist predators (Storch, 2007; Baines et al. 2016; Jahren et al. 2016; Kämmerle et al. 2017) (Figure 1). In this sense, the increase in the carrion availability due to the increase in ungulates is another factor that may have a minor effect compared to other observed factors, but in this case, its easy management compared to the other factors make it more affordable. In addition, the increases in ungulate populations in areas where capercaillie are distributed could have other negative effects, such as competition for food, overgrazing, habitat modification, or even nest trampling (Baines, Wilson & Beeley, 1996; Côté et al. 2004; Jahren et al. 2016). Therefore, increased ungulate densities and carrion availability may have had additive negative effects on capercaillie and grouse populations in the Pyrenees and other boreal forests (Jahren et al. 2016). These effects are suggested by the low abundance and population decreases of capercaillie in the three subpopulations we studied while the ungulate abundance exponentially increased (Figs. 3 and 6, Supporting Information Table S1-S3). There were severe decreases of between 71 and 100% of males counted on leks in the two southern populations (Siall and Tornafort) and a stable number of males counted on leks in Virós (Supporting Information S3). These low and falling population levels show the need for monitoring and conservation management measures to stop or, better still, reverse these declines (Fernández-Olalla et al. 2012; Moreno-Opo et al. 2015; Kämmerle & Storch, 2019). Our data show a temporal overlap between the increase in ungulates and red foxes in hunting bags and a reduction in the abundance of capercaillie on the southern slopes of the Pyrenees. As in northern Europe (Storch, 2007; Jahren et al. 2016), this correlation is presumably causal, and further studies are necessary to clarify the predator/carrion/capercaillie interactions to develop management measures to protect the capercaillie, such as reduce supplementary feeding to predators during the cold seasons (Oro et al. 2013; Newsome et al. 2015).

Management implications

Our data indicate that could exist potential indirect effects of the increase in ungulate populations and the resulting increases in their carrion on capercaillie populations. The progressive decline of the capercaillie population on the southern slopes of the Pyrenees (Canut et al. 2006; Gil et al. 2020; Fig. 3) means that conservation management measures are necessary to save and increase their populations (Fernández-Olalla et al. 2012; Moreno-Opo et al. 2015). However, in many occasions, the management actions required are highly expensive or directly unaffordable. Thus, it is necessary to apply simple measures such as reducing predator abundance on capercaillie breeding areas (Moreno-Opo et al. 2015; Baines et al. 2016; Kämmerle & Storch, 2019). To this end, reductions in the survival and density of mesocarnivores in capercaillie areas could be partially achieved by proper management of carrion from hunting activities and measures to keep carrion out of reach of predator species (Oro et al. 2013; Morales-Reyes et al. 2017) and so the predation pressure on capercaillie could be alleviated. One method of carrion management would be to actively remove harvested animals (combined with increased efforts to find injured animals) followed by suitable disposal of the remains in places where facultative scavengers cannot access them.
(e.g. carrion disposal on vulture restaurants). Another possible interesting approach to investigate is the use of portable electric fencing (Smith et al. 2018), also successfully applied on experimental supplementary feeding sites to prevent non-target species from accessing the food provided (Moreno-Oppo et al. 2012). However, in many cases, this would be very difficult and expensive due to the mountainous terrain, so other approaches should be explored. We suggest that where removal of hunting remains in capercaillie areas is impractical, carcasses should be moved into open areas without forest cover so that vultures can find and consume them, vultures being much more efficient scavengers (Morales-Reyes et al. 2017; Hill et al. 2018). In this way, carcass resources would be exploited by obligate scavengers and minimise subsidies to the food resources of facultative scavengers (Morales-Reyes et al. 2017; Hill et al. 2018). In addition, other food resources used by facultative scavengers that probably are not well managed, such as garbage from ski resorts and the surroundings of mountain villages should be adequately managed, reduced or eliminated in areas inhabited by capercaillie, especially during the winter.

**Acknowledgements**

We acknowledge the forestry rangers of Generalitat de Catalunya for field work. The comments of two anonymous reviewers improved the previous version. This work was funded by the Spanish Ministry of Science, Innovation and Universities (RTI2018-099609-B-C22) and the Spanish Ministry for the Ecological Transition and the Demographic Challenge.

**Conflict of interest**

The authors declare that they have no conflict of interest.

**Ethical approval**

All applicable international, national and/or institutional guidelines for the care and use of animals were followed. All procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted.

**References**

Baines, D., Aebrischer, N.J. & Macleod, A. (2016). Increased mammalian predators and climate change predict declines in breeding success and density of Capercaillie Tetrao urogallus, an old stand specialist, in fragmented Scottish forests. *Biodivers. Conserv.*, 25, 2171–2186.

Baines, D., Wilson, I.A. & Beeley, G. (1996). Timing of breeding in black grouse *Tetrao tetrix* and capercaillie *Tetrao urogallus* and distribution of insect food for the chicks. *The Ibis* 138, 181–187.

Breisjoberget, J.I., Olden, M., Wegge, P., Zimmermann, B. & Andreassen, H. (2018). The alternative prey hypothesis revisited: Still valid for willow ptarmigan population dynamics. *PLoS One* 13, e0197289.

Burnham, K.P. & Anderson, D.R. (2004). Multimodel inference: understanding AIC and BIC in model selection. *Social. Methods Res.*, 33, 261–304. https://doi.org/10.1177/0049124104268644.

Cagnacci, F., Lovari, S. & Meriggi, A. (2003). Capercaillie dependence and food habits of the red fox in an Alpine area. *Ital. J. Zool.* 70, 31–38.

Canut, J., García-Ferré, D., Afonso, I. & Martínez, R. (2006). Situación del urogallo pirenaico (*Tetrao urogallus aquitanicus*) en la comunidad autónoma de Cataluña. In *El urogallo en España. Andorra y Pirineos franceses*. *Situación actual*: 60–70. Robles, I., Ballesteros, F. & Canut, J. (Eds). Madrid, Spain: SEO/Birdlife.

Carricondo-Sanchez, D., Samelius, G., Odden, M. & Willebrand, T. (2016). Spatial and temporal variation in the distribution and abundance of red foxes in the tundra and taiga of northern Sweden. *Eur. J. Wildl. Res.* 62, 211–218.

Cortés-Avizanda, A., Carrete, M., Serrano, D. & Donázar, J.A. (2009). Carcasses increase the probability of predation of ground-nesting birds: a caveat regarding the conservation value of vulture restaurants. *Anim. Conserv.* 12, 85–88.

Coté, S.D., Rooney, T.P., Tremblay, J.P., Dussault, C. & Waller, D.M. (2004). Ecological impacts of deer overabundance. *Annu. Rev. Ecol., Evol., Syst.* 35, 113–147.

Delibes-Mateos, M., De Simon, J.F., Villafuerte, R. & Ferreras, P. (2008). Feeding responses of the red fox (*Vulpes vulpes*) to different wild rabbit (*Oryctolagus cuniculus*) densities: a regional approach. *Eur. J. Wildl. Res.* 54, 71–78.

DeVault, T.L., Rhodes, O.E. Jr & Shivik, J.A. (2003). Scavenging by vertebrates: behavioral, ecological, and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems. *Oikos* 102, 225–234.

Fernández-Olalla, M., Martínez-Abrain, A., Canut, J., García-Ferré, D., Afonso, I. & González, L.M. (2012). Assessing different management scenarios to reverse the declining trend of a relict capercaillie population: a modelling approach within an adaptive management framework. *Biol. Conserv.* 148, 79–87.

Gil, J.A., Gómez-Serrano, M.Á. & López-López, P. (2020). Population decline of the Capercaillie *Tetrao urogallus aquitanicus* in the central pyrenees. *Ardeola* 67, 285–306.

Gomo, G., Mattisson, J., Hagen, B.R., Moa, P.F. & Willebrand, T. (2017). Scavenging on a pulsed resource: quality matters for corvids but density for mammals. *BMC Ecol.* 17, 1–9.

Hill, J.E., DeVault, T.L., Beasley, J.C., Rhodes, O.E. Jr & Belant, J.L. (2018). Effects of vulture exclusion on carrion consumption by facultative scavengers. *Ecol. Evol.* 8, 2518–2526.

Jahren, T., Odden, M., Linnell, J.D. & Panzacchi, M. (2020). The impact of human land use and landscape productivity on population dynamics of red fox in southeastern Norway. *Mammal Res.* 65, 503–516.
Jahren, T., Storaas, T., Willebrand, T., Moa, P.F. & Hagen, B.R. (2016). Declining reproductive output in capercaillie and black grouse–16 countries and 80 years. *Anim. Biol.* 66 (3-4), 363–400.

Jędrzejewski, W. & Jędrzejewska, B. (1992). Foraging and diet of the red fox *Vulpes vulpes* in relation to variable food resources in Bialowieza National Park, Poland. *Ecography* 15, 212–220.

Jiménez, J., Nuñez-Arjona, J.C., Mougeot, F., Ferreras, P., González, L.M., García-Dominguez, F., Muinoz-Igualada, J., Palacios, M.J., Pla, S., Rueda, C., Vilaespesa, F., Nájera, F., Palomares, F. & López-Bao, J.V. (2019). Restoring apex predators can reduce mesopredator abundances. *Biol. Conserv.* 238, 108234.

Kämmerle, J.L., Coppes, J., Ciuti, S., Suchant, R. & Storch, I. (2017). Range loss of a threatened grouse species is related to the relative abundance of a mesopredator. *Ecosphere* 8, e01934.

Kämmerle, J.L. & Storch, I. (2019). Predation, predator control and grouse populations: a review. *Wildl. Biol.* 2019, wib.00464.

Kauhala, K. & Helle, P. (2002). The impact of predator abundance on grouse populations in Finland—a study based on wildlife monitoring counts. *Ornis Fenn.* 79, 14–25.

Kurki, S., Nikula, A.R.I., Helle, P. & Linden, H. (1998). Abundances of red fox and pine marten in relation to the composition of boreal forest landscapes. *J. Anim. Ecol.* 67, 874–886.

Linnell, J.D., Cretois, B., Nilsen, E.B., Rolandsen, C.M., Solberg, E.J., Veiberg, V., Kaczensky, P., Van Moorter, B., Panzacchi, M., Rauten, G.R. & Kaltenborn, B. (2020). The challenges and opportunities of coexisting with wild ungulates in the human-dominated landscapes of Europe’s Anthropocene. *Biol. Conserv.* 244, 108500.

Ludwig, S.C., Roos, S. & Baines, D. (2020). Fluctuations in field vole abundance indirectly influence red grouse productivity via a shared predator guild. *Wildl. Biol.* 2020, wlb.00642.

Maresstrom, V., Kenward, R.E. & Engren, E. (1988). The impact of predation on boreal tetraodonts during vole cycles: an experimental study. *J. Anim. Ecol.* 57, 859–872.

Margalida, A., Colomer, M., Sánchez, R., Sánchez, F.J., Oria, J. & González, L.M. (2017). Behavioral evidence of hunting and foraging techniques by a top predator suggests the importance of scavenging for preadults. *Ecol. Evol.* 7, 4192–4199.

Margalida, A., Colomer, M.Á. & Sanuy, D. (2011). Can wild ungulate carcasses provide enough biomass to maintain avian scavenger populations? An empirical assessment using a bio-inspired computational model. *PLoS One* 6, e20248.

Massei, G., Kindberg, J., Licoppe, A., Gačić, D., Śpren, N., Kamler, J., Baubet, E., Hohmann, U., Monaco, A., Ozolinš, J., Cellina, S., Podgórski, T., Fonseca, C., Markov, N., Pokorny, B., Rosell, C. & Nāhlik, A. (2015). Wild boar populations up, numbers of hunters down? A review of trends and implications for Europe. *Pest Manag. Sci.* 71, 492–500.

Mateo-Tomás, P., Olea, P.P., Moléon, M., Vicente, J., Botella, F., Selva, N., Viñuela, J. & Sánchez-Zapata, J.A. (2015). From regional to global patterns in vertebrate scavenger communities subsidized by big game hunting. *Divers. Distrib.* 21, 913–924.

Milner, J.M., Bonenfant, C., Mysterud, A.T.L.E., GaillardD, J.M., Csányi, S. & Stenseth, N.C. (2006). Temporal and spatial development of red deer harvesting in Europe: biological and cultural factors. *J. Appl. Ecol.* 43, 721–734.

Molón, M., Sánchez-Zapata, J.A., Sebastián-González, E. & Owen-Smith, N. (2015). Carcass size shapes the structure and functioning of an African scavenging assemblage. *Oikos* 124, 1391–1403.

Morales-Reyes, Z., Sánchez-Zapata, J.A., Sebastián-González, E., Botella, F., Carrete, M. & Molón, M. (2017). Scavenging efficiency and red fox abundance in Mediterranean mountains with and without vultures. *Acta Oecol.* 79, 81–88.

Moreno-Opo, R., Afonso, I., Jimenez, J., Fernandez-Ollalla, M., Canut, J., Garcia-Ferré, D., Piqué, J., García, F., Roig, J., Muinoz-Igualada, J., González, L.M. & López-Bao, J.V. (2015). Is it necessary managing carnivores to reverse the decline of endangered prey species? Insights from a removal experiment of mesocarnivores to benefit demographic parameters of the Pyrenean capercaillie. *PLoS One* 10, e0139837.

Moreno-Opo, R., Margalida, A., García, F., Arredondo, A., Rodriguez, C. & González, L.M. (2012). Linking sanitary and ecological requirements in the management of avian scavengers: effectiveness of fencing against mammals in supplementary feeding sites. *Biodivers. Conserv.* 21, 1673–1685.

Needham, R., Odden, M., Lundstadsvseen, S.K. & Wegge, P. (2014). Seasonal diets of red foxes in a boreal forest with a dense population of moose: the importance of winter scavenging. *Acta Theriol.* 59, 391–398.

Newsome, T.M., Dellinger, J.A., Pavey, C.R., Ripple, W.J., Shores, C.R., Wirsing, A.J. & Dickman, C.R. (2015). The ecological effects of providing resource subsidies to predators. *Glob. Ecol. Biogeogr.* 24, 1–11.

Oaten, A. & Murdoch, W.W. (1975). Functional response and stability in predator-prey systems. *Am. Nat.* 109, 289–298.

Oja, R., Soe, E., Valdmann, H. & Saarma, U. (2017). Non-invasive genetics outperforms morphological methods in faecal dietary analysis, revealing wild boar as a considerable conservation concern for ground-nesting birds. *PLoS One* 12, e0179463.

Oro, D., Genovart, M., Tavecchia, G., Fowler, M.S. & Martínez-Abrain, A. (2013). Ecological and evolutionary implications of food subsidies from humans. *Ecol. Lett.* 16, 1501–1514.

Pardo-Barquin, E., Mateo-Tomás, P. & Olea, P.P. (2019). Habitat characteristics from local to landscape scales
combine to shape vertebrate scavenging communities. Basic Appl. Ecol. 34, 126–139.

Peers, M.J., Konkolics, S.M., Lamb, C.T., Majchrzak, Y.N., Menzies, A.K., Studd, E.K., Boonstra, R., Kenney, A.J., Krebs, C.J., Martign, A.R., McCulloch, B., Silva, J., Garland, L. & Boutin, S. (2020). Prey availability and ambient temperature influence carrion persistence in the boreal forest. J. Anim. Ecol. 89, 2156–2167.

Peire la, L.M., Owen-Smith, N. & Moleón, M. (2014). Facultative predation and scavenging by mammalian carnivores: seasonal, regional and intra-guild comparisons. Mamm. Rev. 44, 44–55.

Prigioni, C., Balestrieri, A., Remonti, L. & Cavada, L. (2008). Differential use of food and habitat by sympatric carnivores in the eastern Italian Alps. Ital. J. Zool 75, 173–184.

R Core Team (2020). R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.

Rees, J.D., Crowther, M.S., Kingsford, R.T. & Letnic, M. (2020). Direct and indirect effects of carrion subsidies in an arid rangeland: carrion has positive effects on facultative scavengers and negative effects on a small songbird. J. Arid Environ. 179, 104174.

Ritchie, E.G. & Johnson, C.N. (2009). Predator interactions, mesopredator release and biodiversity conservation. Ecol. Lett 12, 982–998.

Robles, L., Ballesteros, F. & Canut, J. (2006). El urogallo en España, Andorra y Pirineos franceses. Situación actual (2005). Madrid, Spain: SEO/BirdLife.

Saniga, M. (2002). Nest loss and chick mortality in capercaillie (Tetrao urogallus) and hazel grouse (Bonasa bonasia) in West Carpathians. Folia Zool. 51, 205–214.

Selás, V. & Vik, J.O. (2006). Possible impact of snow depth and ungulate carcasses on red fox (Vulpes vulpes) populations in Norway, 1897–1976. J. Zool. 269, 299–308.

Selva, N., Jędrzejewska, B., Jędrzejewski, W. & Wajrak, A. (2005). Factors affecting carcass use by a guild of scavengers in European temperate woodland. Can. J. Zool. 83, 1590–1601.

Smith, T.S., Hopkins, B., Gookin, J. & Thompson, S. (2018). Portable electric fencing for bear deterrence and conservation. Hum.-Wildl. Interact. 12, 3.

Storch, I. (2007). Conservation status of grouse worldwide: an update. Wildl. Biol. 13, 5–12.

Vicente, J., Carrasco, R., Acevedo, P., Montoro, V. & Gortazar, C. (2011). Big game waste production: sanitary and ecological implications. In: Integrated waste management. II: 97–128.

Kumar, S. (Ed). Rijeka, Croatia: InTech.

Walton, Z., Samelius, G., Odden, M. & Willebrand, T. (2017). Variation in home range size of red foxes Vulpes vulpes along a gradient of productivity and human landscape alteration. PLoS One 12, e0175291.

Wegge, P. & Kastdalen, L. (2007). Pattern and causes of natural mortality of capercaillie, Tetrao urogallus, chicks in a fragmented boreal forest. Ann. Zool. Fenn. 44, 141–151.

Wikenros, C., Sand, H., Ahlqvist, P. & Liberg, O. (2013). Biomass flow and scavengers use of carcasses after re-colonization of an apex predator. PLoS One 8, e77373.

Willebrand, T., Willebrand, S., Jahren, T. & Marcstrøm, V. (2017). Snow tracking reveals different foraging patterns of red foxes and pine martens. Mamm. Res. 62, 331–340.

Wilmers, C.C. & Post, E. (2006). Predicting the influence of wolf-provided carrion on scavenger community dynamics under climate change scenarios. Glob. Chang. Biol. 12, 403–409.

Wilmers, C.C., Stahl, D.R., Crabtree, R.L., Smith, D.W. & Getz, W.M. (2003). Resource dispersion and consumer dominance: scavenging at wolf-and hunter-killed carcasses in Greater Yellowstone, USA. Ecol. Lett. 6, 996–1003.

Supporting information

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

S1. Hunting bag trends of ungulate species and red fox at regional scale from Lleida Province.

S2. Hunting bag trends of ungulate species and red fox at local scale from the Controlled Hunting Area (Tornafort study zone).

S3. Data of capercaillie males counted in the monitored leks in the study zones.

S4. Carcass experimental protocol.