Journal of Ornithology
https://doi.org/10.1007/s10336-025-02319-8

ORIGINAL ARTICLE

Effect of proximity to ski slopes on nest predation risk of the Pyrenean Western Capercaillie (*Tetrao urogallus aquitanicus*)

Pablo Ferreras[1] · Fermín Urra[2] · Enrique Castién[3] · Diego Villanúa[2]

Received: 10 March 2025 / Revised: 21 June 2025 / Accepted: 7 August 2025

Abstract
Mountain tourism has shown a strong increase over the last decades. One of the most important activities is skiing, which has a great economic impact on these traditionally less developed areas. However, the massive arrival of people in these habitats can have negative repercussions on the fauna of these ecosystems. An example is the highly endangered Spanish population of Western Capercaillie (*Tetrao urogallus*), which occupies a habitat that often competes with ski facilities. In view of this negative situation, nest predator control is sometimes proposed by managers as a tool to improve the populations of the endangered species. However, experiments assessing the effect of these actions have led to uneven and generally ineffective results. Furthermore, most of the Western Capercaillie's nest predators are also protected species and their lethal control poses ethical and legal limitations. We assessed the relationships between habitat structure and proximity to Nordic ski slopes with Western Capercaillie nest predation rate by monitoring 57 artificial nests in the Pyrenean population (N. Spain). Nest predation rate was estimated as 35.1%, being the corvids the most frequently identified predator (60% of the predated nests), followed by the Red Fox (*Vulpes vulpes*; 20%), the Beech Marten (*Martes foina*) and European Pine Marten (*Martes martes*; 10%) as well as the Wild Boar (*Sus scrofa*; 5%). The distance to ski slopes and to roads were the only variables that showed a significant relationship with nest predation probability, reaching 60% in the area around the ski slopes and less than 10% for nests at distances above 2.5 km. We discuss how this result could be related to a greater presence of generalist predators near the ski slopes attracted by the remains of garbage and what could be the guidelines to follow to reduce this risk of predation.

Keywords Carnivores · Corvids · Human food subsidy · Tetraonids · Tourism

Die Nähe zu Skipisten und die Auswirkungen auf das Nesträuberrisiko beim pyrenäischen Auerhuhn (*Tetrao urogallus aquitanicus*)

Zusammenfassung
Der Bergtourismus ist in den letzten Jahrzehnten stark angestiegen, wobei eine der wichtigsten Aktivitäten das Skifahren mit seiner großen wirtschaftlichen Bedeutung für diese traditionell schwächer entwickelten Gebiete ist. Der massive Ansturm

Communicated by F. Bairlein.

✉ Pablo Ferreras
pablo.ferreras@csic.es

[1] Instituto de Investigación en Recursos Cinegéticos, IREC (CSIC–UCLM–JCCM), Ronda de Toledo 12, 13071 Ciudad Real, Spain

[2] Navarra Environmental Management (Orekan), Padre Adoain, 219 Bajo, 31015 Pamplona, Navarre, Spain

[3] Dirección General de Medio Ambiente. Gobierno de Navarra. C/González, Tablas 9, 31005 Pamplona, Spain

Published online: 19 August 2025

von Menschen in die Lebensräume dort kann jedoch negative Auswirkungen auf die Fauna dieser Ökosysteme haben. Ein Beispiel hierfür ist die stark gefährdete spanische Population des Auerhuhns (Tetrao urogallus), dessen Lebensraum oft mit Skipisten kollidiert. Wegen dieser bedenklichen Situation wird von Managern manchmal die Bekämpfung von Nesträubern als Mittel zur Unterstützung der Populationen der gefährdeten Arten vorgeschlagen. Untersuchungen zur Wirksamkeit dieser Maßnahmen haben jedoch zu widersprüchlichen und durchweg unergiebigen Ergebnissen geführt. Darüber hinaus sind die meisten Nesträuber des Auerhuhns ebenfalls geschützte Arten, deren Bekämpfung ethischen und rechtlichen Beschränkungen unterliegt. Durch die permanente Überwachung von 57 künstlichen Nestern in der Pyrenäenpopulation (Nordspanien) haben wir den Zusammenhang zwischen der Habitatstruktur und Nähe zu Skipisten und der Häufigkeit von Nesträuberei beim Auerhuhn untersucht. Die Rate der Nesträuberei wurde auf 35,1% geschätzt, mit Rabenvögeln als den häufigsten Nesträubern (60% der geplünderten Nester), gefolgt von Rotfüchsen (Vulpes vulpes; 20%), Stein- (Martes foina) und Baummarder (Martes martes; 10%) sowie Wildschweinen (Sus scrofa; 5%). Die Entfernung zu Skipisten und Straßen waren die einzigen Faktoren, die einen signifikanten Zusammenhang mit der Wahrscheinlichkeit von Nesträuberei aufwiesen. Sie erreichten 60% in der Umgebung der Skipisten und weniger als 10% für Nester, die mehr als 2,5 km entfernt waren. Wir erörtern hier, wie dieses Ergebnis mit der größeren Anzahl von Nesträubern in der Nähe der Skipisten, angelockt von Müllresten, zusammenhängen könnte und mit welchen Richtlinien dieses Prädationsrisiko verringert werden könnte.

Introduction

Mountains have had a great attraction for humans since prehistoric times, choosing these sites as locations for the construction of religious temples or places of worship (Río-Rama et al. 2019). Today, this attraction has made mountains one of the top tourist destinations worldwide (UNEP/PNUMA 2007), generating annual economic benefits of more than 70 million dollars (Mohd Taher et al. 2015). This undoubted economic potential must not endanger the great value that mountains have in terms of biodiversity. The climatic and orographic features, together with the inaccessibility of these places to humans until relatively few decades ago, have made it possible for mountain habitats to accumulate more than 80% of the world's bird, mammal and amphibian species (Zhang and Wang 2023) and to be one of the regions with the highest number of endemic species (Noroozi et al. 2018). However, these same peculiarities make these ecosystems highly sensitive to several factors such as global warming, changes in livestock management or the installation of infrastructures associated with tourism (Alba et al. 2022). The analysis of population census of mountain birds in the Giant Mountains (Czech Republic) between 1984 and 2011 revealed a negative trend in the abundance of these species and a shift of them to higher altitudes, significantly related to the progressive increase in average temperatures during the breeding season (Flousek et al. 2015). The land abandonment and the decline of pastoral practices in the Italian Alps caused a rapid scrubbing of alpine pastures, which significantly modified the bird community, allowing the expansion of scrubland species while the more grassland-bound species disappeared from plots located at lower altitudes (Laiolo et al. 2004). Finally, the increased presence of people in the Swiss Alps and Black Forest for hiking, mountain biking and, above all, skiing, has been shown to have a significant negative effect on high mountain species by increasing their stress levels, changing their use of space and altering their species composition, favouring the more generalist species to the detriment of the specialists (Storch and Leidenberger 2003; Thiel et al. 2008, 2011). The Pyrenees are not an exception and more than six million skiers visit the ski slopes of this mountain range every year (Moreno-Gené et al. 2020), which could be having a negative impact on some of the most representative species of this mountain range, such as the Western Capercaillie (*Tetrao urogallus*) (Canut et al. 2011). This species is a large tetraonid characteristic of the Palearctic boreal and high-altitude coniferous forests (Storch 2007). Its distribution in Eurasia covers a relatively continuous strip from Scandinavia far into Russia, to which must be added other fragmented and isolated occurrences in mountain massifs from central and southern Europe (the Alps, the Jura, the Carpathians, the Balkans, the Pyrenees,or the Cantabrian Mountains) and Scotland (BirdLife International 2024). The Iberian Peninsula constitutes the southwest limit for the species, with two populations in the Cantabrian Mountains and the Pyrenees that were isolated from the rest after the last quaternary glaciations, and classified as two different subspecies: *T. u. cantabricus* and *T. u. aquitanicus,* respectively, (Duriez et al. 2007). Both populations have suffered a significant decline in recent decades, with a regression of 83% in the Cantabrian Mountains (Jiménez et al. 2022) and 58% in the Pyrenees (Gil et al. 2020), which has motivated its listing as ‘critically endangered’ at the state level (Robles et al. 2021). Among the factors involved in the decline of Western Western Capercaillie populations throughout its distribution range are hunting (Lohmus et al. 2017), collisions with fences (Baines and Andrew 2003; Canut et al. 2011), habitat loss (Storch 1994; Quevedo et al. 2006; Jahren et al. 2016; Lohmus et al. 2017), predation (Storch 1994; Summers et al. 2004;

Moreno-Opo et al. 2015; Jahren et al. 2016), genetic isolation (Duriez et al. 2007; Clavero et al. 2023; Escoda et al. 2024), climate change (Moss et al. 2001; Summers et al. 2004; Romero et al. 2019), diseases (de Francisco et al. 2023) or disturbances associated with outdoor activities (Thiel et al 2008, 2011; Storch 2013; Moss et al 2014, 2024; Coppes et al. 2017; Rösner et al. 2023). Given that many of these causes are highly interrelated, it is difficult to assess the role of each one separately (Lohmus et al. 2017).

The Pyrenean Western Capercaillie population is exposed to all these risks except hunting, as this activity was banned for the species in Spain in the early 1980s. On the one hand, it occupies forests that are often subjected to heavy logging, which could be causing habitat loss and isolation (Pascual-Horta and Saura 2008). The southern location of this population also raises a problem, as it is particularly sensitive to global warming (Romero et al. 2019), and the fact that it has not been in contact with the rest of the populations for a long time means that it is genetically isolated, with the consequent risk that this entails (Escoda et al. 2024). Finally, it is also subjected to high pressure associated with tourism use of this region, both in winter, on ski slopes, and in summer, in the form of hikers (Zango-Palau et al. 2024).

In the present study, we assess, by monitoring artificial nests, the effect that proximity to a ski resort and the infrastructure associated with tourist uses may have on the risk of Western Capercaillie nest predation. Particularly, we intended to answer the following questions: i) What proportion of nests are predated? ii) Which predators are involved? and iii) Is the risk of predation related to proximity to ski slopes and other human infrastructure or to the surrounding habitat?

Materials and methods

Study area

The fieldwork was carried out in the Larra-Aztaparreta Special Area of Conservation (SAC)(ES0000123; 42º57'N, 0º48'W), located in the Spanish Western Pyrenees at altitudes between 1,400 and 2,400 m.a.s.l. (Figs. 1 and 2).

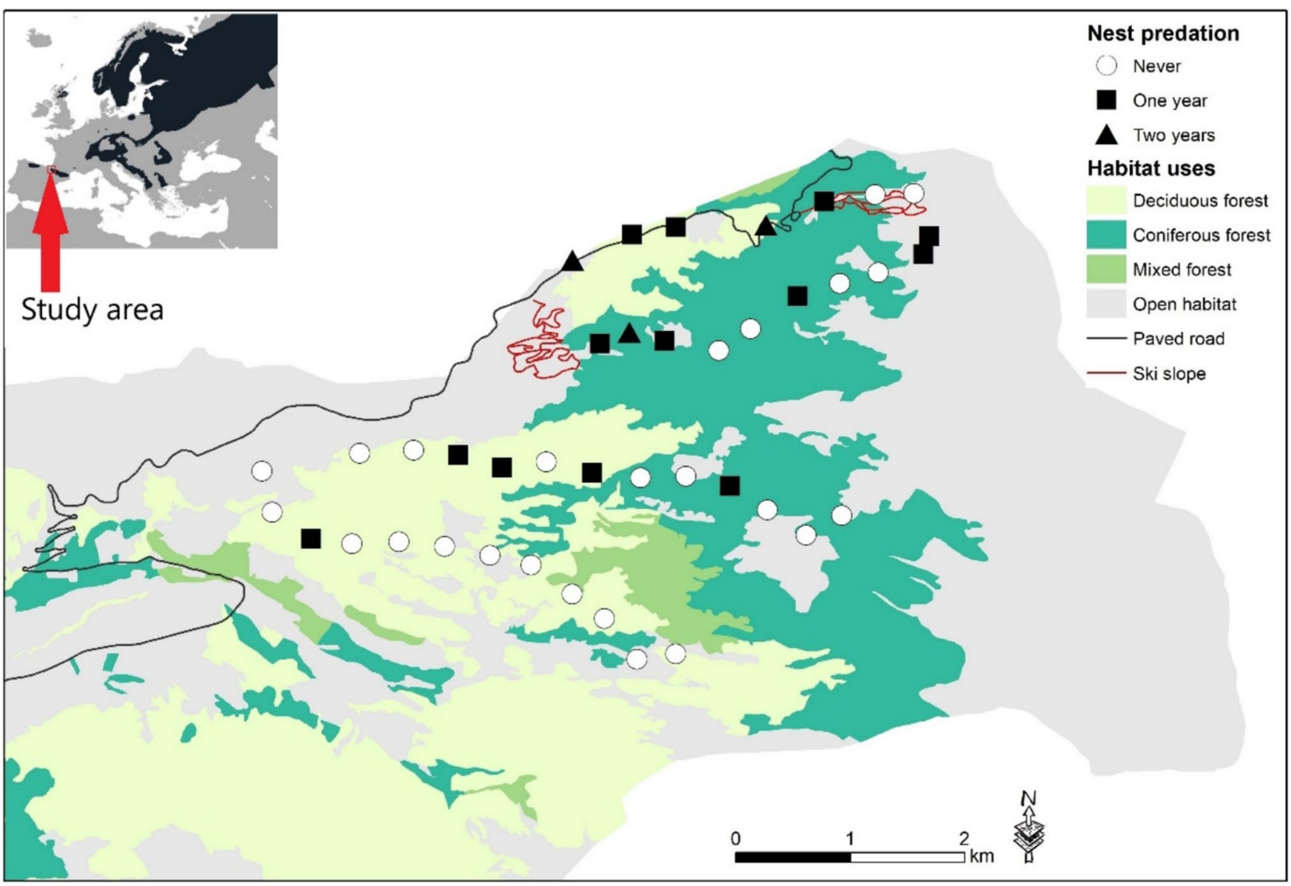


Fig. 1 Western Capercaillie distribution in Europe (IUCN 2025), study area and location of depredated and intact artificial nests in relation to ski slopes, road and habitat

Fig. 2 Example of artificial nest and surrounding habitat

This region is characterized by continental climate (DFb according to Köppen climate classification), with an average temperature of 6 °C to 10ºC (min./max.: −17ºC/34ºC) and with an annual rainfall above 1,500 mm, mostly in the form of snow, which covers the higher altitude areas from January to April (http://meteo.navarra.es/climatologia/fichasclimaticas).

The lower part of the area is occupied by European Beech (*Fagus sylvatica*) forests that are replaced by Mountain Pine (*Pinus uncinata*) forests between 1,600 m and 1,900 m and by subalpine grasslands above 2,000 m. The area is crossed by a single road and includes a small Nordic ski resort (36 km total track length, Fig. 1) which remains open to skiers between December and April. The other authorized uses are sheep, cattle and horse grazing and hiking at a signposted circular route, while hunting and wood extraction are forbidden.

The small population of Western Capercaillie has remained relatively stable since 1990 occupying mainly the mountain pine forest and, to a lesser extent, the beech forests and subalpine grasslands (Government of Navarra unpublished data). The following potential predators of the species are present in this area: the Pine Marten (*Martes martes*), the Beech Marten (*Martes foina*), the Wild Boar (*Sus scrofa*), the Red Fox (*Vulpes vulpes*) and the European Wildcat (*Felis silvestris*) among mammals; the Golden Eagle (*Aquila chrysaetos*) and the Eurasian Goshawk (*Astur gentilis*) within the raptors; the Eurasian Jay (*Garrulus glandarius*), the Carrion Crow (*Corvus corone*) and the Northern Raven (*Corvus corax*) within the corvids (Government of Navarra unpublished data).

Artificial nest installation

To assess the risk of predation on Western Capercaillie nests, we used artificial nests mimicking the species'natural nests (Summers et al. 2009). The artificial nests consisted of a small depression in the ground partially covered by natural vegetation simulating Western Capercaillie nests (Ménoni 1991; Martínez-Vidal 2011) (Fig. 2). Subsequently, the hole was filled with dry plant material and five brown eggs from domestic chickens *Gallus gallus domesticus* were deposited. During field work, we used rubber gloves and cloth gaiters washed with $NaHCO_3$ solution and sprayed with odor-covering solution (Wildlife Research Scent Killer Air & Space – Forest Edge, Wildlife Research Center, inc., MN, USA) before accessing the location of each nest to avoid leaving traces of human scent (Summers et al. 2009; Wegge et al. 2012). Nests were distributed with a separation of 407 m (± 94 SD) between contiguous ones and arranged in lines (Fig. 1). With this distribution, we tried to cover the different habitats present in the area and to obtain a gradient of distances to ski slopes and roads, areas with greater human use. Nest installation was carried out in June 2022 and June 2023 and the nests were kept in the field for approximately 26 days, to match the reproductive phenology of the species in the Pyrenees (Ménoni 1991; Martínez-Vidal 2011). In 2022, 16 nests were installed in the north of the study area and another 41 were installed in 2023 (16 approximately in the same locations as in 2022 and 25 in the southern part of the study area), providing information on a total of 57 artificial clutches (Fig. 1 and electronic supplementary material for details). The identification of the responsible predator species was based on the signs found in the inspection of the nests (Major 1991). Additionally, a camera trap was installed in front of 22 of the nests (38%) to confirm the identification of predator species. The two species of martens (*M. martes* and *M. foina*) were treated as a single predator category (*Martes* sp.) due to the similar marks left in eggshells and the difficulties in differentiating them in camera trap pictures (Tobajas et al. 2022; Palencia and Barroso 2024). Two revisions were carried out, one 15 days after installation and a second one at the time of removal (26 days after installation) (Wegge et al. 2012). A nest was considered as predated if at least one egg was missing or if marks of a predator´s visit were found (Martin and Joron 2003). The potential differences among nests due to differences among persons installing them were minimized by performing the installation by the same team and always following the same protocol.

Habitat and human variables

The habitat surrounding each artificial nest was characterized at two scales: in a 100 m circular buffer, potentially related to the detectability of the nests by predators, and in a 500 m circular buffer, potentially related to predator presence and abundance (electronic supplementary material Table S1). To calculate these variables, the digital layer of the 'Map of crops and uses of Navarra 2021' (OCUPAC_Pol_MCA_VE2021) at a scale of 1:25,000 was used, which contains the land coverage and uses dated in 2021 (available in https://idena.navarra.es/descargas/). The habitat classes considered were: coniferous forest, deciduous forest, mixed forest and open habitat. From this layer, the proportions of each habitat in the 100 m and 500 m buffers were calculated. Since habitat fragmentation can influence predation rates (Angelstam 1986; Chalfoun et al. 2002; Baines et al. 2004; Stephens et al. 2004), edge density (edge length between habitats/total area) was also calculated within the 100 m and 500 m buffers as an index of habitat fragmentation (Cottam et al. 2009). Finally, the distances from each nest to the nearest ski slope and to the nearest road were calculated as variables related to human influence (Storch and Leidenberger 2003). These processes were carried out with the free software *QGIS* v. 3.4 (QGIS.org 2021).

Statistical analysis

To assess the factors potentially related to nest predation risk, generalized linear models (GLM) were fitted with a binomial response (0 = not predated, 1 = predated) and a logit link function. In a first analysis, univariate logistic regression models were fitted with the covariates mentioned above (Table S1), and compared to the null model (constant) using their Akaike information criterion (AIC); the most plausible models were selected according to their AIC value. In a second analysis, generalized linear mixed models (GLMM) were fitted, including the nest ID as random effect, and the different covariates as fixed effects once scaled (average 0 and standard deviation 1) to ease the interpretation of the resulting coefficients. We started from a saturated model that included all the covariates and the values of the variance inflation factor (VIF) were calculated to identify those covariates highly correlated with the rest (VIF > 5). Due to the high correlation between the distance to ski slopes and roads ($r = 0.664$, $p < 0.001$), to build the multivariate models, the distance to roads was discarded as it had lower explanatory value than the distance to ski slopes according to the univariate models (Table 1). Once these covariates were eliminated, an automatic comparison of models (dredge procedure) was carried out from the reduced model, selecting those models with AIC values < 2 to perform a model averaging procedure. To interpret the results, we inspected the coefficients of the covariates included in the resulting averaged model. The analyses were carried out with the free software R v 4.4.2 (R Core Team 2023) through packages *lme4* (Bates et al. 2015), *MuMIn* (Bartón 2023), *car* (Fox and Weisberg 2019), *corrplot* (Wei and Simko 2021) and *boot* (Canty and Ripley 2022).

Results

The overall percentage of predated artificial nests was 35.1% (20/57), with no significant yearly variation (31.3% in 2022 vs 36.6% in 2023) ($chi^2 = 0.005$, $p = 0.944$). There were also no significant differences according to the presence or absence of camera traps (31.8% vs 37.1% with/without camera) ($chi^2 = 0.016$, $p = 0.901$). Corvids were the most frequent predator (60%, 12/20), followed by Red Fox (20%, 4/20), Beech/Pine Marten (10%, 2/20) and Wild Boar (5%, 1/20). The predator involved could not be identified only in

Table 1 Univariate linear models (logistic regression) for the probability of nest predation, fitted with binomial type error and logit link function. Coefficients significantly different from zero are indicated in bold and AIC values that differ by < 2 units from the most plausible model are indicated in italics

	Coefficient	p	g.l	AIC	ΔAIC
Distance to ski slopes	**−0.848 ± 0.356**	**0.017**	2	*70.830*	*0*
Distance to roads	**−0.841 ± 0.383**	**0.028**	2	*71.562*	*0.732*
Null	–	–	1	75.871	5.041
Prop. open habitat 500 m	−0.400 ± 0.320	0.212	2	76.130	5.300
Prop. mixed forest. 500 m	−0.409 ± 0.407	0.316	2	76.506	5.676
Edge density 500 m	−0.326 ± 0.293	0.266	2	76.581	5.751
Prop. deciduous 500 m	0.218 ± 0.279	0.434	2	77.258	6.428
Prop. deciduous 100 m	0.180 ± 0.277	0.515	2	77.448	6.618
Edge density 100 m	0.155 ± 0.278	0.577	2	77.559	6.729
Prop. open habitat 100 m	−0.127 ± 0.285	0.655	2	77.668	6.838
Camera	−0.236 ± 0.576	0.682	2	77.701	6.872
Prop. conif. 500 m	0.104 ± 0.279	0.708	2	77.731	6.901
Prop. conif. 100 m	−0.0667 ± 0.282	0.813	2	77.814	6.985

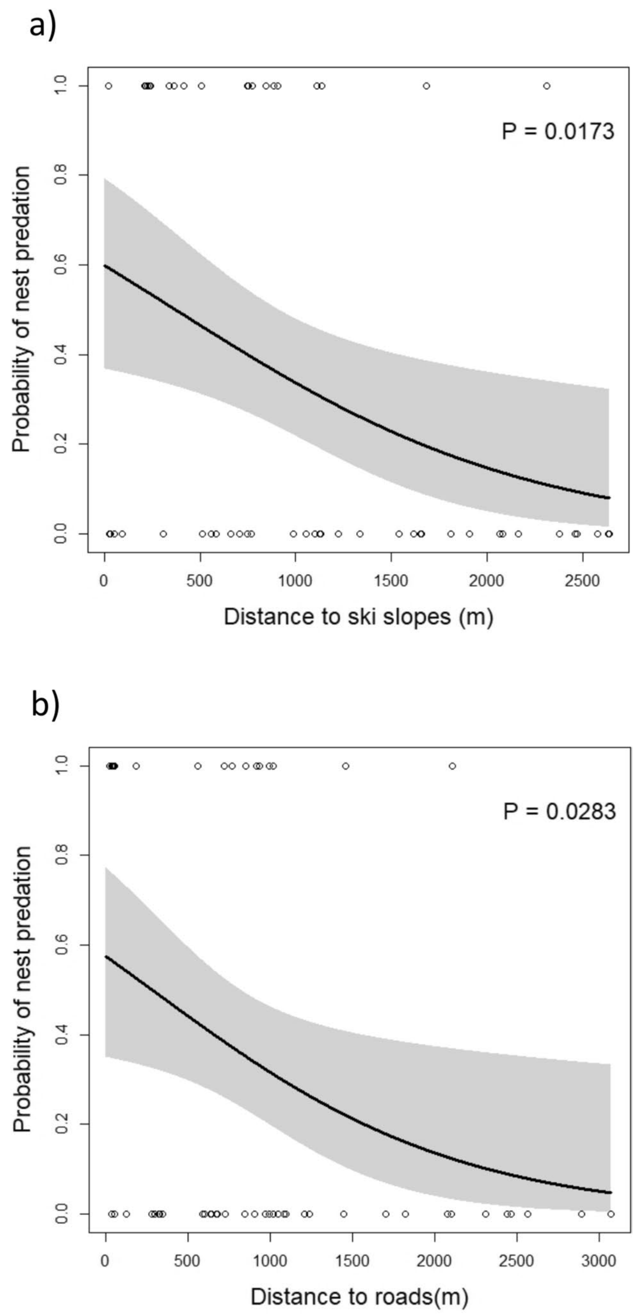


Fig. 3 Probability of nest predation as a function of: **a** distance to ski slopes and **b** distance to roads, according to logistic regression models. The observed values (white dots), the estimated trend (solid black line), the 95% confidence interval (grey area) and the level of significance of the trend (*p*) are shown

one of the predated nests (5%, 1/20) (electronic supplementary material Table S2).

According to the univariate models, the distance to ski slopes and the distance to roads were the variables that best explained the probability of nest predation (Table 1). The expected predation risk of a nest located next to a ski slope or a road would be 60%, and this risk would decrease to values less than 10% for nests at distances above 2.5 km. (Fig. 3). None of the other covariates had a significant relationship with the nest predation probability, and the models with these covariates did not improve the null model according to their AIC (Table 1).

According to the resulting saturated model, the proportions of conifers in 100 m and 500 m, open habitat in 100 m, mixed forest in 100 m, and deciduous forest in 100 m and 500 m were highly correlated with the other variables (VIF > 5), therefore, they were dropped from the model. The obtained reduced model was subjected to automatic comparison (dredge), resulting in selected models (ΔAIC < 2) which included the covariates: distance to ski slopes, edge density in 100 m and proportions of open habitat in 500 m (Table 2, Table S3). The model resulting from model averaging included the distance to ski slopes (negative and significant), the proportion of open habitat in 500 m around the nest (negative and marginally significant), and the edge density in 100 m (positive and not significant; Table 3, Fig. 4).

Discussion

The installation and monitoring of artificial nests is a tool widely used in the study of predation in ground nesters. However, the methodology has important limitations that must be considered when interpreting the results (Storaas 1988; Willebrand and Marcström 1988; Zanette 2002; Burke et al. 2004; Moore and Robinson 2004; Wegge et al. 2012).

First, although artificial nests were aimed to closely mimic the characteristics of natural nests of the species, their location, design and exposure may differ from those of natural nests. For instance, the eggs in natural nests are covered most of the day by the adult who incubates them, as is not the case in artificial nests (Storaas 1988; Summers et al. 2009), which makes them more visually detectable by corvids (Storaas 1988; Willebrand and Marcström 1988). On the other hand, this absence of the adult also implies less

Table 2 Multivariate models selected by automatic comparison (dredge) to explain the probability of nest predation and included in the model average procedure

	Intercept	Distance to ski slopes	Edge density 100 m	Proportion open habitat 500 m	*df*	AICc	ΔAIC
Model 1	−0.8117	−1.0350		−0.5668	4	72.30	0.00
Model 2	−0.7339	−0.8516			3	73.32	1.02
Model 3	−0.7936	−1.0010	0.2519	−0.6457	5	74.06	1.76

Table 3 Coefficients of the covariates included in the averaged model obtained from the top selected models resulting from the dredge procedure. The value of the intercept and the coefficients for the standardized covariates, the standard errors, the values of the *z*-test and the probabilities are indicated, considered significant (*) if $p < 0.05$

	Coefficient	Std. Error	*z*	*pr* (>|z|)
Intercept	−0.7848	0.3340	2.296	0.0216*
Distance to ski slopes	−0.9737	0.4128	2.307	0.0210*
Edge density 100 m	−0.5899	0.3380	1.706	0.0881
Prop. open habitat 500 m	0.2519	0.3215	0.765	0.4442

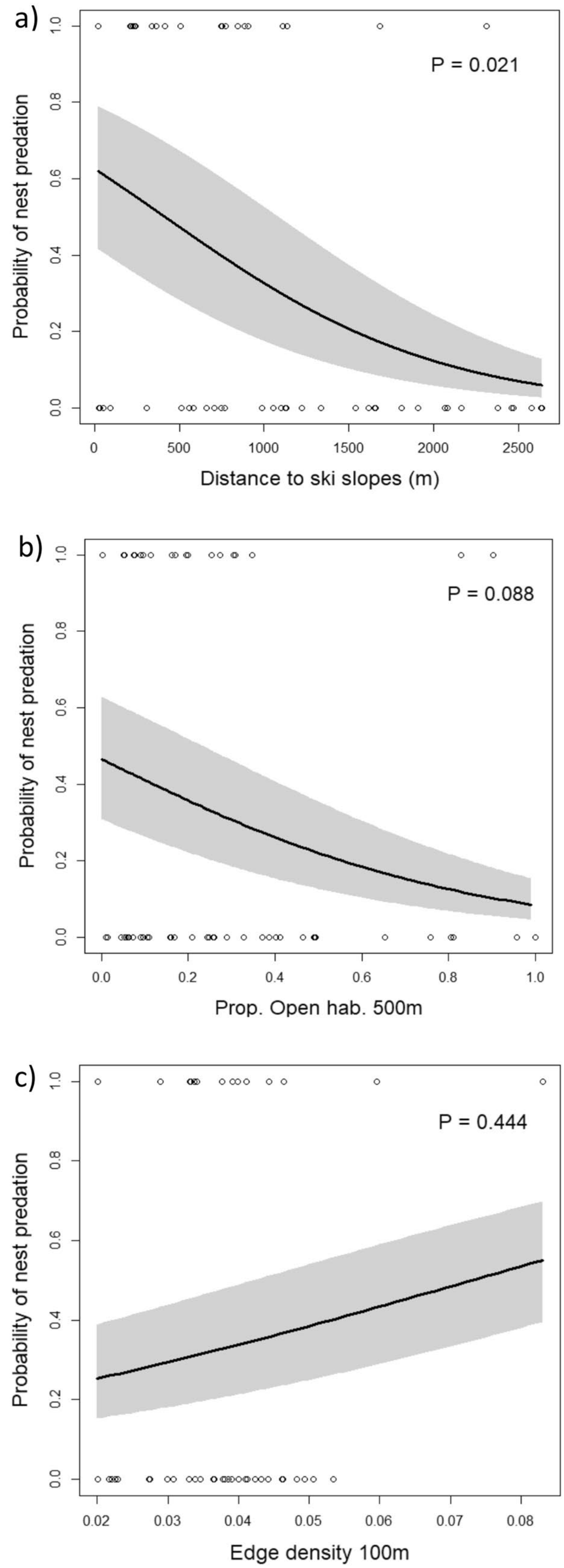
olfactory detection by terrestrial carnivores (Storaas 1988), although this limitation can be partially compensated using chicken-scented hay to build the nests (Palencia and Barroso 2024). Also, traces or human odors left during nest installation may facilitate nest detection by terrestrial carnivores (Burke et al. 2004; Moore and Robinson 2004), and the presence of researchers when installing and reviewing nests may facilitate their detection by corvids, all resulting in increased nest predation compared to natural nests (Burke et al 2004; Moore and Robinson 2004). Finally, installing camera traps next to the nests can also facilitate their detection by predators (Summers et al. 2009). In our case, these limitations would not be as decisive as in other studies, as the aim of the work was not to quantify the predation rate of natural nests in the area, but to assess the possible influence of the surrounding habitat and the proximity to areas heavily used by people on the risk of nest predation.

The proportion of predated artificial nests in our study area (35.1%) is one of the lowest recorded for this species, either estimated from artificial nests (> 50%, Wegge et al. 2012; 88%, Oja et al. 2018; 64.5%, Bamber et al. 2024; 64.6%, Palencia and Barroso 2024), or from natural nests (65%, Saniga 2002; 65%, Summers et al. 2004; 42.4%, Tobajas et al. 2022). Only the work of Holopainen et al. (2024) conducted with artificial nests in Finland found a lower predation rate than ours (22.7%), but in that case the duration of the experiment was only seven days, a shorter time period than established in our work and in most previous studies (20–30 days with revisions every 10–20 days, Wegge et al. 2012; Oja et al. 2018; Tobajas et al. 2022 or Bamber et al. 2024). These different values should not be strictly compared, since field methodology greatly differed among these works (natural or artificial nests, monitoring with or without camera traps, separation between nests…), which can significantly influence the results. A similar situation occurs with the identified predator species since most of the previous works agree with ours in the composition of detected predators (corvids, Red Fox, martens or Wild Boar), although the percentage of nests preyed upon by each of these species varies notably (Saniga 2002; Oja et al 2018; Tobajas et al. 2022; Bamber et al. 2024; Holopainen et al. 2024; Palencia and Barroso 2024; Summers et al. 2004). In this sense, the results from Holopainen et al. (2024) are, again, the most similar to ours, with the highest predation risk posed by corvids followed by the Red Fox and martens.

The most relevant result of our work is the relationship between proximity to ski slopes and nest survival, independently of the composition of the surrounding habitat, at least when the latter parameter is characterized with the precision we have been able to achieve in our work. The increase in the predation rate from less than 10% in nests located more than 2.5 km from the ski slopes to 60% in those adjacent to them shows the important impact of these structures. This negative relationship between ski infrastructure and Western Capercaillie has already been described before. The first study published in this regard was that of Brenot et al. (1996), who found that Western Capercaillie populations adjacent to ski slopes showed a significant decline not detected in populations in the same region but far from ski resorts. More recent work has further explored this question, confirming that Western Capercaillie use areas close to ski slopes less frequently (Thiel et al 2008, 2011; Coppes et al. 2017) and finding higher levels of stress-indicating hormones in the droppings of individuals near these areas (Thiel et al 2008, 2011).

The mountains above 1,500 m where the Western Capercaillie lives and where skiing is practiced in the Pyrenees maintain a constant layer of snow for several months a year, which significantly reduces the availability of trophic resources for mesopredators during that period (Baines et al. 2016; Tobajas et al. 2022; Butler et al. 2023). This situation suggests that, naturally, the abundance of these predators should be low compared to other more beneficial habitats (Tobajas et al. 2022). However, the presence of ski resorts in these areas implies the presence of thousands of people every day during the winter, a new source of food for opportunistic predators in the form of garbage of anthropic origin (Storch and Leidenberger 2003; Canut et al. 2011). This food waste of human origin compensates for the absence of food resources during the winter, allowing higher abundances of potential Western Capercaillie predators, such as the Red Fox, martens or corvids (Storch and Leidenberger 2003; Canut et al. 2011). Furthermore, in the case of Nordic skiing, present in our study area, the creation of 'paths' where people can ski in winter, or hike or cycle when the snow disappears, increases human presence and its negative effects on places previously unreached by humans (Brenot et al. 1996). Finally, the adaptation of the meadows for skiing requires the elimination of scattered bushes and trees (Casagrande-Bacchiocchi et al. 2019), key elements for the Western Capercaillie nesting places and refuge from raptors (Canut et al. 2011), which would again result in a negative impact on the species. In view of this artificial increase in nest

Fig. 4 Probability of nest predation as a function of: **a** the distance to ▶ ski slopes, **b** the proportion of deciduous forest within a 500 m radius and the edge density within a 100 m radius, according to the averaged model from the top GLMMs. The observed values (white dots), the estimated trend (solid black line), the 95% confidence interval (grey area) and the level of significance of the trend (*p*) are shown



predation, the elimination of predators could be proposed as an alternative (Marcström et al. 1988; Kauhala et al. 2000; Baines et al. 2004; Moreno-Opo et al. 2015). However, these actions have a high economical cost (Kauhala et al. 2000; Moreno-Opo et al. 2015; Treves et al. 2019), and generally achieve very low results (Moreno-Opo et al. 2015 and references therein) with great differences among areas (Kauhala et al. 2000) or depending on scale, timing, or intensity of control (Kämmerle et al. 2019). In addition, these control measures are very questionable from an ethical and legal point of view (Treves et al. 2019), given that most of the potential predators of the Western Capercaillie are legally protected. However, new lines of research aim to develop non-lethal methods for predation control that could be useful in the vicinity of ski slopes.

One research line is focused on conditioned food aversion (CFA). This practice is based on introducing into chicken eggs available to generalist predators a chemical that is not lethal to them but produces unpleasant symptoms such as vomiting. When the predator consumes these eggs and suffers the unpleasant symptoms, it learns that this type of food is unpalatable to it and avoids eating it (see Tobajas et al. 2020). Recently, Tobajas et al. (2023) have carried out a CFA experiment in the Pyrenees, assessing the rate of predation of artificial nests of Western Capercaillie in a study area where treated hen eggs had been previously installed and comparing it with a control area with normal hen eggs, finding that fox predation was lower in the area where the treatment had been carried out. Other similar works performed with plover-type nests showed that it is also possible to reduce the rate of egg predation by corvids by causing annoying effects in these birds (Ferguson et al. 2021). However, these techniques were useless for reducing nest predation by mustelids (Norbury et al. 2005; Tobajas et al 2023).

Another non-lethal method tested for reducing the impact of nest predation is 'diversionary feeding'. This technique is based on the installation of other food sources that are attractive and easily detected by generalist predators, so that they focus on eating this food during a specific period, reducing the consumption of other food sources, such as nests (Tobajas et al. 2022). In an experiment of this type carried out in Scotland by Bamber et al (2024) with artificial Western Capercaillie nests and provision of deer meat scraps, it was found that the nest predation rate was significantly lower in the diversionary feeding area than in the control one. In addition, this technique could reduce the predatory activity of all potential predators of grouse nests, as all of them are scavengers to a greater or lesser extent (Tobajas et al. 2022).

Conclusions

The results of this study suggest the negative impact of ski slopes on the Western Capercaillie and require adopting measures to reduce the impact of this type of human activity on the species. Such measures could involve: (1) avoiding new ski resorts to be established in the surroundings of the habitats occupied by the Western Capercaillie, (2) in existing ones, improving garbage collection systems and implementing awareness campaigns among users that allow minimizing the amount of food remains available in the field and (3) testing measures aimed at reducing the impact of predation through alternative non-lethal methods at key phases of the reproductive cycle. If no action is taken, nest predation by opportunistic predators could become a limiting factor in the conservation of the Western Capercaillie in the area.

Ackowledgements

We thank the Environmental Rangers of Ronkal-Salazar, especially Josu Antón, for their help in selecting the routes to place the artificial nests. Anika Meyer helped us with the GIS analysis and Lander Goñi and Fidenciano Márquez helped with the fieldwork. Ester Biescas and Mark den Toom revised the English language. The writing of the article was carried out without any financial help.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10336-025-02319-8.

Funding Field work and initial analyses were funded by the Navarra´s Government through the R&D commission established with the IREC. The rest of the work was carried out without any economic support. Open Access funding was provided by the Spanish National Research Council (CSIC).

Data availability We have made publicly available in our institution repository (DIGITAL.CSIC) the dataset corresponding to our ms. JORN-D-25-00080R2. The link for accessing the dataset is: http://hdl.handle.net/10261/395588.

Declarations

Conflict of interest The authors declare no competing interests.

References

Alba R, Kasoar T, Chamberlain D, Buchanan G, Thompson D, Pearce-Higgins JW (2022) Drivers of change in mountain and upland bird populations in Europe. Ibis 164:635–648

Angelstam P (1986) Predation on ground-nesting birds´ nests in relation to predator densities and habitat edge. Oikos 47:365–373

Baines D, Andrew D (2003) Marking of deer fences to reduce frequency of collisions by woodland grouse. Biol Conserv 110:169–176

Baines D, Moss R, Dugan D (2004) Capercaillie breeding success in relation to forest habitat and predator abundance. J Appl Ecol 41:59–71. https://doi.org/10.1111/j.1365-2664.2004.00875.x

Baines D, Aebischer NJ, 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. https://doi.org/10.1007/s10531-016-1185-8

Bamber JA, Kortland K, Sutherland C, Payo-Payo A, Lambin X (2024) Evaluating diversionary feeding as a method to resolve conservation conflicts in a recovering ecosystem. J Appl Ecol 61(8):1968–1978. https://doi.org/10.1111/1365-2664.14693

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. J Stat Soft 67:1–48. https://doi.org/10.18637/jss.v067.i01

Brenot JF, Catusse M, Ménoni E (1996) Effets de la station de ski de fond du plateau de beille (Ariège) sur une importante population de grand tétras *Tetrao urogallus*. Alauda 64:249–260

Burke DM, Elliott K, Moore L, Dunford W, Nol E, Phillips J, Holmes S, Freemark K (2004) Patterns of nest predation on artificial and natural nests in forests. Conserv Biol 18:381–388. https://doi.org/10.1111/j.1523-1739.2004.00014.x

Butler AR, Evans BE, Mortelliti A, Moll RJ (2023) Forest and snow rather than food or foe limit the distribution of a generalist mesocarnivore in winter. Ecosphere 14:e4706

Canty A, Ripley B (2022) boot: bootstrap R (S-plus) functions. R Package Version 1(3–28):1

Canut J, García D, Afonso I (2011) Manual de conservación y manejo del hábitat del urogallo pirenaico. Serie de Manuales de Gestión de Especies Amenazadas. Ministerio Medio Ambiente y Medio rural y Marino, Madrid

Casagrande-Bacchiocchi S, Zerbe S, Cavieres LA, Wellstein C (2019) Impact of ski piste management on mountain grassland ecosystems in the Southern Alps. Sci Total Environ 665:959–967. https://doi.org/10.1016/j.scitotenv.2019.02.086

Chalfoun AD, Iii FRT, Ratnaswamy MJ (2002) Nest predators and fragmentation: a review and meta-analysis. Conserv Biol 16:306–318. https://doi.org/10.1046/j.1523-1739.2002.00308.x16

Clavero M, Naves J, Lucena-Perez M, Revilla E (2023) Taxonomic inflation as a conservation trap for inbred populations. Evol Appl 17:e13677. https://doi.org/10.1111/eva.13677

Coppes J, Ehrlacher J, Thiel D, Suchant R, Braunisch V (2017) Outdoor recreation causes effective habitat reduction in Capercaillie *Tetrao urogallus*: a major threat for geographically restricted populations. J Avian Biol 48:1583–1594. https://doi.org/10.1111/jav.01239

Cottam MR, Robinson SK, Heske EJ, Brawn JD, Rowe KC (2009) Use of landscape metrics to predict avian nest survival in a fragmented midwestern forest landscape. Biol Conserv 142:2464–2475

Duriez O, Sachet JM, Ménoni E, Pidancier N, Miquel C, Taberlet P (2007) Phylogeography of the capercaillie in Eurasia: what is the conservation status in the Pyrenees and Cantabrian mounts? Conserv Genet 8:513–526. https://doi.org/10.1007/s10592-006-9165-2

Escoda L, Piqué J, Paule L, Foulché K, Menoni E, Castresana J (2024) Genomic analysis of geographical structure and diversity in the capercaillie (*Tetrao urogallus*). Conserv Genet 25:277–290. https://doi.org/10.1007/s10592-023-01567-6

Ferguson AJ, Thomson RL, Nelson-Flower MJ, Flower TP (2021) Conditioned food aversion reduces crow nest predation: an improved framework for CFA trials. J Nat Conserv 60:125970. https://doi.org/10.1016/j.jnc.2021.125970

Flousek J, Telenský T, Hanzelka J, Reif J (2015) Population trends of Central European montane birds provide evidence for adverse impacts of climate change on high-altitude species. PLoS ONE 10:e0139465. https://doi.org/10.1371/journal.pone.0139465

de Francisco ON, Sacristán I, Ewbank AC, Velarde R, Afonso I, Garcia-Ferré D, Martín-Maldonado B, Esperón F, Iglesias I, de la Torre A, Margalida A, Sacristán C (2023) First detection of herpesvirus and hemosporidians in the endangered Pyrenean Capercaillie (*Tetrao urogallus aquitanicus*). Sci Rep 13:21936. https://doi.org/10.1038/s41598-023-48123-3

Gil JA, Gómez-Serrano MA, López-López P (2020) Population decline of the capercaillie *Tetrao urogallus aquitanicus* in the Central Pyrenees. Ardeola 67:285. https://doi.org/10.13157/arla.67.2.2020.ra4

Holopainen S, Selonen V, Krüger H, Kotanen J, Laaksonen T, Miettinen E, Nurmi A, Uusihakala L, Väänänen VM (2024) Forest habitat loss and human land use alter predation of artificial ground nests. For Ecol Manage 561:121858. https://doi.org/10.1016/j.foreco.2024.121858

Jahren T, Storaas T, Willebrand T, Moa PF, Hagrn BR (2016) Declining reproductive output in capercaillie and black grouse – 16 countries and 80 years. Anim Biol 66:363–400. https://doi.org/10.1163/15707563-00002514

Jiménez J, Godinho R, Pinto D, Lopes S, Castro D, Cubero D, Osorio MA, Piqué J, Moreno-Opo R, Quiros P, González-Nuevo D, Hernandez-Palacios O, Kéry M (2022) The Cantabrian capercaillie: a population on the edge. Sci Total Environ 821:153523

Kämmerle JL, Ritchie EG, Sorch I (2019) Restricted-area culls and Red Fox abundance: are effects a matter of time and place? Conserv Sci Pract 1:e115. https://doi.org/10.1111/csp2.115

Kauhala K, Helle P, Helle F (2000) Predator control and the density and reproductive success of grouse populations in Finland. Ecography 23:161–168. https://doi.org/10.1016/j.scitotenv.2022.153523

Laiolo P, Dondero F, Ciliento E, Rolando A (2004) Consequences of pastoral 565 abandonment for the structure and diversity of the alpine avifauna. J Appl Ecol 41:294–304. https://doi.org/10.1111/j.0021-8901.2004.00893.x

Lohmus A, Leivits M, Peterhofs E, Zizas R, Hofmanis H, Ojaste I, Kurlavicius P (2017) The capercaillie (*Tetrao urogallus*): an iconic focal species for knowledge-based integrative management and conservation of Baltic forests. Biodivers Conserv 26:1–21. https://doi.org/10.1007/s10531-016-1223-6

Major RE (1991) Identification of nest predators by photography, dummy eggs, and adhesive. Auk 108:190–195. https://doi.org/10.1093/auk/108.1.190

Marcström V, Kenward RE, Engren E (1988) The impact of predation on Boreal Tetraonids during vole cycles: an experimental xtudy. J Anim Ecol 57:859–872

Martin JL, Joron M (2003) Nest predation in forest birds: influence of predator type and predator's habitat quality. Oikos 102:641–653. https://doi.org/10.1034/j.1600-0706.2003.12040.x

Martínez-Vidal R (2011) Biología de la especie. In: Canut J, García-Ferré D, Afonso I (eds) Manual de conservación y manejo del hábitat del urogallo pirenaico. Dirección General de Medio Natural y Política Forestal. Ministerio de Medio Ambiente, Medio Rural y Marino. Serie manuales de gestión de especies amenazadas, Madrid

Ménoni E (1991) Ecologie et dynamique des populations du grand tétras dans les Pyrénées avec des références spéciales à la biologie de la reproduction chez les poules. PHD, Université Paul Sabatier, Toulouse, Quelques applications à sa conservation

Mohd Taher SH, Jamal SA, Sumarjan N, Aminudin N (2015) Examining the structural relations among hikers' assessment of pull-factors, satisfaction and revisit intentions: the case of mountain tourism in Malaysia. J Outdoor Recreat Tour 12:82–88

Moore RP, Robinson WD (2004) Artificial bird nests, external validity, and bias in ecological field studies. Ecology 85:1562–1567. https://doi.org/10.1890/03-0088

Moreno-Gené J, Daries N, Cristobal-Franse E, Sánchez-Pulido L (2020) Snow tourism and economic sustainability: the financial situation of ski resorts in Spain. Appl Econ 52:5726–5744. https://doi.org/10.1080/00036846.2020.1770683

Moreno-Opo R, Afonso I, Jiménez J, Fernández-Olalla M, Canut J, García-Ferré D, Piqué J, García F, Roig J, Muñoz-Igualada J, González LM, López-Bao JV (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. https://doi.org/10.1371/journal.pone.0139837

Moss R, Oswald J, Baines D (2001) Climate change and breeding success: decline of the capercaillie in Scotland. J Anim Ecol 70:47–61. https://doi.org/10.1111/j.1365-2656.2001.00473.x

Moss R, Leckie F, Biggins A, Poole T, Baines D, Kortland K (2014) Impacts of human disturbance on Capercaillie *Tetrao urogallus* distribution and demography in Scottish woodland. Wildlife Biol 20:1–18. https://doi.org/10.2981/wlb.12065

Moss R, Leckie F, Jones S, Kortland L (2024) Disturbance-related redistribution of Western Capercaillie *Tetrao urogallus* away from woodland tracks. Wildlife Biol 2424:e01151. https://doi.org/10.1002/wlb3.01151

Norbury G, O'Connor CH, Byrom A (2005) Conditioned food aversion to eggs in captive-reared ferrets, *Mustela furo*: a test of seven potential compounds. Appl Anim Behav Sci 93:111–121. https://doi.org/10.1016/j.applanim.2004.12.003

Noroozi J, Talebi A, Doostmohammadi M, Rumpf SB, Linder HP, Schneeweiss GM (2018) Hotspots within a global biodiversity hotspot - areas of endemism are associated with high mountain ranges. Sci Rep 8:10345. https://doi.org/10.1038/s41598-018-28504-9

Oja R, Eliisa P, Soe E, Ligi K, Anijalg P, Laurimaa L, Saarma U, Lõhmus A, Valdmann H (2018) Increased nest predation near protected Capercaillie leks: a caveat against small reserves. Eur J Wildl Res 64:6. https://doi.org/10.1007/s10344-018-1165-2

Palencia P, Barroso P (2024) Disentangling ground-nest predation rates through an artificial nests experiment in an area with Western Capercaillie (*Tetrao urogallus*) presence: martens are the key. Eur J Wildl Res 70:87. https://doi.org/10.1007/s10344-024-01837-9

Pascual-Hortal L, Saura S (2008) Integrating landscape connectivity in broad-scale forest planning through a new graph-based habitat availability methodology: application to Capercaillie (*Tetrao urogallus*) in Catalonia (NE Spain). Eur J for Res 127:23–31. https://doi.org/10.1007/s10342-006-0165-z

Quevedo M, Bañuelos MJ, Obeso JE (2006) The decline of Cantabrian Capercaillie: how much does habitat configuration matter? Biol Conserv 127:190. https://doi.org/10.1016/j.biocon.2005.07.019

Río-Rama M, Maldonado-Erazo C, Durán-Sánchez A, Álvarez-García J (2019) Mountain tourism research. A review. Eur J Tourism Res 22:130–150

Robles L, Martínez Padilla J, Obeso JR, Tirado L, Gil JA, Gómez-Serrano MA, García-Ferré D, López-Jiménez N (2021) Urogallo común, *Tetrao urogallus*. In: López-Jiménez N (ed) Libro Rojo de las Aves de España. SEO/BirdLife, Madrid, pp 252–268

Romero D, Olivero J, Real R (2019) Accounting for uncertainty in assessing the impact of climate change on biodiversity hotspots in Spain. Anim Biodivers Conserv 42:355–367

Rösner A, Schabo DG, Palme R, Lorenc T, Mussard-Forster E, Brandl R, Müller J (2023) High-quality habitats and refuges from tourism reduce individual stress responses in a forest specialist. Wild Res 50:1071–1084. https://doi.org/10.1071/WR21162

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

Stephens SE, Koons DN, Rotella JJ, Willey DW (2004) Effects of habitat fragmentation on avian nesting success: a review of the evidence at multiple spatial scales. Biol Conserv 115:101–110. https://doi.org/10.1016/S0006-3207(03)00098-3

Storaas T (1988) A comparison of losses in artificial and naturally occurring capercaillie nests. J Wildl Manage 52:123–126. https://doi.org/10.2307/3801071

Storch I (1994) Habitat and survival of Capercaillie *Tetrao urogallus* nests and broods in the Bavarian Alps. Biol Conserv 70:237–243. https://doi.org/10.1016/0006-3207(94)90168-6

Storch I (2013) Human disturbance of grouse – why and when? Wildlife Biol 19:39–403. https://doi.org/10.2981/13-006

Storch I, Leidenberger C (2003) Tourism, mountain huts and distribution of corvids in the Bavarian Alps, Germany. Wildlife Biol 9:301–308. https://doi.org/10.2981/wlb.2003.018

Storch I (2007) Grouse: status survey and conservation action plan 2006–2010. IUCN, World Pheasant Association, Fordingbridge

Summers RW, Green RE, Proctor R, Dugan D, Lambie D, Moncrieff R, Moss R, Baines D (2004) An experimental study of the effects of predation on the breeding productivity of Capercaillie and Black Grouse. J Appl Ecol 41:513. https://doi.org/10.1111/j.0021-8901.2004.00891.x

Summers RW, Willi J, Selvidge J (2009) Capercaillie *Tetrao urogallus* nest loss and attendance at Abernethy Forest, Scotland. Wildlife Biol 15:319–327. https://doi.org/10.2981/08-036

Thiel D, Jenni-Eiermann S, Braunisch V, Palme R, Jenni L (2008) Ski tourism affects habitat use and evokes a physiological stress response in capercaillie Tetrao urogallus: a new methodological approach. J Appl Ecol 45:845–853. https://doi.org/10.1111/j.1365-2664.2008.01465.x

Thiel D, Jenni-Eiermann S, Palme R, Jenni L (2011) Winter tourism increases stress hormone levels in the capercaillie. Ibis 153:122–133. https://doi.org/10.1111/j.1474-919X.2010.01083.x

Tobajas J, Descalzo E, Mateo R, Ferreras P (2020) Reducing nest predation of ground-nesting birds through conditioned food aversion. Biol Conserv 242:108405. https://doi.org/10.1016/j.biocon.2020.108405

Tobajas J, Oliva-Vidal P, Pique J, Afonso-Jordana I, García-Ferré D, Moreno-Opo R, Margalida A (2022) Scavenging patterns of generalist predators in forested areas: the potential implications of increase in carrion availability on a threatened capercaillie population. Anim Conserv 25:259–272. https://doi.org/10.1111/acv.12735

Tobajas J, Roig J, Alfonso I (2023) Reducing nest predation of the endangered Western Capercaillie using conditioned food aversion. Proceedings of the 15th International Grouse Symposium, September 11–15, 2023, Bialystok, Poland

Treves A, Krofel M, Ohrens O, van Eeden LM (2019) Predator control needs a standard of unbiased randomized experiments with cross-over design. Front Ecol Evol 7:462. https://doi.org/10.3389/fevo.2019.00462

Wegge P, Ingul H, Pollen VO, Halvorsrud E, Sivkov AV, Hjeljord O (2012) Comparing predation on forest grouse nests by avian and mammalian predators in two contrasting boreal forest landscapes by the use of artificial nests. Ornis Fenn 89:145–156

Willebrand T, Marcström V (1988) On the danger of using dummy nests to study predation. Auk 105:378–379. https://doi.org/10.2307/4087508

Zanette L (2002) What do artificial nests tells us about nest predation? Biol Conserv 103:323–329. https://doi.org/10.1016/S0006-3207(01)00143-4

Zango-Palau A, Jolivet A, Lurgi M, Claramunt-López B (2024) A quantitative approach to the understanding of social-ecological systems: a case study from the Pyrenees. Reg Environ Change 24:9. https://doi.org/10.1007/s10113-023-02177-1

Zhang L, Wang J (2023) Mountain biodiversity, species distribution and ecosystem functioning in a changing world. Diversity 15:799. https://doi.org/10.3390/d15070799

Bartón K (2023) MuMIn: multi-model inference. R package version 1.47.5, https://CRAN.R-project.org/package=MuMIn

BirdLife International (2024) Species factsheet: Western Capercaillie *Tetrao urogallus*. https://datazone.birdlife.org/species/factsheet/western-capercaillie-tetrao-urogallus (accessed 6th March 2024)

Fox J, Weisberg S (2019) An R companion to applied regression. Third edition. Sage, Thousand Oaks CA. https://socialsciences.mcmaster.ca/jfox/Books/Companion/

IUCN (2025) Geographical distribution of the Western Capercaillie *Tetrao urogallus* in Europe. Red List spatial data. https://commons.wikimedia.org/w/index.php?curid=40679949

QGIS.org (2021) QGIS geographic information system. QGIS Association. http://www.qgis.org

R Core Team (2023). R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

UNEP/PNUMA (2007). Tourism and mountains: a practical guide to managing the environmental and social impacts of mountain tours United Nations environment programme. https://wedocs.unep.org/handle/20.500.118

Wei T, Simko V (2021) R package 'corrplot': visualization of a correlation matrix (Version 0.92). Available from https://github.com/taiyun/corrplot