Research article

Camera traps reveal seasonal variation in activity and occupancy of the Alpine mountain hare *Lepus timidus varronis*

EDITOR'S CHOICE

Marjorie Bison[1], **Nigel G. Yoccoz**[2], **Bradley Z. Carlson**[1], **Arthur Bayle**[3] and **Anne Delestrade**[1]

[1]Centre de Recherches sur les Ecosystèmes d'Altitude (CREA Mont-Blanc), Observatoire du Mont-Blanc, Chamonix, France
[2]Department of Arctic and Marine Biology, UiT The Arctic University of Norway, Tromsø, Norway
[3]Université Grenoble Alpes, Université Savoie Mont Blanc, CNRS, LECA, Grenoble, France

Correspondence: Nigel G. Yoccoz (nigel.yoccoz@uit.no)

Mountain hare is a cold-adapted species threatened by climate change, but despite its emblematic nature, our understanding of the causes of population decline remains limited. Camera traps are increasingly used in ecology as a tool for monitoring animal populations at large spatial and temporal scales. In mountain environments where field work is constrained by difficult access and harsh conditions, camera traps constitute a promising tool for surveying rare and elusive species such as the mountain hare. Our study explored the use of camera traps as a tool for studying seasonal habitat occupancy and daily activity patterns of the mountain hare, in order to carry out long-term monitoring of populations. We installed 46 camera traps along elevation gradients in the Mont-Blanc massif (France) from January 2018 to June 2022. We measured habitat variables at each camera trap site in order to define vegetation composition and habitat structure. We performed multi-season and single-season occupancy models to respectively describe habitat occupancy of the mountain hare throughout the year and identify the environmental variables influencing mountain hare presence during the breeding season. Mountain hares occupy coniferous forest in winter, and then switch to mixed areas of shrubland and grassland above treeline in spring and the beginning of summer. In spring, occupancy probability of the mountain hare increases with relative cover of mixed low shrub and herbaceous layer (i.e. the 10–40 cm vegetation layer), suggesting a link to food resources and protection from predation. Our results also confirm the nocturnal and crepuscular activity of the mountain hare during the breeding season, and strictly nocturnal activity in winter. Our results demonstrate the efficiency of camera traps as tools for monitoring mountain hare habitat occupancy in mountain environments and underline the importance of diverse habitat mosaics for the preservation of the species.

Keywords: activity pattern, altitudinal migration, camera traps, habitat, mountain hare, occupancy

www.wildlifebiology.org

Introduction

Population dynamics of the mountain hare *Lepus timidus varronis* are mainly driven by predation, interspecific competition and exposure to disease (Thulin 2003, Newey et al. 2007, Schai-Braun et al. 2019). In the Alps, the mountain hare occupies the high elevation area partly because of direct and indirect (e.g. parasites) competition with the larger, generalist European hare (Parmesan and Yohe 2003, Acevedo et al. 2012, Schai-Braun et al. 2021, Angerbjörn and Schai-Braun 2023, La Morgia et al. 2023). In high elevation alpine areas, air temperatures are increasing at a higher rate than at lower elevations (Pepin et al. 2015, for the Alps: Rebetez and Reinhard 2008, Gobiet et al. 2014), and snow cover duration has significantly shortened since the 1970s (Durand et al. 2009, Pellicciotti et al. 2010, Valt and Cianfarra 2010, Klein et al. 2016, Beniston et al. 2018). Species distribution models predict habitat loss for mountain hare in the Swiss Alps during the coming decades due to warming temperatures during the spring reproductive season (Rehnus et al. 2018). However, due to the conic shape of mountains (Elsen and Tingley 2015), migrating to higher elevations – either caused by competitive exclusion, hybridization or climate change – also implies habitat fragmentation and loss that decreases connectivity and further isolates populations, potentially leading to subsequent population declines (Rehnus et al. 2018). Due to its cryptic nature (mimetic coat colour, nocturnal and hiding behavior) and the difficulty of carrying out field work in mountainous areas, our knowledge of mountain hare habitat occupancy and activity patterns remains limited in alpine regions (Angerbjörn and Schai-Braun 2023). In the face of current climatic and environmental changes, we highlight the need to improve our understanding of the degree of vulnerability of mountain hare populations to several threats (climate change, interspecific competition and hybridization with the European hare, predation and land use change; Thulin 2003, Thulin et al. 2006, Newey et al. 2007, Bisi et al. 2015, La Morgia and Venturino 2017, La Morgia et al. 2023) in order to adapt and optimize mountain hare management and conservation strategies (Angerbjörn and Schai-Braun 2023).

To monitor mountain hare populations in an alpine area highly impacted by climate and land use changes, we installed camera traps along elevation gradients of the Mont-Blanc massif beginning in 2018. Camera traps are now a common tool in ecology for carrying out population surveys at large spatial and temporal scales (Trolliet et al. 2014, Burton et al. 2015, Davis et al. 2018, Depauw et al. 2022). In mountain environments where field work is constrained by harsh conditions – steep slopes, prolonged snow cover duration, difficult access – they represent a promising approach for studying rare and elusive species such as the mountain hare. Considering that detailed knowledge of habitat occupancy and activity patterns is essential for defining effective conservation strategies, in this study we aim to elucidate factors influencing the spatial distribution of the mountain hare, including its use of habitats along elevation gradients

and variation in daily activity rhythm over the course of the year.

While camera traps represent a promising tool for monitoring rare and cryptic species such as the mountain hare, observations are necessarily spatially limited and constrained to sites where cameras have been installed. Habitat mapping using widely available satellite imagery has the potential to extrapolate detected patterns in seasonal habitat occupancy to the landscape scale, which is ultimately the most relevant for conservation and land management efforts (Pettorelli et al. 2014). Furthermore, automated mapping of land cover change allows for monitoring spatial shifts in favorable habitat over time, including changes in tree, shrub and grass ecotones resulting from both climate and land use changes affecting mountain socio-ecosystems (Malinowski et al. 2020).

In Europe, mountain hares occupy heterogeneous habitats offering shelter and food such as forests (Bisi et al. 2013, Rehnus et al. 2016) but they also preferentially select ecotones (Rehnus et al. 2016) with open clearings (Lindlof 1974), moors as in Scotland (Watson and Hewson 1973) or tundra (Angerbjörn and Schai-Braun 2023). A few studies have highlighted elevation shifts in habitat use by hares during the year, with hares migrating from lower elevations in spring to higher elevations in autumn (Rehnus and Bollmann 2020). In contrast, other authors have emphasized the high stability of hare home ranges and habitat use between seasons (Bisi et al. 2010, 2013). We expect that, in mountain environments such as those of the Mont-Blanc massif, hare distribution varies over the year with individuals occupying forested areas in winter and moving upslope to more open habitats in spring and summer following snowmelt (Angerbjörn and Schai-Braun 2023). Within these areas, we hypothesize that mountain hares preferentially select mixed shrubland and grassland areas providing both protection from predators as well as a source of food (reviewed by Angerbjörn and Schai-Braun 2023). Finally, as mountain hare is classified as nocturnal (Angerbjörn and Flux 1995) or crepuscular (Ikeda et al. 2016), we expect to observe a lower activity during the day and assume that activity duration fluctuates depending on the season, with more diurnal activity in the breeding season when days are short (Bisi et al. 2013, Ikeda et al. 2016, Ogurtsov et al. 2018). We also expect daytime activity to be higher in summer than in winter because of higher energy demands linked to reproduction, forcing animals to extend movements in search of high-quality food (Pettigrew et al. 2021).

To test our hypotheses, we performed multi-season and single-season occupancy models to respectively describe habitat occupancy of the mountain hare throughout the year and identify the environmental variables influencing mountain hare presence during the breeding season. Furthermore, in order to extend our findings from localized camera traps to the landscape scale, we mapped the main habitats of the study area using Sentinel-2 satellite imagery and assigned occupancy probabilities to relevant habitat classes in order to assess spatial variability in seasonal habitat

occupancy by the mountain hare. Finally, we discuss the implications of our findings for ongoing monitoring and conservation efforts of mountain hare populations in alpine areas moving forward.

Material and methods

Study site and species

The present study was conducted on the French side of the Mont-Blanc massif above the Chamonix valley (45.83°N, 6.87°E), located in the northern French Alps. The Chamonix valley is characterized by abrupt topography, with an elevation gradient stretching between 800–1000 m a.s.l. in the valley floor to the summit of Mont Blanc at 4810 m a.s.l. Forest occupies lower elevation areas up to 1800–1900 m a.s.l., followed by semi-open habitat characterized by sparse tree and tall shrub cover between 1900 and 2100 m a.s.l., followed by mixed shrublands and grasslands above 2100 m a.s.l. up to talus, cliffs and glaciated habitats generally present above 2700 m a.s.l. These dominant habitats respectively cover 21.5% (75.1 km² of forest), 6% (20 km² of treeline and tall shrub), 11% (63.4 km² of shrub and shrub-meadow habitats) and 5% (17.3 km² of subalpine and alpine grasslands) of the Chamonix valley. Glaciers, rocky and urban areas constitute the remaining habitats (180.5 km², 51.6%).

The mountain hare *L. t. varronis* is a medium-sized mammal that remains active throughout the year. It occupies elevations ranging from 1300 to 4000 m a.s.l. (when alpine pastures exist at this elevation) depending on latitude and habitat structure (Angerbjörn 2023). To cope with seasonal changes in climate and resource availability, mountain hare can use different strategies such as changes in habitat use, in home range size (Gamboni 1997, Slotta-Bachmayr 1998) to decrease movements and accordingly metabolic rate (Pyörnilä et al. 1992, Nieminen and Mustonen 2008, Rehnus et al. 2010), in coat colour change (Flux 1970) for camouflage purposes, and in diet with consumption of low-quality food in winter (Iason and Van Wieren 1999, Hirakawa 2001, Hulbert et al. 2001). More specifically on the subject of feeding, mountain hares are classified as an intermediate feeder, being both grazer and browser (Hulbert et al. 2001) and their foraging strategy depends on resource availability and risk of predation (Rehnus et al. 2013, Schai-Braun et al. 2020). The different types of resources consumed by hares (grasses, forbs, conifers, deciduous trees, shrubs) across studies and seasons is indicative of the seasonal flexibility of their feeding strategies, which are considered generalist herbivores (Rehnus et al. 2013, Angerbjörn and Schai-Braun 2023).

The breeding season of the mountain hare in the Alps extends from April to August (Rehnus 2018), and its reproductive strategy varies with elevation (Schai-Braun et al. 2017). Its average annual home range in the Alps comprises between 11.9 and 77.2 ha in Genini Gamboni (2008), 1.24 and 156.17 ha in Bisi et al. (2010) and 12 and 58 ha in Rehnus et al. (2022), for which reported differences could

be attributed to variation in climate conditions, habitat structure and/or productivity among the studied areas (Bisi et al. 2010). In addition to variations related to the sex (Rehnus et al. 2022), home range tends to increase in summer during breeding (Gamboni 1997, Slotta-Bachmayr 1998, Rehnus et al. 2022) and decrease in autumn and winter in order to reduce energy expenditure (Genini Gamboni et al. 2008, Bisi et al. 2010). The mountain hare is a non-territorial species and overlapping home ranges are common (Genini Gamboni et al. 2008).

In the Mont-Blanc massif, we expect the main predators of mountain hare to be red fox *Vulpes vulpes* and golden eagle *Aquila chrysaetos*, and possibly stoat *Mustela erminea* in particular for leverets, as their presence has been recorded in the massif using camera traps and direct observations (unpubl.). Mountain hare is also known to compete for space with the more common European hare (*L. europaeus*; Thulin 2003, Jansson et al. 2007, Caravaggi et al. 2015, 2017). European hares are colonizing progressively higher elevations due to warming climate conditions and vegetation shifts, which has been shown to increase competition with mountain hare populations (Bisi et al. 2015, LPO PACA, GECEM and GCP 2016, Schai-Braun et al. 2021).

Study design and species identification

We installed 46 camera traps approximately every 200 m of vertical gain along elevation gradients (i.e. transects) in five areas of the Mont-Blanc massif, ranging from 1200 to 2700 m a.s.l. (Fig. 1; see Supporting information for details on camera trap locations). We used covert motion-trigger cameras designed by Moultrie (40i or 50i models) and Reconyx (Hyperfire model). Cameras were fixed to either trees or boulders, and programmed to capture bursts of three images per trigger event, i.e. detected motion. Cameras operated continuously during the year (except when covered by snow or malfunctioning). Given the difficulty of working in mountain environments, it was not possible to perfectly standardize the transects. However, cameras have been positioned along similar gradients in terms of elevation and habitat in order for transects to be considered as replicates. Camera traps were installed to cover the range of habitats throughout the study area (17 in forest, 19 in shrubland and 10 in grassland; see Supporting information for details of the number of camera traps for each altitudinal range and habitat). The lower number of cameras in grasslands is due both to the limited availability of this habitat in the Mont-Blanc massif and to the difficulty of installing them in open areas. Camera traps recorded data between January 2018 and June 2022, although most cameras were placed or active from the spring/summer 2018 onward and some cameras malfunctioned during certain intervals (see Supporting information for details of camera's functioning period). Over this period, 845 pictures of mountain hare have been recorded. Species identification was carried out manually by an expert for 80% of the pictures, and completed by machine learning according to the method of Rigoudy et al. (2023) for the remaining
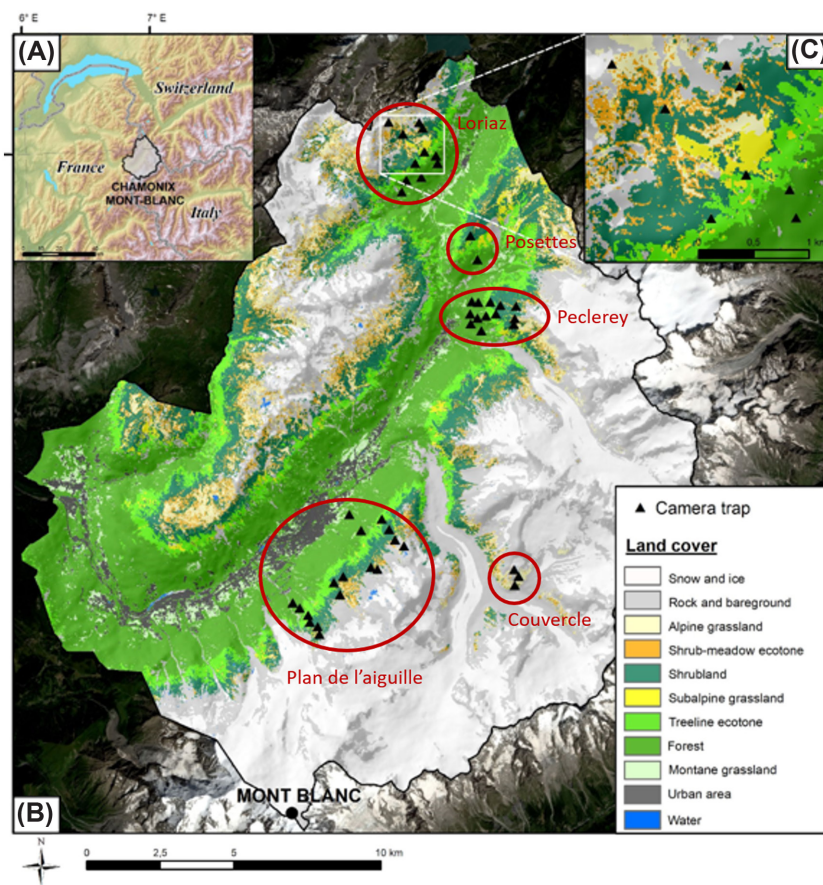
Figure 1. (A) Location of the Chamonix valley within the broader context of the western European Alps. (B) Location of camera traps (n = 46) within the Chamonix valley, overlaid with a habitat map developed specifically for the study area. Red circles indicate the location of the five areas containing elevation gradients. (C) Inset map showing habitat variation at local scale in association with camera traps on Loriaz mountain located on the border with Switzerland.

20% (2022, DeepFaune, www.deepfaune.cnrs.fr). Then they have also been validated by an expert. Identification was based on the ear length relative to the head (longer for the European hare), pelage color in winter (white hair for the mountain hare), shape of the head and the body (rounder for the mountain hare) and leg width (larger for the mountain hare) (Fig. 2). Only one European hare has been detected with our camera traps during the study period. We were not able to differentiate hybrids of European hare and mountain hare from mountain hare; however, only one hybrid out of 298 individuals has been detected by genetic analysis of feces collected within the Mont-Blanc massif (unpubl.). Although we did not account for the possible presence of hybrids in our analysis, we consider their presence to be extremely rare in our study area based on the genetic analyses.

Measuring habitat structure around camera traps

We described each camera trap site according to elevation, camera trap model, habitat and vegetation composition. In July 2022 we measured the proportion of grass, forbs and shrubs, and plant canopy height. We used the estimated proportion of grass, forbs and shrubs, and the tree cover, to classify each camera within a habitat category (forest/shrubland/grassland). Excluding cameras located in forest, we defined the cameras located in grassland as the cameras with > 75% of forbs/grass. The others have been defined as cameras located in shrubland (see Supporting information for details of the proportion of shrubs and forbs/grass around each camera trap). As shrublands are important for mountain hare and widely represented in the Mont-Blanc massif, but are often underestimated in land cover maps (see Supporting information for details of the confusion matrix), the field measurements that we carried out allowed us to accurately describe habitat at the local camera trap scale. At each camera trap site we surveyed 80 contact points, set every 50 cm along two crossed 20 m transects. Transects were positioned in the field of view of each camera trap in order to be representative of the surrounding vegetation. At each point we noted the number of contact points for target functional groups (grass, forbs, shrubs determined at the species level) touching a stake set perpendicular to the ground, as well as the average height of the vegetation, and the type of soil (rock, bare, vegetated or covered with litter). From these data, at the
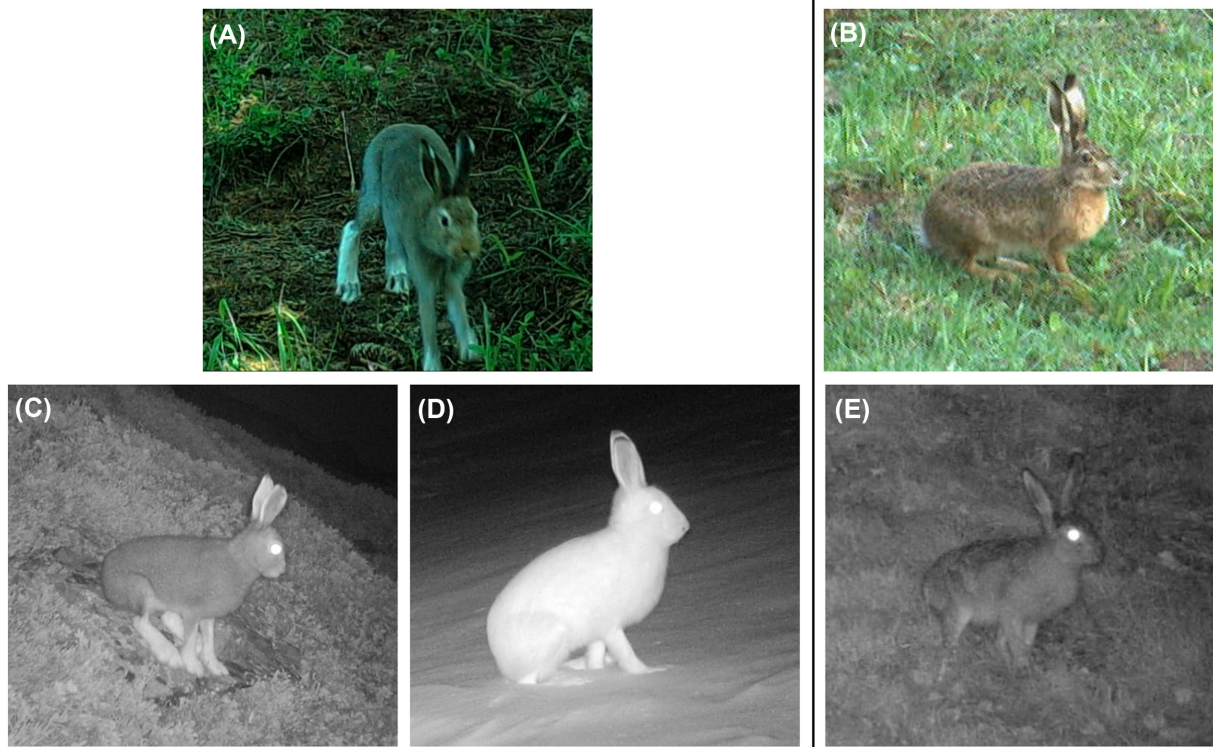
Figure 2. Mont-Blanc massif camera trap pictures of (A, C–D) mountain hare *Lepus timidus varronis* and (B, E) European hare *L. europaeus* demonstrating interspecific differences enabling species identification from both diurnal (A, mountain hare; B, European hare) and nocturnal (C, mountain hare in summer; D, mountain hare in winter; E, European hare) conditions.

camera trap site level (i.e. data from both transects) we calculated mean canopy height as well as the proportion of each vegetation type. In order to quantify vegetation composition surrounding each camera, we performed a PCA on the percentage of each vegetation type (see Supporting information for the PCA performed on the proportion of each vegetation type), and extracted the scores of camera traps along the first two axes of the PCA. At the camera trap site level, we noted the percentage of cover of the tree layer (i.e. vegetation > 4 m, classified from 0 to 5: 0 is no trees, 1 is under 10% of trees, 2 is between 10 and 25% of trees, 3 is between 25 and 50% of trees, 4 is between 50 and 75% of trees and 5 is more than 75% of trees), of the layer < 10 cm (classified from 0 to 5 as for the tree layer: no vegetation under 10 cm to > 75% of vegetation under 10 cm covering the ground), of the layer 10–40 cm (classified from 0 to 5 as for the tree layer: no vegetation between 10 and 40 cm to > 75% of vegetation between 10 and 40 cm covering the ground) and of the layer 40 cm–1.30 m (classified from 0 to 5 as for the tree layer: no vegetation between 40 cm and 1.30 m to > 75% of vegetation between 40 cm and 1.30 m covering the ground). We used the number of vegetation contacts as a proxy of the vegetation biomass in the quadrat. Finally, we used daily timelapse photos taken by each camera to identify the snowmelt-out date for each year and site, provided that camera traps were functioning.

Statistical analyses

Statistical analyses were carried out using R ver. 3.6.2 (www.r-project.org). We used occupancy probability methods for unmarked animals as detailed by Gilbert et al. (2020), and used the 'unmarked' (Fiske and Chandler 2011) and 'camtrapR' (Niedballa et al. 2016) packages to perform subsequent analyses. Statistical analysis were divided in four steps (Table 1). First, we described the raw data with the relative abundance index (RAI) for each month, camera trap and year. Second, we focused on temporal variation of habitat occupancy within the year and we used the multi-season occupancy model (MacKenzie et al. 2003). We then extrapolated the occupancy probabilities modelled via the multi-season model for different months over the whole study area using the habitat map and displayed it for a selected zone. Third, we identified the variables influencing habitat occupancy during the breeding season using a single-season model. Finally, we explored activity patterns of the mountain hare during the four seasons.

Relative abundance index (RAI) analysis

We first calculated the 'RAI' for each month, camera and year. We also averaged RAI values for each year, all cameras and month confounded, to have information about inter-annual variations. RAI corresponds to the number of

Table 1. Statistical analysis, aims and specificity.

Aim	Statistical analysis	Specificity
Describe the raw data	Relative Abundance Index (RAI)	Calculated for each month, camera trap and year
Describe temporal variation of habitat occupancy	Multi-seasons occupancy model	– Years are stacked (years are considered as replicates) – 'Seasons' are the months – Colonization and extinction among months are taken into account in the models
Identification of the variables influencing habitat occupancy during the breeding season	Single-season occupancy model	– Years are stacked (years are considered as replicates) – Focus on the breeding season
Describe the activity pattern among seasons	Density estimation	Performed for each season (spring, summer, autumn, winter)

pictures taken in a given period by the number of days the camera was active during the same period. Even though this index is often used in the literature as an index of population abundance, results have to be interpreted with caution given that RAI does not take detection probability into account (Sollmann et al. 2013, 2018). Here, we only used this index to summarize the raw data.

From counts to presence/absence data
Prior to calibrating occupancy models, we expressed the camera trap data as repeated occasions of detected/non-detected data. Here, we considered that a month (primary occasion) combined the information of six secondary occasions, each lasting five days. If no pictures were taken during the five days, then the species was considered as undetected ('0'). Otherwise, the species was considered as detected ('1'). Hence, for a given month, we had information regarding the detection or non-detection of the species during six secondary occasions (e.g. $1 - 0 - 1 - 1 - 0 - 1$). Occupancy models (MacKenzie et al. 2003) account for detectability by modelling probabilities of being detected or non-detected as resulting from two processes – probability that a site is occupied by hare (true presence) and, given that the site is occupied, probability that a hare is detected or not by camera traps.

Temporal variation of habitat occupancy within the year
Given that we were interested in temporal variation of habitat occupancy and not in turnover rates between years, we used multi-season occupancy models (MacKenzie et al. 2003) with year stacked: years were considered as replicates and 'seasons' as the months. We performed a multi-step model selection in four stages. First, we focused on variables influencing detection probability. We compared the effect of month, effort, habitat, month + effort or month + effort + habitat on detection probability, where effort corresponds to the sampling effort (i.e. the number of days the camera was working during each five-day period). We selected the model with lowest AIC (Burnham and Anderson 2002). Then we repeated the same operations to identify whether the habitat, the month or the interaction habitat × month explained occupation, colonization and extinction probability better than a null model. As previously, we selected the best model depending on AIC. Finally, in order to estimate effect sizes, we predicted occupancy and detection probabilities as a function of covariates retained in the selected model. We performed this

multi-season occupancy model first with habitat as described in the field, and second with habitat as described by satellite data in order to validate the accuracy of the spatially continuous habitat map (sub-section below).

Identification of the variables influencing habitat occupancy during the breeding season
To identify environmental variables influencing the mountain hare occupancy at a site during the breeding season (beginning of April to the end of August), we performed a single-season occupancy model (MacKenzie et al. 2002) with year stacked. We specifically focused on this season as it is decisive for population dynamic. We performed this analysis using years 2019 to 2022 as only seven cameras were active from April to August in 2018. We assumed that the population remained stable during this season (i.e. no migration, emigration, birth or death). No mothers with newborns were detected by camera traps.

We performed a multi-step model selection in two stages. As previously with habitat shift analyses, we first focused on variables influencing detection probability. We compared the effect of month, effort, habitat, month + effort or month + effort + habitat on detection probability. We selected the model with lowest AIC (Burnham and Anderson 2002). As before, we repeated the same operations to identify whether the following habitat variables explained occupancy probability better than a null model: mean canopy height, percentage of each vegetation type (except *Arctostaphylos uva-ursi*, woody forbs, deciduous tree and *Larix decidua* tree which are only recorded around one or two camera traps), the composition of the vegetation (i.e. scores of camera traps along the first two axes of the PCA), slope angle, tree cover, cover of vegetation < 10 cm, between 10 and 40 cm, and between 40 cm and 1.30 m, and the estimated date of snowmelt. We ranked the models according to AIC scores and retained models with ΔAIC lower than 2. Finally, as for multi-season models, we used predicted relationships as measure of effect size.

Activity pattern
We described the activity rhythm of the mountain hare during each season (spring, summer, autumn and winter). We used density estimation to identify peak activity, using time of the day of each observation in hours. To account for the circularity of the data (that is, data are continuous as midnight = 0 = 24 h), we centered the data on midnight and used

the *geom_density()* function in the ggplot2 library, with a bandwidth equal to 1 to better represent short-term variation that the default bandwidth. For each season we used the average time of sunrise and sunset in Chamonix to indicate how activity rhythms were linked to light.

Land cover mapping with Sentinel-2 and spatial extrapolation of habitat occupancy

To contextualise camera traps within spatially continuous habitat variation, we created a 10 m resolution habitat map comprising 11 spatially exhaustive classes (urban areas, water, forest, montane grassland, treeline ecotone, dwarf shrub, subalpine grassland, alpine grassland, shrub-grassland ecotone, rocky areas and snow and ice) for the Chamonix Mont-Blanc municipality (Bayle et al. 2024). First, we conducted photo-interpretation using a high-resolution infrared orthophoto from July 2020, covering the entire study area, to establish training samples for each class. Sampling was carried out in such a way as to minimize the distance between two samples of the same class, and to sample the entire study area to maximize the representativeness of the dataset. Photo-interpretation was carried out solely by BZC to minimize observer bias. Second, we compiled a 10 m resolution stack of eight explanatory variables. We calculated the topographic position index (TPI), the diurnal anisotropic heating index (DAH) and snow-free growing degree days (SF-GDD) as mesotopographic variables (Böhner and Antonić 2009, Gascoin et al. 2019, Barrou Dumont et al. 2021, Choler et al. 2021). Phenology variables were obtained from Tian et al. (2021) available from the Copernicus land monitoring service, and we used the start of the growing season date (SOSD) and the end of season vegetation index value (EOSV). Our spectral variables consisted of three indices, the normalised difference moisture index (NDMI, Gao et al. 1996) computed during summer months (06–01 to 09–01), the brightness index (BI, Escadafal 1989) and the normalised difference anthocyanin index (NARI, Bayle et al. 2019), both of which were computed during the fall (09–01 to 11–01). Further details on computation methods can be found in the Supporting information.

We implemented a random forest analysis to model the 11 classes, using training samples and the eight explanatory variables detailed above (Breiman 2001). We partitioned the data set into a model training subset (two thirds of pixels) and a model evaluation subset (one third of pixels) and calibrated the model using the *train* function in the 'caret' R package (Kuhn 2008). We repeated this procedure 1000 times, meaning that we implemented one random forest model for each dataset, to assess classification quality. For the final classification, we used a similar random forest model approach without partitioning between training and evaluation subsets. We applied this model across the study area, defined by the Chamonix Mont-Blanc municipality boundary (Fig. 1). See Supporting information for details of the random forest model.

We combined results from the multi-season model with the habitat map in order to visualize spatial variation in mountain hare occupancy probability for different months. To achieve this, we assigned probabilities modelled for camera trap sites to corresponding mapped habitat classes. Considering that camera traps were categorized as forest, grassland or shrub based on field surveys, we matched occupancy probabilities with the following mapped habitats: forest directly to forest, shrubland as both the shrub and shrub-grassland ecotone classes, and grassland as either subalpine or alpine grassland. To visualise spatial shifts in occupancy probability between winter and late spring, we mapped mountain hare occupancy probabilities for relevant habitats in January and May, respectively, for a selected zone.

Results

Relative abundance index (RAI)

Over the course of the study period, 37 out of 46 cameras detected mountain hares, and RAI values were variable from one site to another and across months, with values varying from 0 (i.e. no pictures of hare taken during the month) to 0.35 (i.e. around one picture taken every three days during the month, Fig. 3). Small variations were also observed across years with values ranging from 0.015 to 0.027 (Fig. 3). Mountain hare were contacted between 1400 and 2500 m a.s.l. and none were observed by camera traps located above 2500 m.

Temporal variation of habitat occupancy

Sampling effort, month and habitat influenced the detection probability of the mountain hare (Table 2, Fig. 4). Predicted detection probability was positive for the three variables and increased with the sampling effort. Detection probabilities were similar between habitats and varied among months with the lowest values observed in February and December. Habitat as described in the field influenced occupancy probability, and the interaction between habitat and month influenced colonization probability, while no variable influenced extinction probability in the selected model (Table 2). Mountain hare mainly occupied forest from December to March ('forest' in Fig. 5–6). In parallel, predicted occupancy probability increased in mixed shrubland during this period (Fig. 5 – 'shrubland'). Then, from April to August, predicted occupancy probability decreased in forest and in mixed shrubland to reach low predicted occupancy probability values at the end of summer and in autumn (Fig. 5). Low variation was predicted in grassland habitat within the year (Fig. 5 – 'grassland'). Spatial extrapolation of occupancy probability values revealed a pronounced shift in habitat occupancy between January and May, with higher values of mountain hare occupancy in the forested areas below 2000 m a.s.l. in January and increased occupancy probability in above-treeline shrub and shrub-meadow habitats above 2000 m a.s.l. in May (Fig. 6). Finally, the best performing model was the same with habitat as described by satellite data and predicted occupancy probabilities for each habitat were similar to results obtained with habitat as described in the field (see Supporting information for details of the confusion matrix).

Figure 3. Relative Abundance Index (RAI) according to the camera trap sites ordered by elevation (from low elevation at the bottom of the figure to high elevation at the top of the list). The more intense the color, the higher the number of contacts for each functioning day of the camera. Grey squares correspond to months where camera traps were not working.

Identification of the variables influencing habitat occupancy during the breeding season

Four models were selected according to AIC values. Sampling effort and habitat influenced detection probability of mountain hare from April to August (Table 3). Cover of the layer 10–40 cm, proportion of *Calluna vulgaris* and proportion of *Vaccinium vitis-idaea* positively affected occupancy probability, while the cover of the tree layer negatively affected occupancy probability (Table 4, Fig. 7). The effect of *V. vitis-idaea*

was entirely driven by two cameras with a high percentage of *V. vitis-idaea* compared to others, and this prevented a robust estimate of the relationship.

Activity pattern

Activity of the mountain hare was higher during the night than during the day, and higher during summer than during winter. During spring and summer (i.e. approximately during the breeding period), activity was highest at sunset, then

Table 2. Model selection of variables influencing detection probability (~ p), occupancy probability (~ psi), colonization probability (~ gamma) and extinction probability (~ epsilon) of the multi-season model. Habitat corresponds to the habitat described on the field. Bold entries show the sequential fitting of models, first with detection probability, last with extinction probability.

| Model selection	AIC
~ p ~ 1 ~ 1 ~ 1	
~ Month + Effort + Habitat ~ 1 ~ 1 ~ 1	3750.99
~ Effort + Month ~ 1 ~ 1 ~ 1	3753.29
~ Month ~ 1 ~ 1 ~ 1	3759.52
~ Effort ~ 1 ~ 1 ~ 1	3767.94
~ 1 ~ 1 ~ 1 ~ 1	3775.27
~ Habitat ~ 1 ~ 1 ~ 1	3779.17
~ p ~ psi ~ 1 ~ 1	
~ Month + Effort + Habitat ~ Habitat ~ 1 ~ 1	3746.40
~ Month + Effort + Habitat ~ 1 ~ 1 ~ 1	3750.99
~ p ~ psi ~ gamma ~ 1	
~ Month + Effort + Habitat ~ Habitat ~ Habitat*Month ~ 1	3699.82
~ Month + Effort + Habitat ~ Habitat ~ 1 ~ 1	3737.18
~ Month + Effort + Habitat ~ Habitat ~ Habitat ~ 1	3746.40
~ p ~ psi ~ gamma ~ epsilon	
~ Month + Effort + Habitat ~ Habitat ~ Habitat*Month ~ 1	3699.82
~ Month + Effort + Habitat ~ Habitat ~ Habitat*Month ~ Habitat	3703.71
~ Month + Effort + Habitat ~ Habitat ~ Habitat*Month ~ Habitat*Month	3727.73
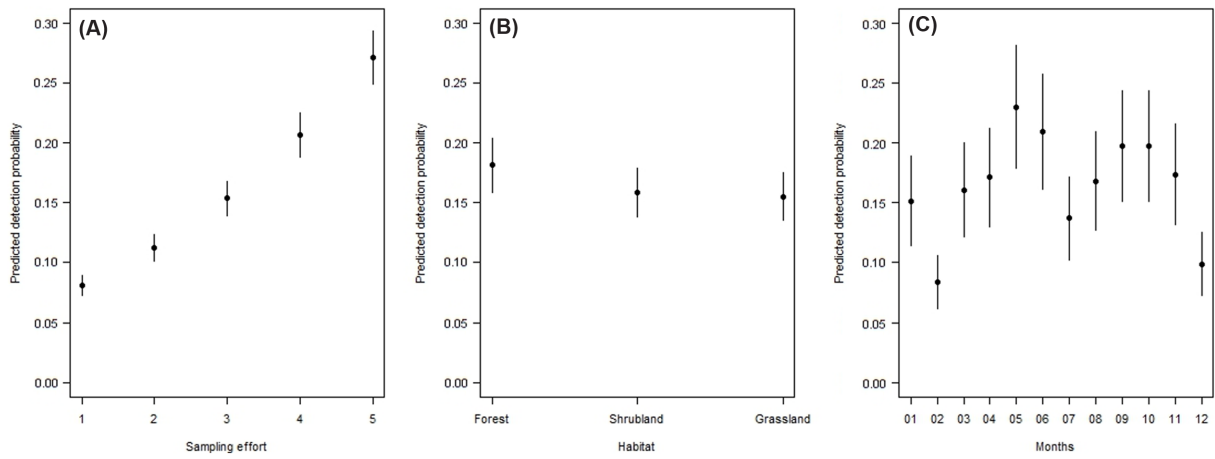
Figure 4. Detection probability predicted by the best multi-season occupancy model according to (A) the sampling effort, (B) the habitat and (C) the months. Error bars represent the 95% confidence interval.

stayed at a lower level during the night and started decreasing again around one hour before sunrise (Fig. 8). In winter, activity decreased around one and a half hour before sunrise, and increased around one hour after sunset (Fig. 8). Activity was at an intermediate level in autumn. Activity of mountain hare is crepuscular and nocturnal in summer, and nocturnal in winter (Fig. 8).

Discussion

On the Chamonix side of the Mont-Blanc massif, mountain hares occur between 1400 and 2500 m a.s.l., and occupy forests, shrublands and grasslands distributed along this elevation gradient (Bisi et al. 2013, Rehnus et al. 2013, 2016, Sultaire et al. 2016, Rehnus et Bollman 2020, La Morgia et al. 2023). The absence of mountain hares in camera traps above 2500 m a.s.l. in our study contrasts with the results from La Morgia et al. (2023), who observed the highest occurrence of this species within pioneer and rocky areas above 2470 m a.s.l. While they may occur at higher elevations in the Mont-Blanc massif (Angerbjörn and Flux 1995, pers. obs.), in our study the camera traps set up at elevations above 2500 m were located in an isolated area surrounded by glaciers and not connected to forests or shrublands (Fig. 1). For the future, additional cameras in grasslands and above 2500 m could
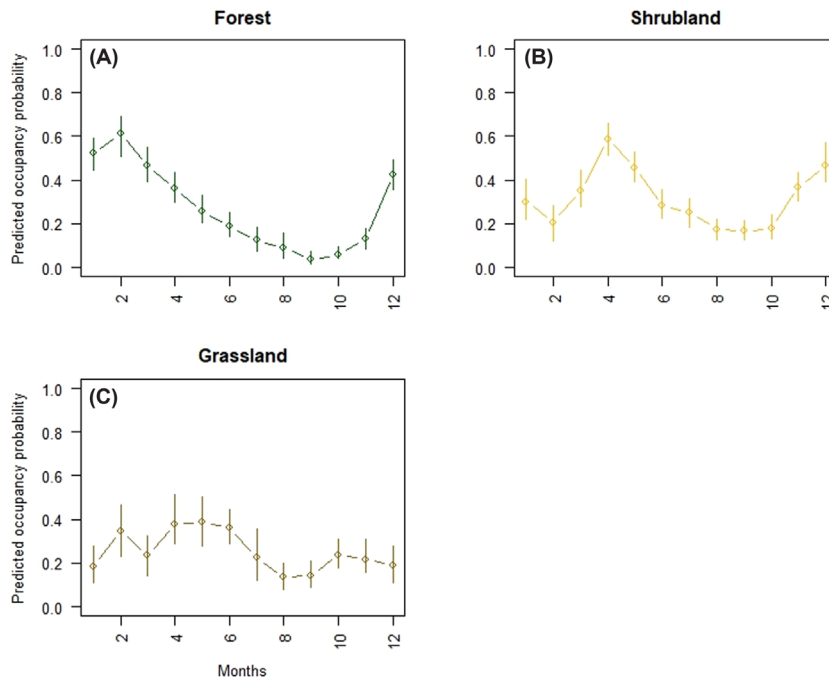

Figure 5. Intra-annual variation of the predicted occupancy probability of the three habitats included in the multi-season occupancy model: (A) forest, (B) shrubland, (C) grassland.
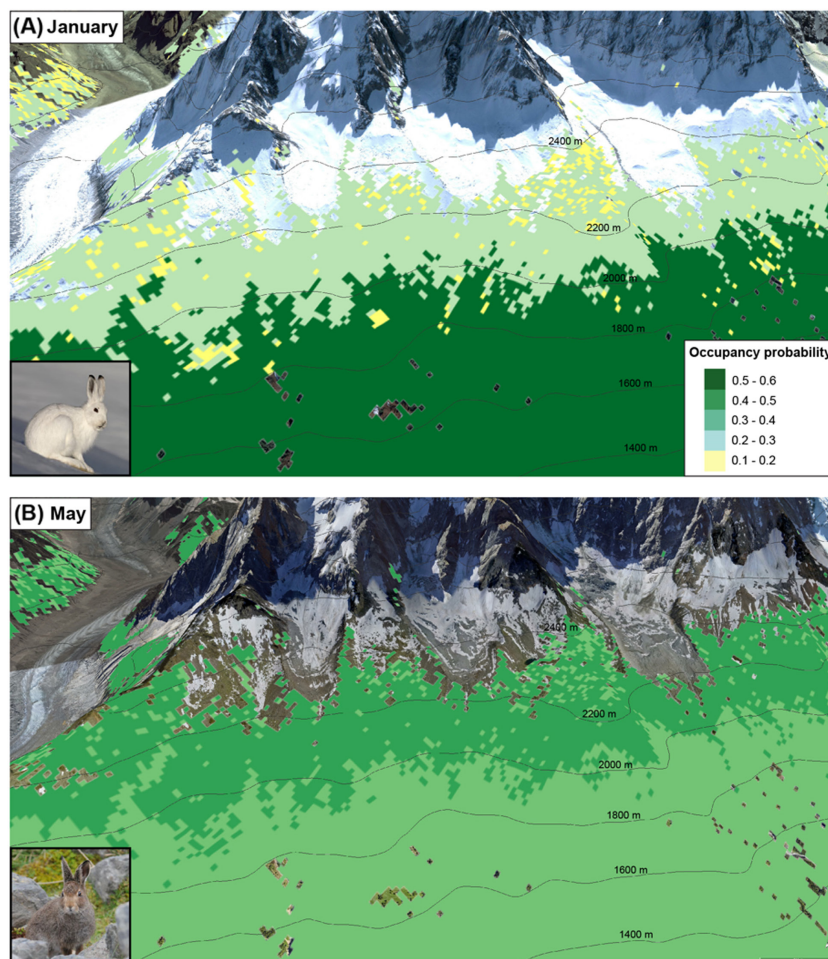
Figure 6. Mountain hare occupancy probability extrapolated to the 10 m habitat map for the months of (A) January and (B) May, indicating seasonal variation in potential favorable habitat. In January, mountain hares show high probability of occupying forest habitat, with lower probability in open shrub and grassland habitats. In May, hare populations tend to move upslope into shrubland and mixed grass and shrub habitats above the treeline. Seasonal background images are provided by Google Earth. Mountain hare photo credits: C. Robion (A) and F. Moutou (B).

be set up in other areas of the massif in order to provide a wider view of mountain hare distribution in higher elevation areas. However, we are limited by topographical configuration of the massif where many areas above 2500 m at present are either glaciated or rocky cliff habitat. In the future, the emergence of vegetated ecosystems in glacier forefields caused by glacial retreat (Bayle et al. 2023, Bosson et al. 2023) in the Mont-Blanc massif could appear as new potential habitat for mountain hare at higher elevation areas. In addition, in high elevation areas, a fecal survey (such as used in Rehnus

Table 3. Model selection of variables influencing detection probability (~ p) and occupancy probability (~ psi) of the single-season model performed during the breeding season.

Model selection	AIC
~ p ~ 1	
~ Effort + Habitat ~ 1	1637.28
~ Habitat ~ 1	1640.85
~ Effort ~ 1	1641.66
~ 1 ~ 1	1644.83
~ p ~ psi *	
~ Effort + Habitat ~ Tree layer	1629.60
~ Effort + Habitat ~ Proportion of *Calluna vulgaris*	1630.42
~ Effort + Habitat ~ Layer 10–40 cm	1630.57
~ Effort + Habitat ~ Proportion of *Vaccinium vitis-idaea*	1631.45

*We only present the four models for which ΔAIC < 2.

Table 4. Outputs of the three selected models: estimate, standard error and p-value of the variables influencing occupancy and detection probability (only shown for the model with the tree layer as variations are similar for the other ones) of the single-season model performed during the breeding season. Occupancy (psi) and detection (p) probability.

	Estimate	SE	p-value
~ psi			
Cover of the tree layer	−0.36	0.12	0.003
Cover of the layer 10–40 cm	0.42	0.15	0.005
Proportion of *Calluna vulgaris*	12.28	5.2	0.02
Proportion of *Vaccinium vitis-idaea*	13.74	8.33	0.10
~ p			
Intercept	-4.56	1.56	0.003
Sampling effort	0.53	0.31	0.09
Shrubland	0.42	0.17	0.02
Grassland	0.41	0.21	0.05

and Bollmann 2020) could be used to complete observations of camera traps and improve our understanding of habitat occupancy above 2500 m.

Occupancy varied among seasons and habitats. In winter (December to April), mountain hares were mainly found in forest (< 1800 m a.s.l.), probably to reduce energy expenditure caused by cold temperatures, find food resources and be less exposed to predation. At the end of winter and beginning of spring, mountain hare migrated to higher elevations (Rehnus and Bollmann 2020) and occupied mixed areas of shrublands. Indeed, within the cameras classified in shrublands, proportion of shrub varies from 37 to 87%, while the remaining percentage is composed of forbs/grass species, offering a wide panel of mixed vegetation type within the shrubland habitat (see Supporting information for details of the proportion of shrubs and forbs/grass around each camera trap). We suppose that these heterogeneous habitats offer

food and protection from predators for mountain hares during the breeding period (Hiltunen et al. 2004, Hiltunen and Kauhala 2006, Rehnus et al. 2013, 2016). Habitats with a high degree of shelter provided by the vegetation canopy limit visual contacts from predators and give a higher chance of allowing the mountain hare to flee (Rehnus et al. 2013). In addition, shrub vegetation decreases wind exposure and hence reduces the heat loss of animals (Grace and Easterbee 1979). Variation of predicted occupancy probability of mountain hare in grassland is low compared to other habitats, but results still show that they can occupy high elevation areas (2300–2500 m a.s.l.). We suppose that open habitats such as grasslands are generally not preferred to reduce the risk of predation, but they still might be visited to find high-quality food (Rehnus et al. 2016), or may constitute transient habitats used by males during the reproductive season to find females (Rehnus et al. 2022). Predicted occupancy probability of mountain hare decreases at the end of the summer and in autumn in all habitats. We expect that after the high spring and summer activity related to the search for food resources, breeding and mating (Pettigrew et al. 2021), mountain hares reduce their activity to decrease predation risk and energy expenditure (Bisi et al. 2010). As both animal movement and population density influence occupancy estimates (Neilson et al. 2018, Rogan et al. 2019), we suggest that the lower level of activity of mountain hare at the end of summer and in autumn is associated to less movement within their home range (Genini Gamboni et al. 2008, Bisi et al. 2010), a pattern that we observed in the field (pers. obs.). This leads to a reduced number of contacts per camera traps, preventing us from accurately estimating habitat occupancy of mountain hare during this period. To summarize, occupancy is not a direct measure of abundance as it is influenced by animal movement and population density, which could explain the lower values of occupancy during this period. Combining studies of movement (e.g. with GPS collars) and camera traps is needed to understand this fully.
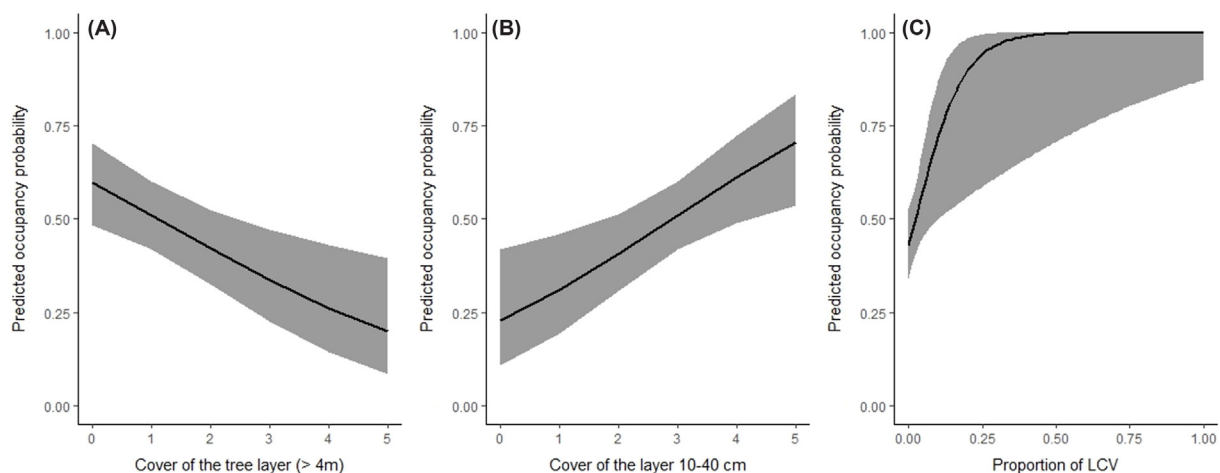

Figure 7. Predicted occupancy probability according to the three selected environmental variables included in the single-season model performed during the breeding season: (A) the cover of the tree layer, (B) the cover of the layer 10–40 cm and (C) the proportion of *Calluna vulgaris*.
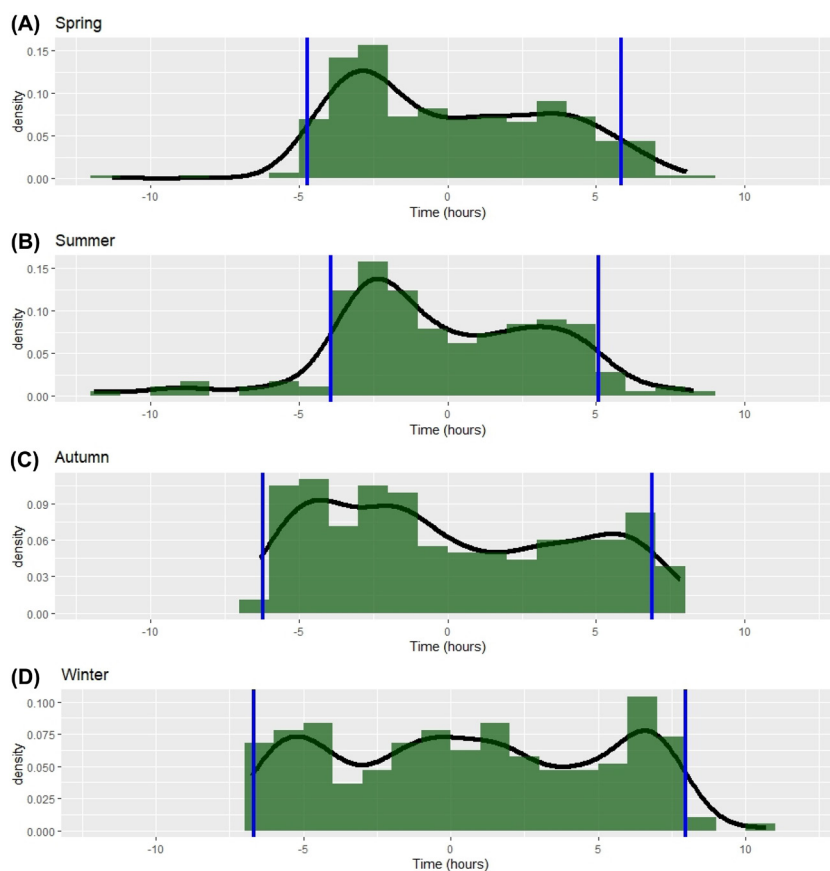
Figure 8. Activity pattern of mountain hare centered on midnight in (A) spring (March, April, May), (B) summer (June, July, August), (C) autumn (September, October, November) and (D) winter (December, January, February). Vertical lines indicate average time of sunrise and sunset in Chamonix for each season.

Extending our findings from localized camera traps to the landscape scale using habitat maps is relevant for management purposes. However, in this case we would not recommend extrapolating to a scale broader than the French side of the Mont-Blanc massif. Indeed, mountain ranges can be very different in terms of environmental variables (percentage of shrubland/forest, slopes, connectivity of different areas) and biotic interactions, such as the presence of European hare that can influence the distribution of the mountain hare. Models of this study have been performed with habitat variables instead of elevation, which allowed the extrapolation within the French side of the Mont-Blanc massif. However, extrapolation at a scale broader than the French side of the Mont-Blanc massif would require further validation, because the Mont-Blanc massif has some specificities such as steep slopes and a high percentage of shrubland areas, compared to the Italian side for example. Studies of habitat use have shown that it can be influenced by the availability of each habitat (e.g. Mysterud and Ims 1998), but this is not something we could assess in the study.

With respect to vegetation cover, we found that the predicted occupancy probability of mountain hare increases with the cover of the mixed low shrub and herbaceous layer (i.e. 10–40 cm vegetation layer) during the breeding period

(April–August). Occupancy probability is negatively correlated with the tree layer during the breeding period, which is consistent with the decrease of occupancy probability in forest during this period.

In the Alps, mountain hares have a higher activity level during the night than during the day, in agreement with the nocturnal or crepuscular activity pattern found in other regions (Bisi et al. 2013, Ikeda et al. 2016, Ogurtsov et al. 2018, Pettigrew et al. 2021). Lengths of activity periods vary between seasons in parallel with the variations of the night and day cycles. Higher levels of activity are supposedly related to food searching (Bisi et al. 2013). Unlike Pettigrew et al. (2021, Scotland) and contrary to our expectations, diurnal activity in summer is low for mountain hares in the Mont-Blanc massif. We suppose that this reduced activity could be a strategy to avoid predators such as golden eagles or foxes, and less constraint due to longer nights at lower latitudes than in Scotland. During the breeding period, activity of mountain hare is crepuscular and nocturnal while it is only nocturnal in winter (Ikeda et al. 2016).

In the Alps, agricultural decline (abandonment of grazing by cows, sheep and goats) and subsequent reforestation can be detrimental to mountain fauna that depend on semi-open environments and mixed habitats (Patthey et al. 2012).

Indeed, increasing forest cover leads to a homogenization of vegetation cover and a structural loss of biodiversity by increasing the dominance of trees in the long term (Rehnus et al. 2016). Our study confirms the importance of mosaics of forested habitats and mixed areas of shrubland and grassland for mountain hares. Thus, natural (avalanches, herbivory by wildlife) or anthropogenic (pastoralism, forest management) disturbances carried out at the forest edge are considered favorable for maintaining suitable habitats for the mountain hare, in order for them to optimize trade-offs between food resources and shelter depending on the season (Rehnus et al. 2016). In our study area, the relatively low percentage of mixed shrub and grassland habitat (4% or 13 km²) highlights the need for land management strategies aimed at conserving the remaining semi-open habitats above treeline and ongoing monitoring of ecotone shifts in the years ahead. Lastly, as underlined by Rehnus et al. (2014), it is also important to limit tourist activity – the Mont-Blanc massif is a highly and seasonally touristic area – in the areas used by mountain hares, as frequent human disturbance negatively impacts the energy budget of the mountain hare through changes in physiology and behavior, particularly in winter when snow limits the access to food resources (Rehnus et al. 2014).

In conclusion, our results show that camera traps provide detailed information on mountain hare ecology in mountain environments and confirm the importance of access to a mosaic of habitats over short distances. Further long-term surveys are needed to investigate how climate change, predation, interspecific competition and hybridization with the expanding European hare *L. europaeus* might impact altitudinal migration, habitat shift, nutritional needs, activity pattern and population dynamics of the mountain hare. Deepening our understanding of these processes would allow us to define optimal management strategies depending on the region, either directly, e.g. through more restrictive hunting regulations or human recreational activities, or indirectly, e.g. through forest and habitat management.

Author contributions

Marjorie Bison: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Visualization (lead); Writing – original draft (lead). **Nigel G. Yoccoz**: Conceptualization (equal); Formal analysis (equal); Methodology (equal); Validation (equal); Visualization (equal); Writing – original draft (equal). **Bradley Z. Carlson**: Conceptualization (equal); Formal analysis (equal); Visualization (equal); Writing – original draft (equal). **Arthur Bayle**: Methodology (equal); Writing – original draft (equal). **Anne Delestrade**: Conceptualization (equal); Investigation (equal); Project administration (equal); Supervision (equal); Visualization (equal); Writing – original draft (equal).

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.b2rbnzsp7 (Bison et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

References

Acevedo, P., Jiménez-Valverde, A., Melo-Ferreira, J., Real, R. and Alves, P. C. 2012. Parapatric species and the implications for climate change studies: a case study on hares in Europe. – Global Change Biol. 18: 1509–1519.

Angerbjörn, A. and Flux, J. E. C. 1995. *Lepus timidus*. – Mamm. Species 495: 1–11.

Angerbjörn, A. and Schai-Braun, S. C. 2023. Mountain hare *Lepus timidus* Linnaeus, 1758. – In: Hackländer, K. and Zachos, F. E. (eds), Handbook of the mammals of Europe. Springer International Publishing, pp. 1–29.

Barrou Dumont, Z., Gascoin, S., Hagolle, O., Ablain, M., Jugier, R., Salgues, G., Marti, F., Dupuis, A., Dumont, M. and Morin, S. 2021. Brief communication: evaluation of the snow cover detection in the Copernicus high resolution snow & ice monitoring service. – Cryosphere 15: 4975–4980.

Bayle, A., Carlson, B. Z., Thierion, V., Isenmann, M. and Choler, P. 2019. Improved mapping of mountain shrublands using the sentinel-2 red-edge band. – Remote Sens. 11: 2807.

Bayle, A., Carlson, B. Z., Zimmer, A., Vallée, S., Rabatel, A., Cremonese, E., Filippa, G., Dentant, C., Randin, C., Mainetti, A., Roussel, E., Gascoin, S., Corenblit, D. and Choler, P. 2023. Local environmental context drives heterogeneity of early succession dynamics in alpine glacier forefields. – Biogeosciences 20: 1649–1669.

Bayle, A., Carlson, B. Z., Nicoud, B., Francon, L., Corona, C., Lavorel, S. and Choler, P. 2024. Uncovering the distribution and limiting factors of Ericaceae-dominated shrublands in the French Alps. – Front. Biogeogr. 16: e61746.

Beniston, M. et al. 2018. The European mountain cryosphere: a review of its current state, trends, and future challenges. – Cryosphere 12: 759–794.

Bisi, F., Nodari, M., Dos Santos Oliveira, N. M., Masseroni, E., Preatoni, D. G., Wauters, L. A., Tosi, G. and Martinoli, A. 2010. Space use patterns of mountain hare (*Lepus timidus*) on the Alps. – Eur. J. Wildl. Res. 57: 305–312.

Bisi, F., Nodari, M., Dos Santos Oliveira, N. M., Ossi, F., Masseroni, E., Preatoni, D. G., Wauters, L. A. and Martinoli, A. 2013. Habitat selection and activity patterns in alpine mountain hare (*Lepus timidus varronis*). – Mamm. Biol. 78: 28–33.

Bisi, F., Wauters, L. A., Preatoni, D. G. and Martinoli, A. 2015. Interspecific competition mediated by climate change: which interaction between brown and mountain hare in the Alps? – Mamm. Biol. 80: 424–430.

Bison, M., Yoccoz, N. G., Carlson, B. Z., Bayle, A. and Delestrade, A. 2024. Data from: Camera traps reveal seasonal variation in activity and occupancy of the Alpine mountain hare *Lepus timidus varronis*. – Dryad Digital Repository, https://doi.org/10.5061/dryad.b2rbnzsp7.

Böhner, J. and Antonić, O. 2009. Land-surface parameters specific to topo-climatology. – Dev. Soil Sci. 33: 195–226.

Bosson, J. B., Huss, M., Cauvy-Fraunié, S., Clément, J. C., Costes, G., Fischer, M., Poulenard, J. and Arthaud, F. 2023. Future emergence of new ecosystems caused by glacial retreat. – Nature 620: 562–569.

Breiman, L. 2001. Random forests. – Mach. Learn. 45: 5–32.

Burnham, K. P. and Anderson, D. R. 2002. Model selection and multi-model inference: a practical information-theoretic approach. – Springer-Verlag.

Burton, A. C., Neilson, E., Moreira, D., Ladle, A., Steenweg, R., Fisher, J. T., Bayne, E. and Boutin, S. 2015. Wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. – J. Appl. Ecol. 52: 675–685.

Caravaggi, A., Montgomery, W. I. and Reid, N. 2015. Range expansion and comparative habitat use of insular, congeneric lagomorphs: invasive European hares *Lepus europaeus* and endemic Irish hares *Lepus timidus hibernicus*. – Biol. Invas. 17: 687–698.

Caravaggi, A., Leach, K., Santilli, F., Rintala, J., Helle, P., Tiainen, J., Bisi, F., Martinoli, A., Montgomery, W. I. and Reid, N. 2017. Niche overlap of mountain hare subspecies and the vulnerability of their ranges to invasion by the European hare; the (bad) luck of the Irish. – Biol. Invas. 19: 655–674.

Choler, P., Bayle, A., Carlson, B. Z., Randin, C., Filippa, G. and Cremonese, E. 2021. The tempo of greening in the European Alps: spatial variations on a common theme. – Global Change Biol. 27: 5614–5628.

Davis, C. L. et al. 2018. Ecological correlates of the spatial co-occurrence of sympatric mammalian carnivores worldwide. – Ecol. Lett. 21: 1401–1412.

Depauw, L., Blondeel, H., De Lombaerde, E., De Pauw, K., Landuyt, D., Lorer, E., Vangansbeke, P., Vanneste, T., Verheyen, K. and De Frenne, P. 2022. The use of photos to investigate ecological change. – J. Ecol. 110: 1220–1236.

Durand, Y., Giraud, G., Laternser, M., Etchevers, P., Mérindol, L. and Lesaffre, B. 2009. Reanalysis of 47 years of climate in the French Alps (1958–2005): climatology and trends for snow cover. – J. Appl. Meteorol. Climatol. 48: 2487–2512.

Elsen, P. R. and Tingley, M. W. 2015. Global mountain topography and the fate of montane species under climate change. – Nat. Clim. Change 5: 772–776.

Escadafal, R., Girard, M.-C. and Courault, D. 1989. Munsell soil color and soil reflectance in the visible spectral bands of Landsat MSS and TM data. – Remote Sens. Environ. 27: 37–46.

Fiske, I. and Chandler, R. 2011. unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. – J. Stat. Softw. 43: 1–23.

Flux, J. E. C. 1970. Colour changes of mountain hares (*Lepus timidus scoticus*) in north-east Scotland. – J. Zool. 162: 345–358.

Gamboni, A.-S. 1997. Comportement spatio-temporel d'une population de lièvre variable (*Lepus timidus varronis*) au sud des Alpes. – MSc thesis, Univ. de Neuchatel, Switzerland.

Gao, B.-C. 1996. NDWI – a normalized difference water index for remote sensing of vegetation liquid water from space. – Remote Sens. Environ. 58: 257–266.

Gascoin, S., Grizonnet, M., Bouchet, M., Salgues, G. and Hagolle, O. 2019. Theia Snow collection: high-resolution operational snow cover maps from Sentinel-2 and Landsat-8 data. – Earth Syst. Sci. Data 11: 493–514.

Genini Gamboni, A.-S., Bisi, F., Masseroni, E., Nodari, M., Preatoni, D. G., Wauters, L. A., Martinoli, A. and Tosi, G. 2008. Home range dynamics of mountain hares (*Lepus timidus*) in the Swiss Alps. – Hystrix Int. J. Mammal. 19: 157–163.

Gilbert, N. A., Clare, J. D. J., Stenglein, J. L. and Zuckerberg, B. 2020. Abundance estimation of unmarked animals based on camera-trap data. – Conserv. Biol. 35: 88–100.

Gobiet, A., Kotlarski, S., Beniston, M., Heinrich, G., Rajczak, J. and Stoffel, M. 2014. 21st century climate change in the European Alps – a review. – Sci. Total Environ. 493: 1138–1151.

Grace, J. and Easterbee, N. 1979. The natural shelter for red deer (*Cervus elaphus*) in a Scottish glen. – J. Appl. Ecol. 16: 37–48.

Hiltunen, M. and Kauhala, K. 2006. Selection of sapling stand habitats by the mountain hare (*Lepus timidus*) during winter. – Mamm. Biol. 71: 183–189.

Hiltunen, M., Kauhala, K. and Lindén, H. 2004. Habitat use of the mountain hare *Lepus timidus* in summer: the importance of different vegetation layers. – Acta Theriol. 49: 479–490.

Hirakawa, H. 2001. Coprophagy in leporids and other mammalian herbivores. – Mamm. Rev. 31: 61–80.

Hulbert, I. A., Iason, G. R. and Mayes, R. W. 2001. The flexibility of an intermediate feeder: dietary selection by mountain hares measured using faecal n-alkanes. – Oecologia 129: 197–205.

Iason, G. and Van Wieren, S. 1999. Digestive and ingestive adaptations of mammalian herbivores to low-quality forage. – In: Olff, H., Brown, V. K. and Drent, R. H. (eds), Herbivores: between plants and predators. Blackwell, pp. 337–370.

Ikeda, T., Uchida, K., Matsuura, Y., Takahashi, H., Yoshida, T., Kaji, K. and Koizumi, I. 2016. Seasonal and diel activity patterns of eight sympatric mammals in northern Japan revealed by an intensive camera-trap survey. – PLoS One 11: e0163602.

Jansson, G., Thulin, C.-G. and Pehrson, Å. 2007. Factors related to the occurrence of hybrids between brown hares *Lepus europaeus* and mountain hares *L. timidus* in Sweden. – Ecography 30: 709–715.

Klein, G., Vitasse, Y., Rixen, C., Marty, C. and Rebetez, M. 2016. Shorter snow cover duration since 1970 in the Swiss Alps due to earlier snowmelt more than to later snow onset. – Clim. Change 139: 637–649.

Kuhn, M. 2008. Building predictive models in R using the caret package. – J. Stat. Softw. 28: 1–26.

La Morgia, V. and Venturino, E. 2017. Understanding hybridization and competition processes between hare species: implications for conservation and management on the basis of a mathematical model. – Ecol. Modell. 364: 13–24.

La Morgia, V., Martini, I., Tosatto, E., Mazza, E., Bertolino, S. and Santovito, A. 2023. Global warming is promoting the rapid invasion of the mountain hare range by the European hare in the Alps. – Biodivers. Conserv. 32: 3875–3891.

Lindlof, B. et al. 1974. On activity, habitat selection and diet of the mountain hare (*Lepus timidus* L.) in winter. – Viltrevy 9: 27–43.

LPO PACA, GECEM and GCP. 2016. Les mammifères de Provence-Alpes-Côte d'Azur. – Biotope, 344 pp.

MacKenzie, D. I., Nichols, J. D., Lachman, G. B., Droege, S., Andrew Royle, J. and Langtimm, C. A. 2002. Estimating site occupancy rates when detection probabilities are less than one. – Ecology 83: 2248–2255.

MacKenzie, D. I., Nichols, J. D., Hines, J. E., Knutson, M. G. and Franklin, A. B. 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. – Ecology 84: 2200–2207.

Malinowski, R., Lewiński, S., Rybicki, M., Gromny, E., Jenerowicz, M., Krupiński, M., Nowakowski, A., Wojtkowski, C., Krupiński, M., Krätzschmar, E. and Schauer, P. 2020. Automated production of a land cover/use map of Europe based on Sentinel-2 imagery. – Remote Sens. 12: 3523.

Mysterud, A. and Ims, R. A. 1998. Functional responses in habitat use: availability influences relative use in trade-off situations. – Ecology 79: 1435–1441.

Neilson, E. W., Avgar, T., Burton, A. C., Broadley, K. and Boutin, S. 2018. Animal movement affects interpretation of occupancy models from camera-trap surveys of unmarked animals. – Ecosphere 9: 15.

Newey, S., Dahl, F., Willebrand, T. and Thirgood, S. 2007. Unstable dynamics and population limitation in mountain hares. – Biol. Rev. 82: 527–549.

Niedballa, J., Sollmann, R., Courtiol, A. and Wilting, A. 2016. camtrapR: an R package for efficient camera trap data management. – Methods Ecol. Evol. 7: 1457–1462.

Nieminen, P. and Mustonen, A. M. 2008. A preliminary study on the seasonal body temperature rhythms of the captive mountain hare (Lepus timidus). – Cryobiology 56: 163–167.

Ogurtsov, S. S., Zheltukhin, A. S. and Kotlov, I. P. 2018. Daily activity patterns of large and medium-sized mammals based on camera traps data in the central forest nature reserve, Valdai upland, Russia. – Nat. Conserv. Res. 3: 68–88.

Parmesan, C. and Yohe, G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. – Nature 421: 37.

Patthey, P., Signorell, N., Rotelli, L. and Arlettaz, R. 2012. Vegetation structural and compositional heterogeneity as a key feature in Alpine black grouse microhabitat selection: conservation management implications. – Eur. J. Wildl. Res. 58: 59–70.

Pellicciotti, F., Bauder, A. and Parola, M. 2010. Effect of glaciers on streamflow trends in the Swiss Alps. – Water Resour. Res. 46: 10522.

Pepin, N. et al. 2015. Elevation-dependent warming in mountain regions of the world. – Nat. Clim. Change 5: 424–430.

Pettigrew, G. W., Di Vita, V., Pettigrew, M. and Gilchrist, J. S. 2021. The diel activity pattern of mountain hare (Lepus timidus) on managed heather moorland in Scotland. – Ecol. Evol. 11: 7106–7113.

Pettorelli, N., Safi, K. and Turner, W. 2014. Satellite remote sensing, biodiversity research and conservation of the future. – Philos. Trans. R. Soc. B 369: 20130190.

Pyörnilä, A., Putaala, A., Hissa, R. and Sulkava, S. 1992. Adaptations to environment in the mountain hare (Lepus timidus): thermal physiology and histochemical properties of locomotory muscles. – Can. J. Zool. 70: 1325–1330.

Rebetez, M. and Reinhard, M. 2008. Monthly air temperature trends in Switzerland 1901–2000 and 1975–2004. – Theor. Appl. Climatol. 91: 27–34.

Rehnus, M. and Bollmann, K. 2020. Mountain hare Lepus timidus follow the green-up wave in the pursuit of high quality food. – Wildl. Biol. 2020: 1–5.

Rehnus, M., Palme, R., Filli, F. and Hackländer, K. 2010. Seasonal glucocorticoid secretion in mountain hares (Lepus timidus). – Mammalia 74: 347–350.

Rehnus, M., Marconi, L., Hackländer, K. and Filli, F. 2013. Seasonal changes in habitat use and feeding strategy of the mountain hare (Lepus timidus) in the central Alps. – Hystrix 24: 161–165.

Rehnus, M., Wehrle, M. and Palme, R. 2014. Mountain hares Lepus timidus and tourism: stress events and reactions. – J. Appl. Ecol. 51: 6–12.

Rehnus, M., Braunisch, V., Hackländer, K., Jost, L. and Bollmann, K. 2016. The seasonal trade-off between food and cover in the alpine mountain hare (Lepus timidus). – Eur. J. Wildl. Res. 62: 11–21.

Rehnus, M., Bollmann, K., Schmatz, D. R., Hackländer, K. and Braunisch, V. 2018. Alpine glacial relict species losing out to climate change: the case of the fragmented mountain hare population (Lepus timidus) in the Alps. – Global Change Biol. 24: 3236–3253.

Rehnus, M., Bollmann, K., Gugerli, F., Brodbeck, S. and Schenker, L. 2022. Le lièvre variable: dynamique de population et utilisation de l'habitat. – Fauna 41: 2–7.

Rigoudy, N. et al. 2023. The DeepFaune initiative: a collaborative effort towards the automatic identification of European fauna in camera-trap images. – Eur. J. Wildl. Res. 69: 113.

Rogan, M. S., Balme, G. A., Distiller, G., Pitman, R. T., Broadfield, J., Mann, G. K. H., Whittington-Jones, G. M., Thomas, L. H. and O'Riain, M. J. 2019. The influence of movement on the occupancy-density relationship at small spatial scales. – Ecosphere 10: 13.

Schai-Braun, S. C., Gander, J., Jenny, H. and Hackländer, K. 2017. Is reproductive strategy of Alpine mountain hares adapted to different elevations? – Mamm. Biol. 85: 55–59.

Schai-Braun, S. C., Posautz, A., Alves, P. C. and Hackländer, K. 2019. Gastrointestinal parasite infestation in the alpine mountain hare (Lepus timidus varronis): are abiotic environmental factors such as elevation, temperature and precipitation affecting prevalence of parasite species? – Int. J. Parasitol. Parasites Wildl. 9: 202–208.

Schai-Braun, S. C., Lapin, K., Bernhardt, K.-G., Alves, P. C. and Häcklander, K. 2020. Effect of landscape type, elevation, vegetation period, and taxonomic plant identification level on diet preferences of Alpine mountain hares (Lepus timidus varronis). – Eur. J. Wildl. Res. 66: 57.

Schai-Braun, S. C., Jenny, H., Ruf, T. and Hackländer, K. 2021. Temperature increase and frost decrease driving upslope elevational range shifts in alpine grouse and hares. – Global Change Biol. 27: 6602–6614.

Slotta-Bachmayr, L. 1998. Biologie und Ökologie des Alpenschneehasen (Lepus timidus varronis Miller 1901): Verbreitung, Raumnutzung, Aktivität und Habitatwahl in den hohen Tauern. – PhD thesis, University of Salzberg, Austria.

Sollmann, R., Mohamed, A., Samejima, H. and Wilting, A. 2013. Risky business or simple solution–relative abundance indices from camera-trapping. – Biol. Conserv. 159: 405–412.

Sultaire, S. M., Pauli, J. N., Martin, K. J., Meyer, M. W. and Zuckerberg, B. 2016. Extensive forests and persistent snow cover promote snowshoe hare occupancy in Wisconsin. – J. Wild. Manage. 80: 894–905.

Thulin, C. G. 2003. The distribution of mountain hares Lepus timidus in Europe: a challenge from brown hares L. europaeus? – Mamm. Rev. 33: 29–42.

Thulin, C. G., Fang, M. and Averianov, A. O. 2006. Introgression from Lepus europaeus to L. timidus in Russia revealed by mito-

chondrial single nucleotide polymorphisms and nuclear microsatellites. – Hereditas 143: 68–76.

Tian, F., Cai, Z., Jin, H., Hufkens, K., Scheifinger, H., Tagesson, T., Smets, B., Van Hoolst, R., Bonte, K., Ivits, E., Tong, X., Ardö, J. and Eklundh, L. 2021. Calibrating vegetation phenology from Sentinel-2 using eddy covariance, PhenoCam, and PEP725 networks across Europe. – Remote Sens. Environ. 260: 0034-4257.

Trolliet, F., Huynen, M.-C., Vermeulen, C. and Hambuckers, A. 2014. Use of camera traps for wildlife studies. A review. – Biotechnol. Agron. Soc. Environ. 18: 446–454.

Valt, M. and Cianfarra, P. 2010. Recent snow cover variability in the Italian Alps. – Cold Reg. Sci. Technol. 64: 146–157.

Watson, A. and Hewson, R. 1973. Population densities of mountain hares (*Lepus timidus*) on western Scottish and Irish moors and on Scottish hills. – J. Zool. 170: 151–159.