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Non-invasive estimation of brown hare density in Mavrovo National Park, North Macedonia, using the REST model

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Abstract

Effective conservation of predators requires a comprehensive understanding of their prey populations. Being a specialised hunter, the survival of the critically endangered Balkan lynx (*Lynx lynx balcanicus*) depends on ample amount of the two main prey species, roe deer (*Capreolus capreolus*) and brown hare (*Lepus europaeus*). We used the REST model to calculate the density of brown hare in Mavrovo National Park (MNP), North Macedonia. To that aim, we selected four sites near villages within MNP, as the park harbours the majority of the Balkan lynx population. We randomly placed 10 camera-traps with at least 200 m distance in between, aiming at a survey period of 28 days. We focused on agroecosystems with a mix of active and inactive pastures and small agricultural fields. During the entire trapping period we collected 230 videos with hare observations, obtained over a total trapping effort of 867 active trapping nights. The site-specific diel activity pattern of the brown hare reveals distinct periods of inactivity from early morning to late afternoon, with activity levels peaking shortly after this interval. Results show that the density ranged from 3.38–16.45 (SE = 2.08–5.37) brown hares per one km^2. This study offers the first-ever density estimation of brown hare in the Balkan lynx range. If repeated and updated, this could potentially inform better management measures for the conservation of the Balkan's rare cat.

Keywords: brown hare, prey, REST, density

Introduction

Effective conservation of predators requires a comprehensive understanding of their prey populations. The Critically Endangered status of the Balkan lynx (*Lynx lynx balcanicus*) has been long recognised (Breitenmoser & Breitenmoser-Würsten 2001), but its official IUCN Red Listing came 10 years after the onset of the Balkan Lynx Recovery Programme (Melovski et al. 2015). The main threats rendering this status range from inbreeding-related maladies to poaching, prey depletion and habitat destruction, and these are relevant throughout its range – North Macedonia, Albania and Kosovo (Melovski et al. 2021). Being a specialised hunter, the survival of the Balkan lynx depends on ample amount of the two main prey species, roe deer (*Capreolus capreolus*) and brown hare (*Lepus europaeus*). Estimating the density of the prey population can ensure their proper management while safeguarding the predator's population. Although the roe deer in the Balkan lynx range has already been estimated (Halotel 2020), a reliable density estimation dedicated only to the brown hare is so far missing.

The brown hare is a native species throughout most of Eurasia and it is confirmed as Least Concern in Europe on the IUCN Red List of Threatened Species (Hackländer and Schai-Braun 2019). Throughout its geographic range it is widespread and it is most abundant in agricultural landscapes such as pastures or farmland even though it most likely evolved in a steppe grassland habitat (Vaughan et al. 2003; Canova et al. 2020). In association with habitat changes caused by the intensification and mechanisation of agricultural practices, there is some evidence of a decline in the hare numbers from the beginning of the 20th century onward (Hackländer & Schai-Braun 2019; Canova et al. 2020). Due to

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these population declines in recent decades, some European countries have already classified the brown hare as Near Threatened or Threatened on their Red Lists (e.g. Norway, Switzerland, Germany and Austria) (Reichlin et al. 2006). Therefore, obtaining population density estimates in different parts of Europe is increasingly important.

The innovative Spatially Explicit Capture–Recapture (SECR) density estimation has shown promising results for species with distinct coat patterns, such as the Eurasian lynx (Zimmermann et al. 2016). However, accurately estimating population densities in unmarked individuals poses significant challenges, prompting researchers to explore various alternative methods for assessing brown hare density. These methods include capture-mark-recapture, plot-based techniques, line transects, spotlight counts, direct observations, and faecal pellet surveys (Langbein et al. 1999). While effective, many of these approaches can be time-consuming and may disturb the animals. A noteworthy advancement in this field is the Random Encounter and Staying Time (REST) model, which leverages camera-trapping data to provide reliable density estimate (Nakashima et al. 2017). This method has also been successfully applied to snowshoe hares (Jensen et al. 2022), demonstrating its potential for non-invasive population monitoring.

This study uses the REST model to calculate the density of the brown hare in Mavrovo National Park, North Macedonia. The park harbours the majority of the Balkan lynx population in North Macedonia (Melovski et al., 2018) and is therefore the most important site to assess the density of their prey species, the brown hare.

Materials and methods

Study area

The study was conducted in Mavrovo National Park, located in the western part of North Macedonia and covering a protected area of ca. 730 km^2. The park consists of three Alpine mountain systems; the Shar Planina, Bistra and Korab mountains, all belonging to the Scardo-Pindic Mountain massif. It is characterised by a diverse relief of high mountain pastures, steep slopes, canyons and valleys, ranging between altitudes of 611 to 2,764 m above sea level (Melovski et al. 2020). There are 37 villages within the boundaries of the park, all of varying sizes and with a total number of around 5,660 houses, around 30% of which are still considered as active households (State Statistical Office of the Republic of Macedonia, 2021).

The habitat consists mostly of forests of King Boris fir (*Abies borisii-regis*), European beech (*Fagus sylvatica*), mixed fir-beech forest communities and a variety of oak species (*Quercus spp.*). Alpine mountain vegetation can be found only on Mt. Korab, while sub-alpine vegetation is represented on Shar Mt. and Bistra (Melovski et al. 2020). Other large mammals present in the park, apart from brown hare and the Balkan lynx, are roe dear, red fox, grey wolf, brown bear, wildcat, chamois, badger and wild boar (Melovski et al. 2009).

Study species

The brown hare is most common in grasslands, open farmland and woodlands but tends to favour a heterogeneous mosaic of grasses, hedgerows and arable fields (Albayrak & Sarıçam 2017). During their inactive periods in the day, hares usually reside in or near their form in more structured landscapes, whereas during their active period, at night, they go out to feed in more open landscapes with short vegetation (Tapper & Barnes 1986; Neumann et al. 2011). In areas with smaller field sizes and, therefore, higher landscape heterogeneity, brown hare home ranges tend to be smaller (Schai-Braun & Hackländer 2014). Home-range size, according to the literature and based on similar conditions to our study sites, ranged from 12–29.4 ha (Schai-Braun & Hackländer 2014; Levänen et al. 2019). The reproductive season of brown hare starts 2–4 weeks after the winter solstice (Flux 1965) and the first litters can be expected in late February. However, the prime months of reproduction are only from June to August (Olesen & Asferg 2006). One of the assumptions of the REST model is that animal density stays constant during the research period. This assumption should be maintained as one can expect that the biggest population change will occur during those prime reproductive months more so than during our research period, from 22 March to 27 April.

Study-site selection

For our study-site selection we focused on agro-ecosystems within the national park with a mix of active and inactive pastures and small agricultural fields. We selected four sites (near the villages of Tanushe, Bitushe, Trebishte and Nistrovo, all in Mavrovo National Park), each with a size of 34.8 ha (Fig. 1). All sites were known to be within the range of the Balkan lynx (Melovski et al. 2020). The methodology behind the selection of study sites was based on the study conducted by Jensen et al. (2022), who obtained reliable density estimates with their methodology using the REST model. The size of the selected sites was calculated to comprise the majority of the home range of two snowshoe hares. Their selection of home range size was based on literature on hares in similar habitat and calculated by GPS data and 90% isopleths. For brown hares, however, home range size can vary greatly based on the landscape type and calculation methods (Kunst et al. 2001; Stott 2003; Rühe & Hohmann 2004; Smith et al. 2004; Schai-Braun & Hackländer 2014; Levänen et al. 2019). Therefore, home range size for our study was chosen, in line with Jensen et al. (2022), based on the literature using GPS data and similar landscapes to our study population. To assess home-range size we only consulted the literature where the study area was comprised of small field sizes to resemble our study area and where the home range was calculated using GPS data. As a result, the home-range size, obtained as the mean home range according to the literature, measured 20.7 ha. Since it is believed that home ranges of neighbouring hares overlap by 32% (Rühe & Hohmann 2004), this means that the combined area used by two neighbouring hares would typically be around 34.8 ha, which corresponds to the size of our study sites.

Camera set-up

In each site, 10 camera-traps (Cuddeback C123, and Cuddeback PowerHouse IR 20MP - Model G-5024 ©) were placed randomly with at least 200 m in between each trap. This was done in an attempt to obtain independent data points, which is one of the assumptions of the REST model. We opted for 10 camera-traps per site as it is thought to be more likely to obtain successful density calculations with a high camera-trap density of five camera-traps per hare home range (Jensen et al. 2022). The first cameras were placed on 22 March and the last cameras removed on 28 April. Not all sites had the cameras placed on the same day but for each site we aimed for a survey period of 28 days. This was done as study shows that after two to three weeks of trapping, there is a great improvement in detection rate accuracy and estimates are likely to be within 10% of the estimates of a study with a sampling period of 60 days (Kays et al. 2020).

Each camera was set at a height of 30 cm above the ground, facing 0°N or moved clockwise until at least 6 m were visible in front of the camera. The camera was set to take 30-second videos upon trigger. When the hare remained in the area of detection after those 30 seconds, there was a minimal recovery time of 5 seconds before the camera was activated again and we counted this as the same observation. Detection of one brown hare individual was defined as an observation of a hare separated by at least 1 hour from any other hare observation video to minimize the risk of counting multiple individuals over a short period of time when in reality it is the same individual (Jensen et al. 2022). When multiple individuals were seen together in the same video they were counted as multiple observations, and if morphologically different individuals passed separately in front of the camera within the hour, they were also counted as different observations. A defining object was placed at a known distance from the camera to meet the model assumption of ensuring 100% accuracy of detectability (Nakashima et al. 2020). Any hare observed behind this object was not included in the analysis. The object was never placed further than 7 m from the cam-

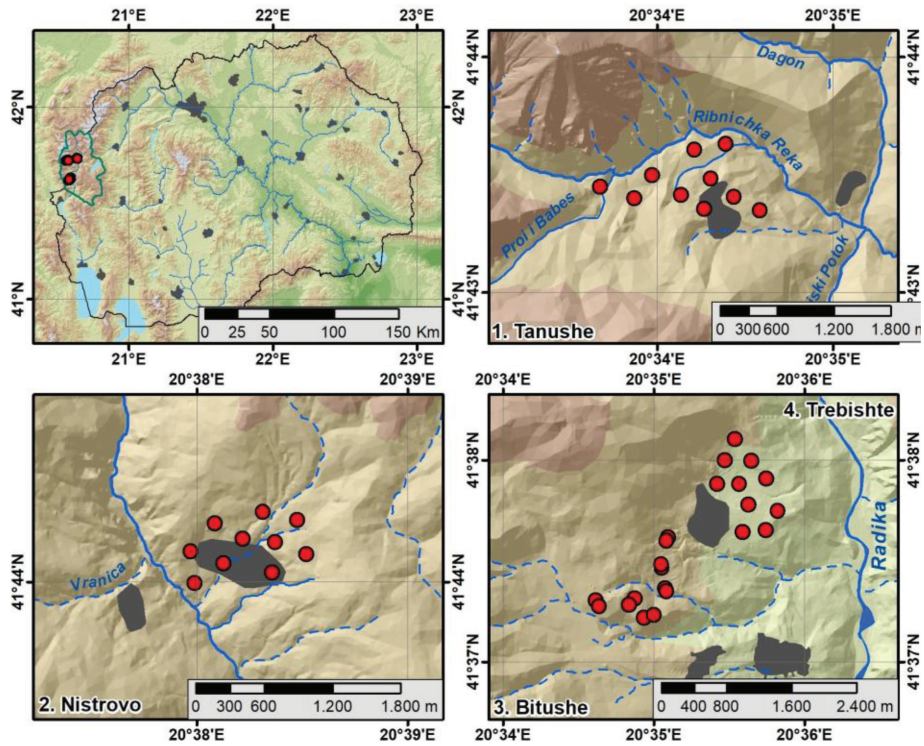

Fig. 1. Satellite images of the study sites. From left to right: The outline of the country of North Macedonia with the outline of the study area, Mavrovo National Park and the location of the four study sites within the park represented by the numbers; close-up of each study site, Tanushe, Nistrovo and Bitushe and Trebishte with the locations of the camera-traps represented by the red dots.

era since the infrared (IR) flash poorly illuminated night images at a distance past this even with the strobe power set to maximum. IR flash was used to ensure that we met the model assumption of not affecting the behaviour or movement of our study animal by the presence of the camera-traps (Nakashima et al. 2020). We aimed at checking each camera halfway during the survey period, but due to time constraints, we were only able to do this for Nistrovo, as all cameras at Trebishte were removed halfway through the study period after villagers complained and two cameras were stolen or vandalised.

Since not all cameras were able to record footage for the whole 28-day period, different subsets of the acquired data were composed. These different datasets were created to ensure sampling effort is the same within each dataset. This is necessary to be able to compare densities. Within each of these datasets the survey effort was the same (trapping nights, number of sites and cameras). However, each dataset was composed of a different combination of trapping nights, cameras and sites to cover as many combinations as possible with our limited data. We can observe an inverse relationship between the number of cameras included in the dataset and the number of trapping nights: as the number of cameras increases, the number of trapping nights decreases, and vice versa.

REST model/modelling

To calculate brown hare density, we used the REST model developed by Nakashima et al. (2017). This is a likelihood-based model adapted from the random encounter model (Rowcliffe et al. 2008). The advantage of the REST model is that density estimates can be obtained within approximately one month, while cameras can be placed by a single researcher and need minimal attention during the research period. It describes the relationship between density, trapping rate and staying time. More specifically, the density calculation is based on the average time the hare spends in front of the camera (staying time), the detectable area in front of the camera and the survey effort. The detectable area in front of each camera was calculated based on the known distance from the camera within which we have 100% detection accuracy and the camera detection angle. The distance was 7 m for all but one camera where the distance was only 6 m. The camera detection angle was 42 degrees for all cameras. The average staying time per camera was calculated by dividing the total number of seconds each brown hare individual remained in front of the camera by the total number of hare detections for that camera.

To ensure all model assumptions were met, we accounted for the time of the day where hares are inactive and therefore undetectable by the camera-traps (Nakashima et al. 2020). Specifically, we multiplied our survey effort by the proportion of the day during which hares are active. This proportion was quantified by performing a circular kernel regression in R (version 2023.03.0+386 "Cherry Blossom") using the R package "activity" with a bandwidth multiplier of 1.5 as it yielded the most robust activity-level estimation with our sample size (Rowcliffe et al. 2014). Due to the unforeseen variation in sampling effort across the sites, the time of the day (in radians) of all the hare observations recorded during the entire study period was pooled and used to compute the circular kernel regression. First the dataset was cleaned to remove all observations that were recorded within 15 minutes of one another.

To calculate the brown hare density (D) at the camera level we used the following formula:

$$D = \frac{numberofdetections * stayingtime}{detectableare * (surveyeffort * animaldielactivity)}$$

The density at camera level was calculated for all cameras and averaged across each site to obtain the brown hare density estimates per site. To acquire the 95% CIs around these estimates we used 1,000 bootstrapped samples quantified in R.

Results

During the entire trapping period we collected 230 videos with hare observations within the area with 100% detection accuracy. This was obtained over a total trapping effort of 867 active trapping nights, of which 228 in Nistrovo, 142 in Trebishte, 222 in Bitushe, and 275 in Tanushe. The number of detections at the camera level ranges from 0 to 30 based on a one-hour detection interval across all sites for the entire survey period. The average amount of detections per site ranges from 3 to 6.78 per camera and the average staying time per camera ranges from 0 to 47.13 s across the entire survey period and across all sites.

The variation in trapping nights across the sites is caused by inactivity of several cameras during all or multiple trapping nights due to different factors. There were nine cameras inactivated by bears or livestock, three cameras were inactivated by humans, five cameras were stolen, three of which only were backed up midway through the study, five cameras failed for several to all trapping nights due to unknown problems with the camera itself.

Taken all combined values into account, the density ranged from 3.38–16.45 (SE = 2.08–5.37) brown hares per one km^2 (Table 1). Based on the bootstrapped confidence intervals around the density calculations we can see that the datasets with the higher number of cameras yield the narrowest confidence intervals and smallest SE even though the amount of trapping nights is lowest. Therefore the dataset in Table 1, with 8 cameras per site and 16 trapping nights, is our preferred dataset.

The site-specific diel activity pattern of the brown hare reveals distinct periods of inactivity from early morning to late afternoon, with activity levels peaking shortly after this interval (Figure 2). Due to the variation in sampling effort across the sites, the hare diel activity value of 0.306 is used in the density calculations; this value is obtained by pooling all the observations across the sites (Table 2).

Discussion

This is the first-ever attempt to quantify the density of the brown hare in North Macedonia using camera-trapping . As one of the main prey species of the critically endangered Balkan lynx (Melovski et al. 2015), the brown hare plays an important role in the diet of this elusive cat (Ivanov et al. 2018; Melovski et al. 2022). The hare study sites overlap with the known distribution of the Balkan lynx and more specifically are located at a close distance to known kill sites (Melovski et al. 2020). Therefore, knowing the hare density in these locations can have important implications for the protection and management of the Balkan lynx and the brown hare as well as the management of their habitats.

Following the calculations of the preferred dataset, the density estimates for all sites combined is 8.75 (SE = 2.01) hares per km^2. In Europe, the natural brown hare population density is about 2 hares per km^2 but it can reach up to 275 individuals per km^2 in optimal habitats (Schai-Braun & Hackländer 2016). On higher altitudes, from 800 m to over 1000 m above sea level (similar to the study sites), average densities are much lower, ranging from 4.46–5.90 individuals per km^2, based on a study in the Czech Republic (Pikula et al. 2004). This measure approaches the calculations acquired in our study for several sites. However, since the calculations are based on a relatively novel approach for calculating density, we recommend repeating the study with a more robust dataset. This should increase the reliability of the results.

It is also important to mention that hare density can vary between the pre-breeding period, from March to April, and the post-breeding period, from October to November (Canova et al. 2020). The REST model only estimates the average density during the research period. So, to aquire the density during the post-breeding season, another study needs to be conducted during autumn (Rowcliffe et al. 2008).

Due to technical issues preventing several cameras from recording throughout all trapping nights, we were unable to deploy the planned 10 cameras at each of the four locations. This, however, did not render the data unusable. When it comes to calculating animal density through the REST model, the precision of the density calculations increases as the research efforts increase.

Table 1 Density calculations of the brown hare in Mavrovo National Park based on camera-trap data, REST model calculations and bootstrapped 95% CIs around the density calculations.

Location	Number of Cameras	Trapping Nights	Mean Staying Time (s)	Amount of Detections	Density (Hares/km2)	95% CI	SE
Nistrovo	5	28	11.08	15	3.88	0.19 - 8.17	2.04
Bitushe	5	28	15.20	22	7.11	0.83 - 14.66	3.53
Tanushe	5	28	19.41	43	18.80	1.78 - 49.74	12.23
All Combined	**15**	**28**	**15.23**	**80**	**9.93**	**2.71 - 21.10**	**4.69**
Nistrovo	6	23	16.32	16	6.31	1.43 - 11.99	2.69
Bitushe	6	23	19.26	36	15.29	3.55 - 29.52	6.63
Tanushe	6	23	11.87	33	6.73	1.12 - 14.80	3.49
All Combined	**18**	**23**	**15.82**	**85**	**9.44**	**4.17 - 15.27**	**2.83**
Nistrovo	8	19	11.97	14	3.88	0.36 - 7.33	1.78
Bitushe	8	19	19.93	48	16.62	5.89 - 27.31	5.47
Tanushe	8	19	10.45	26	4.64	0.99 - 9.43	2.15
All Combined	**24**	**19**	**14.12**	**88**	**8.38**	**4.07 - 13.65**	**2.44**
Nistrovo	7	18	22.64	13	5.54	1.48 - 10.71	2.35
Bitushe	7	18	18.43	46	16.63	6.73 - 26.57	5.06
Tanushe	7	18	13.48	28	9.27	1.55 - 21.39	5.06
Trebishte	7	18	13.57	26	6.03	3.46 - 8.89	1.38
All Combined	**28**	**18**	**17.03**	**113**	**9.37**	**5.27 - 13.79**	**2.17**
Nistrovo	8	16	7.00	10	3.38	0.000 - 8.14	2.08
Bitushe	8	16	17.46	46	16.45	6.31 - 27.35	5.37
Tanushe	8	16	10.76	25	6.43	1.41 - 13.78	3.15
Trebishte	8	16	16.35	30	8.75	4.65 - 13.94	2.37
All Combined	**32**	**16**	**12.89**	**111**	**8.75**	**5.16 - 13.04**	**2.01**

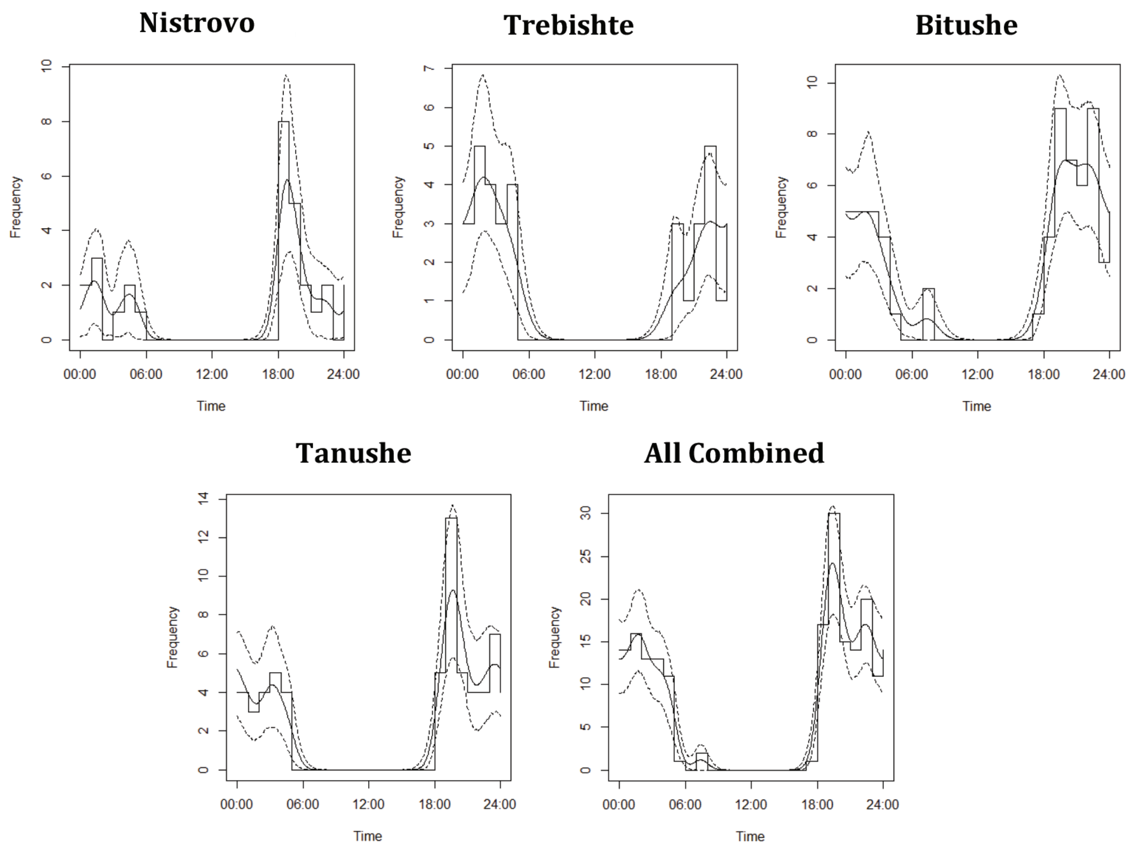

Figure 2. Site-specific diel activity patterns of brown hare (*Lepus europaeus*) derived from hare detections on camera-traps over the entire survey period. The dotted line shows the 95% CI around the estimate

More specifically, increasing the number of cameras improves the precision of the calculations, rather than increasing the amount of trapping nights (Nakashima et al. 2017). In fact, our bootstrapped confidence intervals around the density estimates support these findings. The narrowest confidence intervals and smallest SE are found in datasets with the highest number of cameras albeit at the expense of trapping nights.

The lowest hare density is found in Nistrovo. This village is inhabited year-round and is characterised by steep, small pastures that are very actively grazed although by low numbers of livestock such as sheep, horses and cows. Hares typically do not favour pastures that are heavily grazed by sheep (Smith et al. 2004) and this could have led to the lower density estimates. The site of Trebishte is also located near an active village where keeping livestock is one of the main agricultural activities. This site however, has the second highest hare density estimate.

There are many different factors that can influence hare density or home range size in a certain type of habitat. For instance, brown hares typically have smaller home ranges in sites with high levels of habitat heterogeneity, such as structured landscapes with field margins, as they have to move less far between their resting and feeding sites (Smith et al. 2004). Therefore, we can expect higher densities in this habitat type (Olesen & Asferg 2006; Smith et al. 2004). However, to confidently explain the difference in hare densities between the sites based on habitat type, quantification of habitat variables would have been necessary.

Table 2. Diel activity values of the brown hare in Mavrovo National Park based on the camera trap data from the entire study period and bootstrapped 95% CIs.

Site	Estimate	SE	95% CI	n
Nistrovo	0.192	0.055	0.114 - 0.315	27
Trebishte	0.318	0.049	0.190 - 0.378	32
Bitushe	0.364	0.044	0.239 - 0.400	61
Tanushe	0.260	0.050	0.174 - 0.362	58
All Combined	0.306	0.037	0.238 - 0.377	178

The brown hare plays a notable, though secondary, role in the diet of the critically endangered Balkan lynx. According to Melovski et al. (2022), while the Balkan lynx primarily targets ungulates—such as roe deer and chamois—hares and smaller mammals are also utilized, particularly in areas with lower densities of larger prey. Although brown hares constitute a smaller proportion of kills compared to ungulates, their widespread distribution across the lynx's habitat means they can serve as an important nutritional buffer when main prey are less available. This ecological flexibility underscores the hare's value in sustaining lynx populations under variable environmental conditions and reinforces the need to maintain balanced prey communities to support the Balkan lynx's survival and ongoing genetic restoration efforts (Melovski et al. 2022).

This pilot study aims to gain insight into the brown hare population density in the Mavrovo area, rather than quantifying environmental factors or human disturbances for site comparison. However, since we have no means of testing the accuracy of our results by comparing against previous studies or a less novel methodology, including a comparative study across the sites based on the quantification of the natural environment could at least add some credibility to our estimates. This way we can hypothesise density differences across the sites based on the already available literature describing how densities and home ranges change based on habitat structure and human disturbances. If the calculated densities follow the patterns typically discussed in the literature, this will give extra credibility to the data.

Constraints and recommendations

We believe that there might be a negative bias towards the density estimation. This is because one of the REST model assumptions was not always met because of a slight delay in the triggering time of our cameras (Nakashima et al. 2017). On certain videos we would notice that the recording only started when the hare was already well within the detection range and therefore the few seconds of the hare entering the field of vision were not quantified. This could reduce the average staying time per camera, which has direct effects on the density calculations and could give a value smaller than the true density. Still, when the hare stayed in front of the camera for longer than 30 seconds and another video would start recording, we would add the 5 seconds of recovery time to the staying time so no extra bias was added here. To reduce the possible negative bias on our density estimates in future research it will be beneficial to use different camera-traps with a faster trigger time. Another way to reduce this bias would be to reduce the area with 100% detection probability. This can be done by reducing the detection angle in all the recorded videos to the real angle within which all hares are observed to enter. Unfortunately, this could not be achieved with our footage due to certain observations with such a low trigger time that it would have reduced the new detection angle to 0°.

Another way that hare density can be overestimated is by not meeting the assumption that animal behaviour is unaffected by the camera traps. In our study, the hares did not seem greatly affected by the cameras or the distance markers. And if this were to be the case, it is important that the staying times during which the hares show investigative behaviour towards equipment, such as smelling, staring or rubbing, are removed from the dataset.

Due to the loss of a large amount of data because of camera-trap failure and theft, we suggest that another study be conducted to obtain more reliable results. Seeing that the accuracy of the density estimates increases with the number of cameras in place (Nakashima et al. 2017), it will be crucial that all the cameras deployed are recording well. Therefore, we suggest that 10 cameras be placed in a similar fashion as with this study, and that camera functionality is checked and the data collected one or two weeks after placement. In case not all cameras were functional, the study design should be such that extra time is available for the cameras to remain active for a longer period of time, to make up for the time lost due to camera failure.

To reduce the probability of theft, it would also be recommended to have a meeting with the villagers (local community) to ask for permission to place cameras in their fields and to explain the aim of the project. Signs should be placed on each camera explaining our research and who to contact if there are any further questions or problems. Liaising with villagers will be beneficial to the project not only to reduce theft or vandalism by humans but also by livestock and wildlife. If they understand the nature of the experiment and have been asked for permission, they will perhaps be more likely to pick up a camera that has been pushed over by a bear or livestock or to inform us if they notice a camera has gone missing. To avoid cameras being pushed over by livestock or bears, however, it is important that the camera stakes are pushed into the ground deep enough and the camera is connected to the stake by two connection points to avoid rotation. To this note, we recommend increasing the frequency of checks, although this will increase the financial cost of the study.

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Trial of another density calculation method, the faecal pellet count, was done beforehand within the 2021 Balkan lynx camera-trapping survey in Mavrovo National Park. Lena Soumpasis explored methods and made the study design. Yon Halotel also helped the actual count in the field. Ekrem Veapi helped camera-trap deployment and checks. Andrej Gonev, as part of the BLRP lynx team, also assisted in the fieldwork. The experience gained from this trial helped look into another density calculation method later led by Marie Busschots. Vasko Avukatov produced the maps. We are also grateful for the constructive and helpful comments by Inés Moreno when writing the manuscript.

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Ethics declarations

Competing interests
The authors declare no competing interests.

Contributions

MB designed the research; all authors performed the research; MB wrote the manuscript and prepared figures; all authors reviewed the manuscript.
Corresponding author: Marie Busschots.

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