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Hopping with the seasons: Weather and landscape features affect seasonal and diurnal movement of mountain hares

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Abstract

Context.

Although animals are well adapted to natural weather fluctuations and have different strategies to adjust their space use to environmental conditions, climate change may lead to more frequent and unpredictable extreme weather events.

Objectives.

We investigated how landscape composition and seasonally varying weather conditions affect mountain hare (*Lepus timidus*) movement behaviour in southeastern Norway.

Methods.

We estimated monthly range sizes and movement distances of 26 GPS-collared mountain hares (> 8000 'hare days' and > 100,000 GPS locations) and investigated the effect of landscape variables, weather conditions (for movement distances only), season, and sex on ranging behaviour.

Results.

Overall home range sizes (95% KDE) ranged from 43 to 363 ha (mean estimate: 174 ha; 95% CI: 138–210 ha). Males used larger monthly ranges and moved further than females, especially during the breeding season, whereas hares generally moved shorter distances in fall. The effect of temperature on movement differed among seasons, suggesting that hares adjusted their movements to thermal conditions and seasonal energy demands. Wind, rainfall, and fresh snowfall had smaller and more variable effects, potentially related to energy conservation, shelter use, or anti-predator behaviour.

Conclusions.

Combined, our study shows that mountain hare movement behaviour is shaped by sex, season, landscape, and weather variables. This provides important information for this species, which is predicted to encounter increasing pressure and challenges in the future. Population-level consequences of hares will not only depend on changing weather conditions, but also on the availability of suitable food and sheltered microhabitats and on the hares' capacity to adjust their behaviour.

1. Introduction

Movement is a fundamental aspect of life for most organisms, and contains important information about the spatial requirements of individuals and populations (Nathan et al. 2008). Over time, repeating patterns of movement result in the creation of an individual's home range, defined as "the area traversed by the individual in its normal activities of food gathering, mating, and caring for young" (Burt 1943). Animals have different strategies to adjust their space use in response to changing environmental conditions, such as seasonal shifts and temporal shifts in space use in response to altered resource

availability, predation risk, reproductive timing (Powell and Mitchell 2012; Thies et al. 2006). While some species migrate to track favourable conditions, leading to seasonally shifting ranges (Kauffman et al. 2021), others remain within their home range and alter space use in response to shifting environmental conditions (Borowik et al. 2024; Mayer et al. 2019). Similarly, predation risk can alter movement by causing animals to avoid high-risk habitats, or reduce movement when the risk of detection is high (Bleicher 2017; Böhme et al. 2025). Landscape characteristics, including habitat composition, resource availability, and shelter, can further constrain or facilitate animal movement by determining the spatial arrangement and connectivity of suitable habitats (Doherty et al. 2019).

In addition, weather conditions, such as precipitation, wind and temperature, are important abiotic factors that may directly influence animal movement behaviour (McMillan et al. 2022; Price-Rees et al. 2014; Rivrud et al. 2010). High temperatures may lead to thermal stress, causing animals to seek shelter and reduce their movement to avoid overheating (Mutwedu et al. 2021). Conversely, low temperatures may limit animal movement to conserve energy and body heat (Giroux et al. 2022). Moreover, because scent will remain for longer in colder conditions (Gutzwiller 1990), predation-risk may increase with decreasing temperatures as predators are better at detecting prey (Ruzicka and Conover 2012). Similarly, increased wind speed can mask both sound and scent (Ruzicka and Conover 2011), thereby reducing both the predators' and preys' ability to detect each other (Cherry and Barton 2017). Rain can also affect movement, as wet fur reduces insulation, and therefore increase heat loss (McArthur and Ousey 1994), which might increase shelter-seeking behaviour and reduce movement. Finally, snow cover can limit the accessibility of habitats and increase the energetic costs of movement (Bryce et al. 2022).

Although animals are adapted to natural weather fluctuations, climate change leads to more frequent and unpredictable extreme weather events (Cai et al. 2014). These changes may increase the importance of weather-related constraints on movement, habitat selection and survival. Combined with habitat loss and fragmentation, invasive species and pathogens, it contributes to increasing challenges for wildlife (Abrahms et al. 2023; Surasinghe 2011).

Generally, little is known about how weather conditions and landscape factors affect movement behaviour in leporids. Mayer et al. (2019) investigated how weather conditions impacted habitat selection and home range of GPS-collared European hares (*Lepus europaeus*) and found partial adjustments in habitat selection as a response to temperature, humidity and wind speed during winter, suggesting thermal constraints. Similarly, juvenile European hares decreased their activity with increasing wind speed (Sokos et al. 2015), and rainy weather conditions may lower the survival of young European rabbits (*Oryctolagus cuniculus*) in spring and might generally facilitate the outbreak or spread of diseases in rabbits as well as in hares (Rödel and Dekker 2012).

To date, no studies have investigated how weather affects the movement of mountain hares (*L. timidus*). This is important, because mountain hares occur in areas that are predicted to experience pronounced changes in climate and associated vegetation composition (Serreze et al. 2000). Moreover, mountain hares are an optimal animal model to investigate weather effects on movement behaviour, because they

do not hibernate, do not use any shelters or burrows, and experience vastly varying weather conditions throughout the year. Driven by photoperiod (day length), mountain hares undergo a seasonal moult, changing from summer brown to winter white during fall, and back to summer brown in the spring to maintain their camouflage to the changing environment (Stokes et al. 2023; Stokes et al. 2025; Zimova et al. 2018). In Scandinavia, mountain hare populations have declined in recent decades, likely due to changes in predator-prey dynamics, with generalist predators, especially red fox (*Vulpes vulpes*), shifting their diet on hares when rodent densities are low (Pedersen and Pedersen 2012; Thulin et al. 2021; Tyson and Lutscher 2016). Moreover, mountain hares experience increasing seasonal coat colour mismatch, which reduces camouflage in environments with seasonal snow cover (Stokes et al. 2025), and encounter potential competition and hybridization with European hares that are expanding across Scandinavia (Bach et al. 2023; Thulin 2003). With these increasing challenges for the mountain hares, understanding their movement and space use is important for management and conservation efforts.

The aim of this study was to investigate how movement behaviour in mountain hares is influenced by seasonal variation in weather conditions. We first describe seasonal variation in monthly range size and then quantify how weather conditions affected movement distances by mountain hares conditional on the time of the year while accounting for other variables, such as sex and land cover. Specifically, we predicted larger monthly range sizes and movement distances during spring as a response to the start of the mating season (Merwe and Racey 1991), and we expected this to be more pronounced for males. Moreover, we predicted that hares would reduce their movement distances with increasing wind speed and precipitation as it may negatively impact their ability to detect predators and preserve energy. Concerning ambient temperature, we expected seasonal differences, with reduced movement with increasing temperature during the warmer months due to risk of thermal stress, and increased movement during the colder months as a response to increased foraging due to increased metabolic needs.

2. Material and methods

2.1 Study areas and species

The study was conducted in the eastern parts of Norway, in the municipalities of Tydal, Trøndelag and Stor-Elvdal, Innlandet (Fig. 1). Landcover in Stor-Elvdal municipality is dominated by mountains and forest, mainly spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*), but deciduous trees, such as birch, aspen and willow are also present (Gundersen et al. 2004). Tydal municipality is in a mountainous region of Trøndelag county, dominated by birch (*Betula ssp.)* forest, interspersed wih open areas of mountains. Other tree species like rowan (*Sorbus aucuparia*) and willow (*Salix spp*) are also present (Rekdal 2013). Both areas experience continental climate with cold winters and warm summers, with temperature extremes being more pronounced in Stor-Elvdal (daily mean temperatures range from − 33.4°C in the winter to 32.0°C in the summer) compared to Tydal (daily mean temperatures range from − 28.5°C to 22.2°C; seklima.met.no). The average annual precipitation is 835 mm in Stor-Elvdal and around 900 mm in Tydal.

Mountain hares are primarily nocturnal and crepuscular (Pettigrew et al., 2021), but with some activity also during the day (Pierquin, in review JAE). The red fox is the hares' most important predator, but lynx (*Lynx lynx*), Eurasian eagle owl (*Bubo bubo*), pine marten (*Martes martes*), goshawk (*Accipiter gentilis*) and wolverine *(Gulo gulo*) also predate on hares (Angerbjörn 1995; Lindström et al. 1994). The diet of the mountain hare varies seasonally. Birch is the staple food during winter, but aspen (*Populus tremula*) and willow are preferred when available (Pulliainen and Tunkkari 1987). In spring and summer their diet consists more of grasses and herbs, while in fall they mostly graze on bilberry leaves and shoots (Schai-Braun et al. 2025).

2.2 Hare captures and collaring

We GPS-collared a total of 26 hares (13 males, 13 females; Table S1) from February to April 2024 and January to April 2025, with some collars recording GPS data until 15 May 2026 (our cutoff for this study). For captures, we placed cage traps (80 × 80 × 30 cm) baited with hay and/or birdseeds, on strategic locations throughout the study areas. Traps were inactive for the first few days/weeks after deployment, until hares started to visit them regularly. We then activated the traps, and were notified through camera traps with instant messaging triggered by movement. When captured, hares spent on average 56 min (range: 11 to 164 min) inside the trap before we arrived. Five individuals were recaptured using long nets encircling their updated GPS position. When a hare was captured (either in trap or net) we covered its eyes with a sock (with the end cut off), and placed it in a cloth bag, before we weighed it and fitted a GPS-collar (OrniTrack-NR40 GPS-GSM transmitter). We used two collar types; one with a smaller battery (45 g total weight), and one with a heavier battery (55 g) depending on hare body mass. Total weight was less than 2% of the hares' body mass. The handling took approximately 10–15 min before the hare was released at the capture site.

2.3 Ethical note

The study was approved by the Norwegian Environment Agency (Miljødirektoratet), and the Norwegian Food Safety Authorities (Mattilsynet), and trapping was conducted with permission from landowners. One individual died during capture, likely due to stress. Another one died several months after collaring, likely directly linked to complications with the collar. During recapture, one hare exhibited minor skin abrasions (likely resulting from collar removal), and was therefore not recollared as a precaution. One hare was evaluated to be stressing too much during the handling procedure; this hare was released without further processing. Apart from these cases, we observed no evident short- or long-term negative effects of the capture, handling and collaring.

2.4 Estimating home ranges, monthly ranges, and distance moved

GPS locations were registered every 2, 2.5 or 3.5 h (depending on battery size; Table S1) and were sent through the Global System for Mobile Communications (GSM) network every two weeks, stored in the Movebank repository (www.movebank.org, ID 3575092655). To exclude potentially un-natural behaviour and movement as a result of the stress experienced during capture (Mayer et al. 2021), we excluded the

first 5 days after capture in our analyses. For one individual that dispersed during the tracking period (Pedersen et al. 2026), we only retained data in its established home range after the dispersal movement was completed. When a GPS collar stopped moving for more than 24 h, we backtracked the movement to determine the date and cause of the event. In case a dead hare was moved by predators/scavengers, we excluded both the date of incident, as well as the day prior to the incident from the analysis. As a part of a parallel project, we occasionally approached the hares in their daytime resting sites to quantify coat colour. These days (n = 71 hare days) were also excluded from the analyses. We initially conducted a stationary test using one collar and estimated that the mean location error of GPS positions was 5.8 m (unpublished data). Moreover, all GPS locations with a satellite count < 4 and a Horizontal Dilution of Precision (HDOP) value > 5 were excluded to ensure only including accurate GPS locations in our analyses (Lewis et al. 2007). Finally, clear outliers, defined as way-and back movements of > 1000 m between 3 consecutive GPS locations, were also excluded.

We used Kernel Density Estimation (KDE) to estimate the home range size of the hares, using the *adehabitatHR* package (Calenge 2024). We calculated the general home range of each individual for the period it was GPS-collared (Table S1). We used 95% KDE, referring to the full home ranges and 50% KDE, referring to core areas. Thereafter, we calculated monthly 95% KDE (hereafter monthly ranges), only including individuals that had > 25 days of GPS data in the given month.

We estimated the straight-line distance between consecutive GPS positions (hereafter distance moved), using the *distGeo()* function from the R package *geosphere* (Hijmans 2026), separately for the three fix rates (2 h, 2.5 h and 3.5-h).

2.5 Weather and land cover data

We obtained hourly data of ambient temperature, rain and snow precipitation, wind speed, and snow depth for the centre of each study area from historic raster data at 0.1° resolution (https://open-meteo.com/en/docs/historical-weather-api). We estimated the cumulative rainfall and snowfall (the latter was only included in the spring, fall and winter analyses) per day due to massive zero-inflation and little variation of the hourly precipitation data and because cumulative precipitation is a better indication of wet conditions within a given day.

A digital elevation model raster was obtained at 30 arc second resolution from a digital elevation model provided by the European Environment Agency. From this, we estimated terrain ruggedness in QGIS using the “Raster terrain analysis” tool. Forest type classes, defined as pine-dominated, spruce-dominated, deciduous-dominated, or NA (other non-forest land cover, mostly consisting of moors and mountain areas) were obtained as raster file from the ‘Skogressurskart (SR16)’ (https://www.nibio.no/tema/skog/kart-over-skogressurser/skogressurskart-sr16).

We then extracted the weather variables, terrain ruggedness, and land cover class for each GPS position. For the monthly home ranges, we estimated the average terrain ruggedness, elevation, and the

proportion of pine, spruce, and deciduous forest cover using the R package ‘exactextractr’ (Baston 2023).

2.6 Statistical analysis

To investigate the factors affecting home range size, we used generalized additive mixed models (GAMM) of the R package ‘mgcv’ with a Gaussian error distribution using a restricted maximum likelihood (REML) approach (Wood and Wood 2015). We used monthly range size (95% KDE; log-transformed) as response variable, including sex as parametric term and month as a cyclic function, terrain ruggedness, elevation, and the proportion of spruce forest cover as smooth terms. Terrain ruggedness was highly correlated with the proportion of pine forest cover (Pearson’s r = -0.76) and deciduous forest cover (0.84), as was the proportion of pine and deciduous forest cover (-0.87). Thus, pine and deciduous forest cover proportions were not included in the analysis. We included the two-way interaction of month and sex to test if female and male range sizes differed conditional on month. Hare ID and study area were included as a random effect to account for individual variation and unmeasured differences between the study areas. We did not explicitly include weather variables in this analysis because they correlated with month (warmer temperatures in summer, snowfall in winter, etc.).

To investigate variation in distance moved (log-transformed; response variable) we used GAMMs, with a Gaussian distribution and logarithmic link function. We ran separate analyses for each season to avoid higher-order interactions and because we predicted that the effects of the weather variables differed among seasons (e.g. increasing temperature could have a negative effect on hare distance moved in summer but a positive effect in winter). We defined seasons as winter from December to 14 March (usually complete snow cover), spring from 15 March to May, summer from June to 14 September, and fall from 15 September to November. Spring and fall were defined based on the moulting period of mountain hares in this area (Stokes et al. 2023) and varying presence of snow cover during these transition periods.

Fixed effects included fix rate (2 h, 2.5 h, and 3.5 h), sex, and land cover as parametric terms, and hour of the day, using a cyclic function, terrain ruggedness, and elevation as smooth term. Additionally, we included the two-way interactions of hour with the weather variables to specifically investigate if hares adjusted their distance moved throughout the day conditional on weather conditions. Hare ID and study area were included as a random intercept.

We built 4 candidate models for the monthly home range analysis and 5 candidate models for the distance moved analysis (Table S2, Table S3), selecting the model with the lowest AICc value using the *MuMIn* package (Barton 2020). Model fit was evaluated and confirmed by using the *DHARMa* package to perform residual diagnostics, outlier tests, and quantile deviance tests (Hartig 2021). All statistical analysis were performed in R version 4.5.2 (R Core Team 2024).

3. Results

3.1 Overall home range and monthly range size

Overall home range sizes (95% KDE) of mountain hares ranged from 43 to 363 ha (mean estimate: 174 ha; 95% CI: 138–210 ha) and core areas (50% KDE) ranged from 7 to 77 ha (mean: 30 ha; 95% CI: 24–37 ha), with both showing considerable inter-individual variation (Table S1). There was no clear difference between home range areas between Stor-Elvdal (mean 95% KDE: 195 ha; 95% CI: 134–256 ha) and Tydal (mean 95% KDE: 159 ha; 95% CI: 110–208 ha; t-test: t = 1.0, df = 21, p-value = 0.33), but males generally had larger home ranges compared to females (male mean: 213 ha; 95% CI: 159–267 ha versus female mean: 136 ha; 95% CI = 91–181 ha; t-test: t = -2.4, df = 23, p-value = 0.025).

We could estimate a total of 258 monthly ranges for the 26 individual hares, with variation in monthly home range size best explained by the full model, which explained 26.6% of the variation in monthly home range size through fixed effects and 99.4% when including both fixed and random effects (Table S2, Table S4). The interaction of month and sex showed that male monthly ranges were generally larger than female ranges, with the difference between males and females being smallest between August and October, when range sizes were generally smallest (Fig. 2a). Moreover, monthly range size was smaller between 500 and 700 m elevation compared to higher and lower areas (Fig. 2b), increased with increasing terrain ruggedness (Fig. 2c), which correlated positively with deciduous forest cover and negatively with pine forest cover, and was comparatively larger when the ranges included intermediate proportions of spruce cover (Fig. 2d, Table S4).

3.2 Distance moved

When predicted for a 2.5 h fix rate, hares moved on average 32 to 86 m depending on season, with greater movement distances in spring, summer, and winter compared to fall, and males moving greater distances than females during spring but not the other times of the year (Fig. 3a, Table S3). Land cover also partly affected movement distances but this effect was generally small (Fig. 3b, Table S5). Similarly, distance moved changed conditional on elevation, with hares moving greater distances at elevations > 800 m during spring, fall, and winter, but moved shorter distances at higher elevations during summer (Fig. 3c). Differences in movement distances in relation to elevation were less clear at lower elevations (Fig. 3c). Diel movement patterns varied across seasons, with movement primarily occurring during crepuscular hours and nighttime (Fig. 4).

The full model including all predictor variables best explained hare movement distances in spring, while the full model excluding sex best explained hare movement distances during the rest of the year (Table S3). Temperature was the most important weather variable explaining movement distance by mountain hares, but windspeed and precipitation partly also played a role (Table S5). During spring, when ambient temperatures were comparatively colder, hares moved greater distances during the evening and night but there was no difference during the rest of the day (Fig. 4a). In summer, hares shifted their movement distances depending on temperature, moving more during the evening hours until midnight, but less from midnight until morning when temperatures were comparatively colder (and vice versa when it warmer)

(Fig. 4b). During fall and winter, hares concentrated movement during the crepuscular times of the day when temperatures were comparatively colder and moved greater distances around midnight when temperatures were comparatively warmer (Fig. 4c-d). The effect of wind speed on distance moved was generally small, but mountain hares moved somewhat less on windy nights (from midnight to ca. 5:00) during spring and summer, and more during fall, with no effect in winter (Fig. 4e-h). Similarly, rainfall generally had little impact on movement distances by hares (Fig. 4i-l), except in fall when they moved less during rainy nights (Fig. 4k).

Movement distances were partly also affected by snow conditions, with mountain hares moving less on days with more snowfall during fall and winter, a trend also observed during spring (Fig. 5a-c). Snow depth had comparatively little impact on distance moved, with hares tending to move more during nights when snow cover is higher in fall, but less in winter and spring (Fig. 5d-f). Finally, distance moved correlated positively with terrain ruggedness during fall and winter but not in spring and summer (Table S5).

4. Discussion

This study investigated how seasonal and diel movement behaviour of mountain hares is shaped by sex differences, landscape and weather effects. Male mountain hares moved more than females, and range size was larger in more rugged terrain. Movement was mainly crepuscular and nocturnal, with seasonal differences in movement distances related to elevation and partly weather conditions. Temperature was the most important weather variable, while wind, rainfall, and snow conditions generally had smaller effects. Below, we compare our home range estimates with those reported from other geographic regions and discuss the potential mechanisms underlying the observed movement patterns, as well as how these patterns may affect mountain hare populations in the future.

Comparison with home range estimates from other studies

The home range estimate from this study, on average 213 ha for males and 136 ha for females, is similar to previous estimates from Finland (between 105 and 206 ha) (Kauhala et al. 2005; Levänen et al. 2019) and Sweden (280 ha for males and 116 ha for females) (Dahl and Willebrand 2005). In contrast, average home range sizes in other areas of Europe were much smaller, including Scotland (113 ha for males and 89 ha for females in Hewson and Hinge (1990) and 22 ha in Hulbert et al. (1996)), Ireland (50 ha for males and 22 ha for females) (Wolfe and Hayden 1996), the European alps (between 38 and 54 ha) (Bisi et al. 2011; Gamboni et al. 2008). The most likely explanation for this difference between Fenno-Scandia and other regions of Europe is that net primary productivity in the former region is considerably lower due to its colder climate, reducing food availability and thereby forcing hares to move over larger areas to meet their energetic needs. This is supported by the finding that there was a negative correlation between home range size and the available green biomass of grass in a mountain hare population in Scotland (Hulbert et al. 1996). Additionally, differences in landscape configuration, affecting resource distribution, as well as animal community composition, affecting interspecific competition and predation

risk, may have affected home range sizes among these areas (Bjørneraas et al. 2012; Messinger et al. 2019; Trombulak 1985). It is important to note that, apart from ecological and landscape differences, variation in home range size among studies partly may have been related to methodological differences such as the choice of home range estimator (Nilsen et al. 2007), and positioning technology. For example, while we used KDE estimates based on frequent GPS data, Kauhala et al. (2005) used VHF tracking and Levänen et al. (2019) used GPS data and adaptive Local Convex Hulls to estimate home ranges.

Sex differences and seasonal variation

We found that males utilized larger home ranges than females similar to mountain hares in Sweden, Scotland, and Ireland (Dahl and Willebrand 2005; Hewson and Hinge 1990; Wolfe and Hayden 1996), while other studies from Finland and the European Alps found no sex differences in home range size (Bisi et al. 2011; Kauhala et al. 2005). We speculate that these differences were related to variation in resource distribution among geographic areas, thereby affecting home range overlap between males and females, with males in areas with less overlap having larger ranges to visit multiple females. Again, methodological differences, e.g. related to the sample size may have influenced these differences, so this finding should be interpreted cautiously.

The sex differences observed in our study were likely explained by the reproductive biology of mountain hares. While range sizes of males were generally larger than female ranges, the difference was greatest during winter and spring, when home ranges were largest, as shown in other studies (Bisi et al. 2011; Dahl and Willebrand 2005; Kauhala et al. 2005). Similarly, males moved the greatest distances during spring, coinciding with the principal mating season (Angerbjörn 1986). This can be explained by sex-specific reproductive strategies, with males searching greater areas in order to maximize access to females, as shown in other species (Frafjord 2016; Mayer et al. 2019; Sprogis et al. 2016), and females being constrained to smaller areas to take care of dependent young (Aronsson et al. 2016). More generally, larger range sizes and movement distance during late winter and early spring may be related to food limitations during this time of year, forcing hares to cover larger areas to meet their energetic needs. Even after accounting for sex differences and within-home range landscape composition, there was substantial variation in individual home range sizes, which may be explained by animal personality and age, as well as finer-scale (unmeasured) resource availability in the different hare home ranges (Hertel et al. 2021; Spiegel et al. 2017).

Both males and females had the smallest home ranges and moved the shortest distances during fall, when hares typically have the lowest body mass (Merwe and Racey 1991) after a period of high energy use due to breeding activities (Bisi et al. 2011). Thus, the reduced movement may be an energy-conserving strategy to increase body mass before winter. Additionally, reduced movement during fall might be an anti-predator response, both because it is the hares' hunting season and since hares moult during fall, potentially leading to coat colour mismatch with the surrounding environment (Bisi et al. 2011; Pedersen et al. 2017; Stokes et al. 2025). This is supported by the finding that mismatched

mountain hares were less active during daytime in response to moult mismatch (Pierquin et al in review), but see (Zimova et al. 2024).

Landscape and weather effects

Monthly range sizes by mountain hares were smaller between 500 and 700 m elevation compared to higher and lower areas. This elevation range generally correlates with a higher proportion of open mixed-deciduous forest and shrubs (Moen and Lillethun 1999), likely providing high-quality food resources, allowing hares to move over smaller areas. These areas often have a higher proportion of spruce (rather than pine) forest, explaining smaller ranges when the proportion of spruce forest was larger. Similarly, at elevations above 800 m, i.e. close to or above the forest line (Bryn and Potthoff 2018), hares moved greater distances during most of the year, probably because there are fewer shrubs and edible plants above the treeline, except during summer. Increasing terrain ruggedness, which correlated positively with deciduous forest cover and negatively with pine forest cover, led to larger monthly range sizes, and hares moved greater distances in more rugged terrain. This suggests that hares may avoid rugged areas, thereby increasing their moving behaviour.

Temperature was the weather variable most strongly associated with movement distances, but its effect varied seasonally. In summer, on comparatively warmer days, hares moved more between midnight and the early morning, i.e., the time of the day when temperatures were comparatively colder. This suggests that, while mountain hares are well adapted to cold conditions (Thirgood and Hewson 1987), they may be vulnerable to heat stress, adjusting activity periods (reflected in reduced movement distances) during warmer days in summer, a finding similarly reported for brown hares (Stiegler et al. 2023). Conversely, in fall and winter, when temperatures were comparatively colder, hares concentrated movement during the crepuscular times of the day while, when temperatures were comparatively warmer, they moved greater distances around midnight. These longer movements around comparatively warmer midnight temperatures are consistent with reduced energetic costs of travelling and foraging under less thermally challenging conditions. Moreover, reduced movement during colder periods may reflect behavioural energy conservation, potentially including prolonged use of forms or other sheltered microsites that reduce exposure to wind and heat loss (Thirgood and Hewson 1987). Combined, these patterns suggest that temperature may influence mountain hare movement through a combination of thermoregulatory constraints and seasonal changes in activity requirements, rather than through one consistent response to cold or warm conditions. This makes sense provided the large seasonal variation in temperatures. Our study areas differed by 23°C between its warmest (July) and coldest (January) average monthly temperature and experienced a 60°C difference between its coldest (-31°C) and warmest (29°C) day during the study period. This exemplifies the large weather variation animals are exposed to, including consequences for vegetation growth and resource availability (Wang et al. 2018). Importantly, because we did not measure resting-site selection or microclimatic conditions directly, the role of shelter remains speculative rather than a demonstrated mechanism.

The effect of wind speed on movement distance was relatively small. In spring, hares moved shorter distances during the early morning hours on windy days, while moving longer distances on windy days in fall. Similar, to our results for spring, snowshoe hares (*Lepus americanus*) decreased their activity during heavy wind (Studd et al. 2022). The noise of the wind may negatively impact their ability to detect predators (Ruzicka and Conover 2011), and therefore increase their shelter-seeking behaviour. We have no good explanation for increased movement distances on windy days in fall but speculate that hares may show more responsive movements under windy conditions as anti-predator responses (e.g. when pursued by hunting dogs), thereby leading to larger movement distances. The effect of rainfall was negligible during most of the year, but during fall, hares moved shorter distances during rainy nights. This was probably related to reduced activity, with hares potentially seeking shelter to avoid heat-loss, as shown for other leporids (Seltmann et al. 2009).

Finally, we found little impact of snow depth on movement distances, likely because this measure was not a detailed enough. For example, if the snow surface is a hard crust, underlying snow depth will not impede movement as mountain hares are well adapted to moving in snow (Iason and Newey 1995). Conversely, when we directly measured daily snowfall (which is usually soft enough that hares will sink in), hares moved shorter distances on days with more snowfall. Thus, hares likely avoid moving on days with large amounts of fresh snow to conserve energy. Additionally, carnivores and humans may use fresh snow tracks to find hares; thus, reduced movement after snowfall could also be an anti-predator behaviour.

5. Conclusions

Our study shows that mountain hare movement behaviour is shaped by sex, season, landscape, and weather variables. This provides important information for this species, which is predicted to encounter increasing pressure and challenges in the future (Pedersen et al. 2017; Schai-Braun et al. 2024; Stokes et al. 2023; Stokes et al. 2025). Temperature was the most important weather-related predictor of movement distance, with hares responding to temperature conditional on the time of the year. This flexibility may help individuals accommodate moderate changes in weather, for example by shifting activity towards thermally favourable periods or reducing movement when conditions are energetically costly. Nevertheless, the consequences of future climatic change are likely to depend on the balance between potentially favourable and unfavourable effects (Hof et al. 2012). Warmer conditions may reduce thermoregulatory costs and facilitate movement during cold parts of the year but could constrain activity during warm summer periods, and facilitate the expansion of brown hares, potentially leading to increased interspecific competition (Larroque et al. 2026). Similarly, more variable weather may create short-term constraints on movement during heat, fresh snowfall, rain, or strong winds, while also altering vegetation growth, snow characteristics, and resource availability. The population-level consequences will therefore depend not only on changing temperatures, but also on the availability of suitable food and sheltered microhabitats and on the hares' capacity to adjust their behaviour. Maintaining heterogeneous landscapes that provide these resources may support this behavioural flexibility under future environmental change.

Declarations

Competing Interests

The authors have no relevant financial or non-financial interests to disclose.

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Author Contribution

All authors contributed to the study conception, design, and fieldwork/data collection. Data preparation and statistical analyses were performed by Martin Mayer and Stian Kalleberg. The first draft of the manuscript was written by Martin Mayer and Stian Kalleberg and all authors commented on consecutive versions of the manuscript. All authors read and approved the final manuscript. Simen Pedersen obtained funding for the study and is the overall project leader. Simen Pedersen and Martin Mayer supervised Stian Kalleberg.

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Data Availability

All underlying raw GPS data is available on Movebank (https://www.movebank.org/cms/webapp?gwt_fragment=page=studies,path=study3575092655).

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Figures

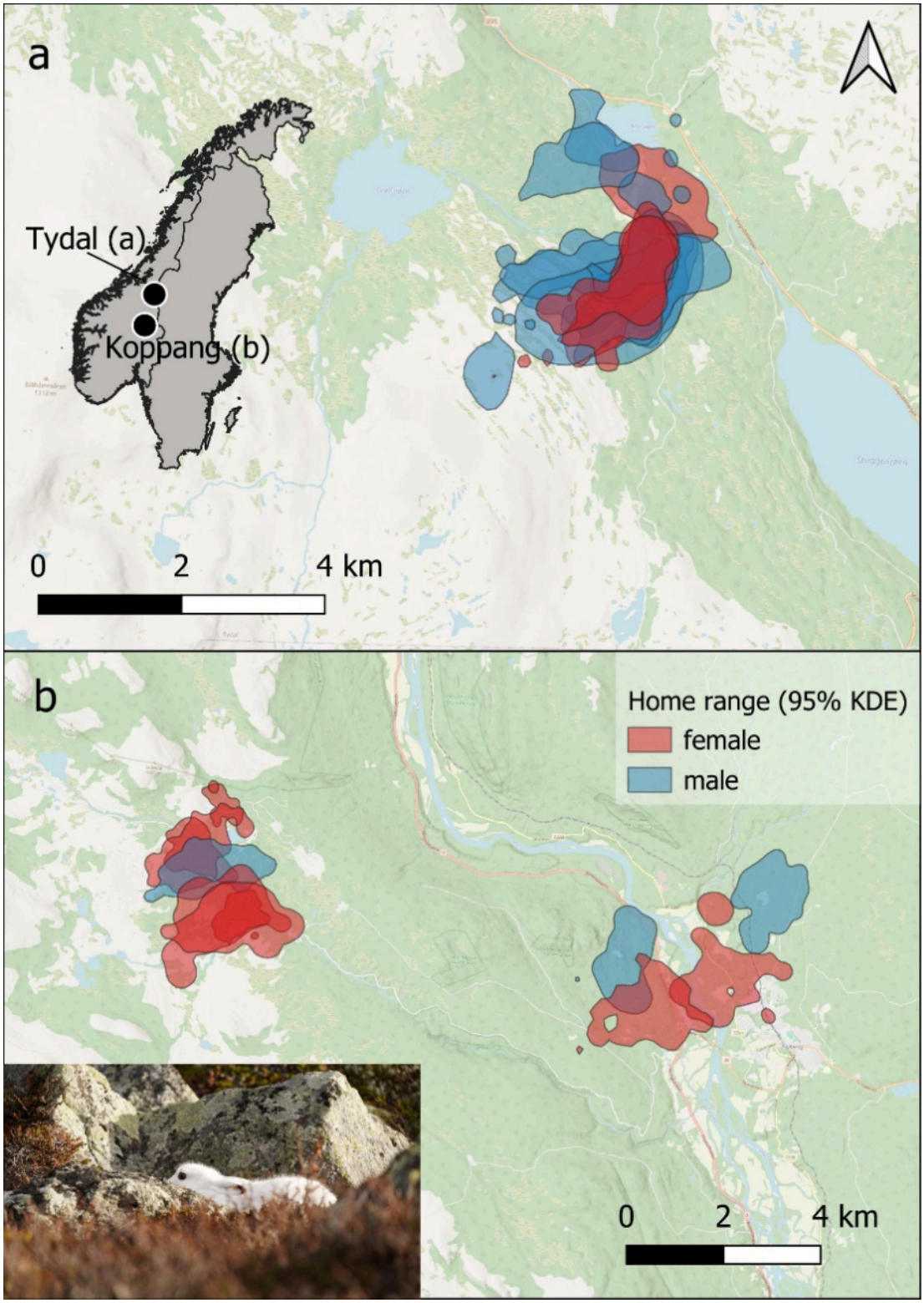


Figure 1

Overview of the overall home ranges, estimated as 95% Kernel density estimates (KDE), separately for 13 female (red shading) and 13 male (blue shading) mountain hares (inset picture) in (a) Tydal and (b) Koppang, Stor-Elvdal. The location of the study areas within Norway as indicated as black dots in the inset map. Note that the maps are on different scales. Picture: Martin Mayer.

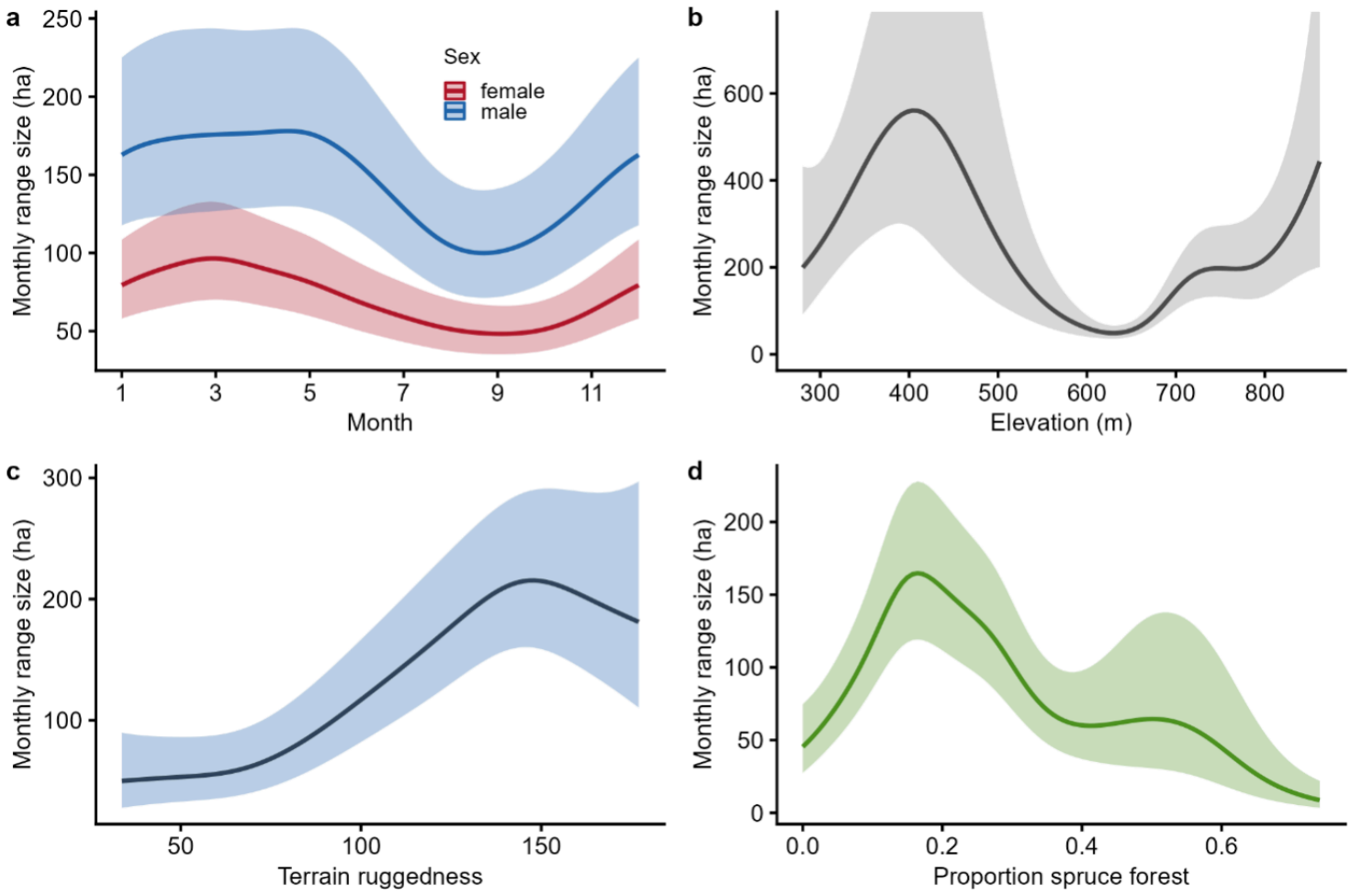


Figure 2

Predicted monthly range size, estimated as 95% Kernel density estimate (KDE) by mountain hares as a function of (a) month separately for females and males, (b) elevation, (c) terrain ruggedness, and (d) the proportion of spruce forest within the monthly range. The 95% confidence intervals are shown as shading. Note that the y-axis scale differs among plots.

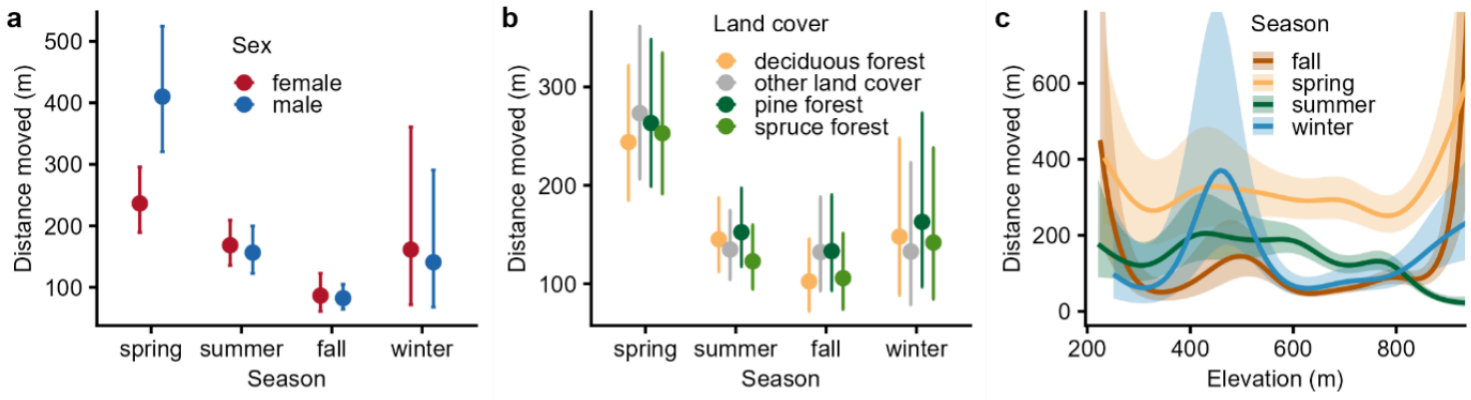


Figure 3

The predicted distance moved (predicted for 2.5 h fix rate) by mountain hares as a function of (a) season separately for females and males, (b) land cover type separately by season, and (c) elevation separately by season. The 95% confidence intervals are shown as bars (a-b) or shading (c).

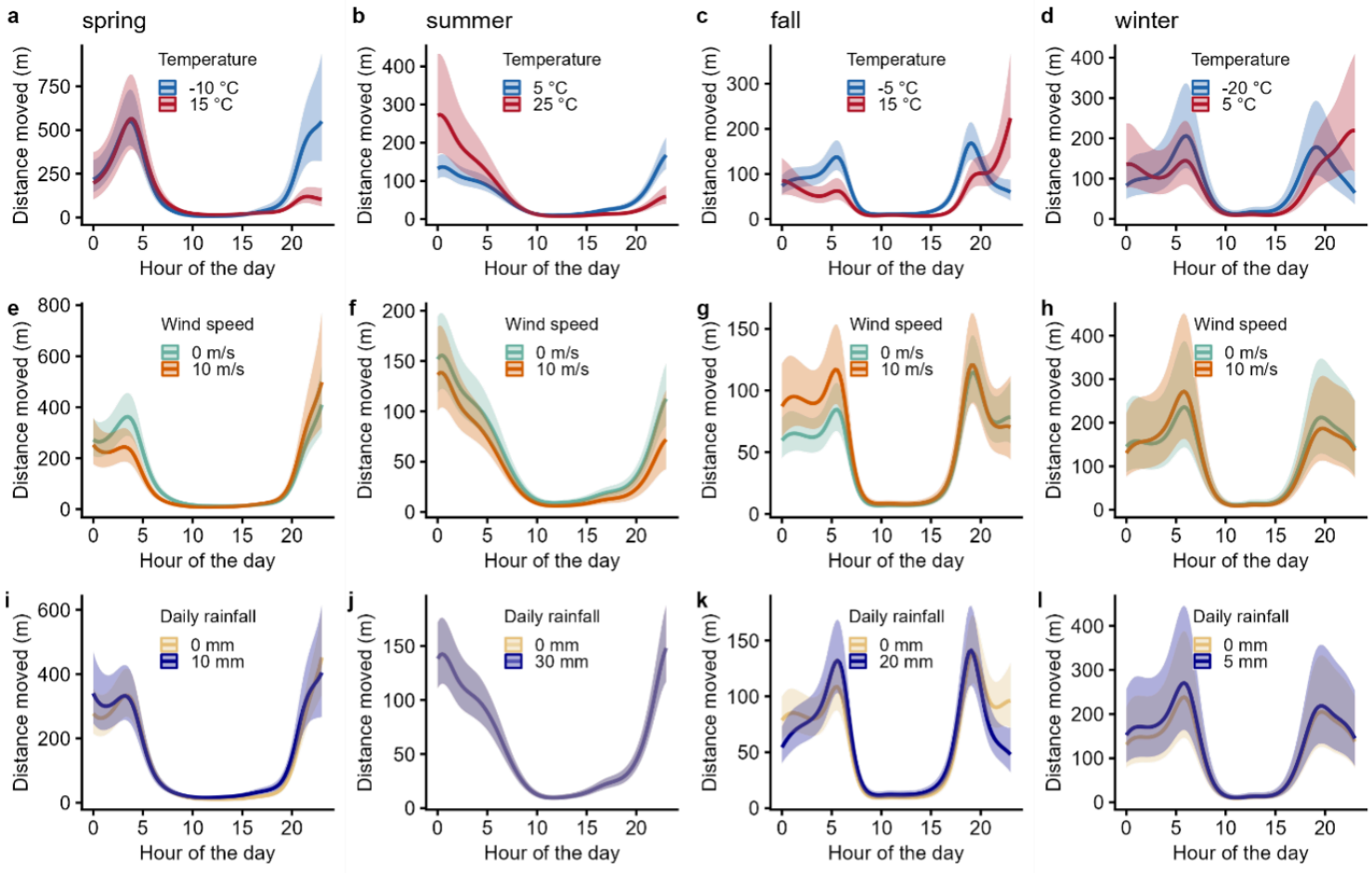


Figure 4

Predicted distance moved (predicted for 2.5 h fix rate and for males and females combined) by mountain hares in response to the hour of the day in interaction with ambient temperature (a-d), wind speed (e-h), and daily rainfall (i-l), shown separately for spring (left), summer (middle left), fall (middle right), and winter (right). The 95% confidence intervals are shown as shading. Note that the y-axis scale and predicted temperature and rainfall differ among plots (based on seasonal differences).

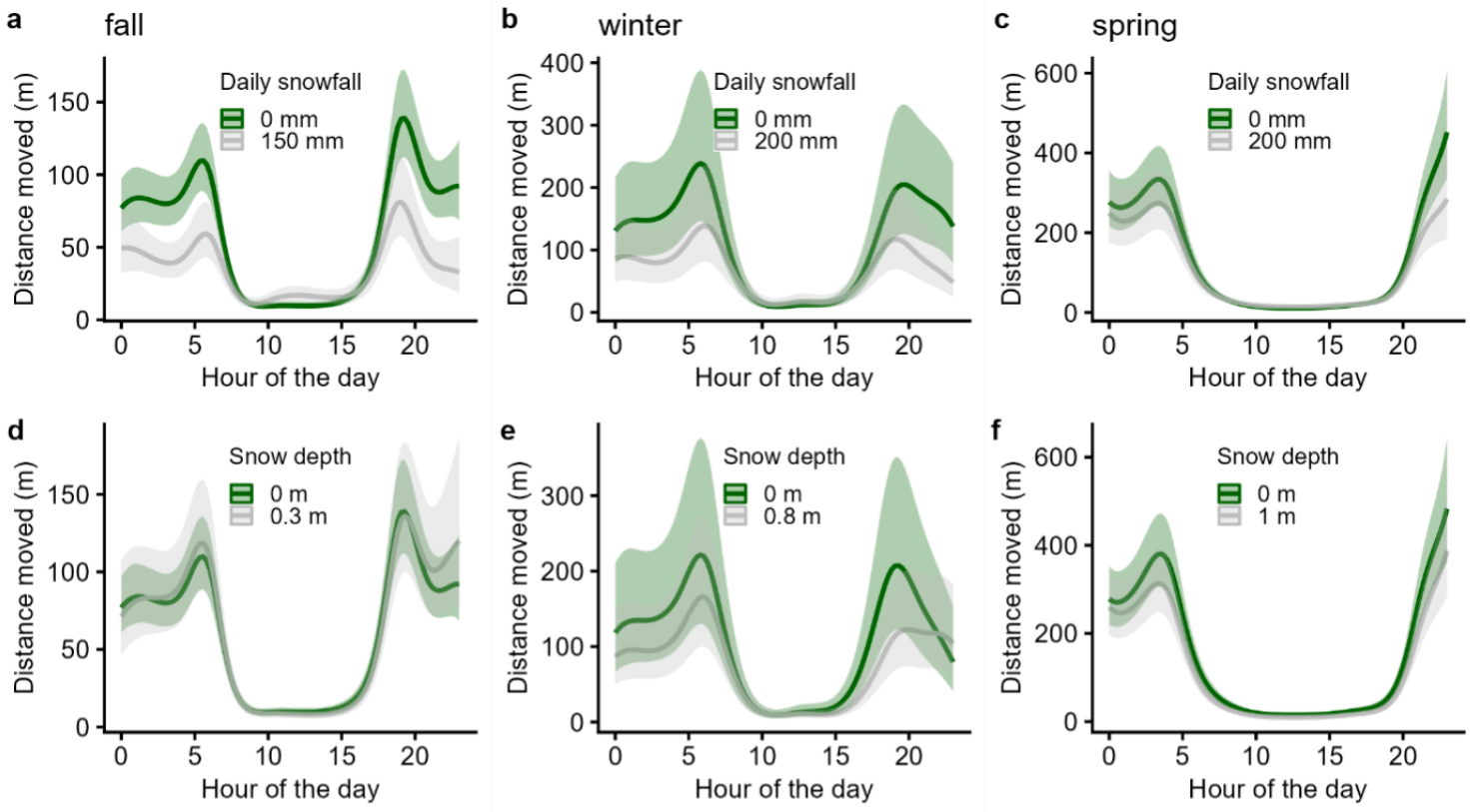


Figure 5

Predicted distance moved (predicted for 2.5 h fix rate and for males and females combined) by mountain hares in response to the hour of the day in interaction with daily snowfall (a-c) and snow depth (d-f) shown separately for fall (left), winter (middle), and spring (right). The 95% confidence intervals are shown as shading. Note that the y-axis scale and predicted snowfall and snow depth differ among plots (based on seasonal differences).

Supplementary Files

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