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The influence of snow cover, elevation, and latitude on fur colour in the mountain hare

Anna Göransson[1], Davide Carniato[2,*], Lars Hillstrom[1], Petter Hillborg[1], Marcus Larsson[3], Antonio J. Carpio[4]

(1) Department of Electrical Engineering, Mathematics and Science, Faculty of Engineering and Sustainable Development, University of Gävle, 801 76 Gävle, Sweden.
(2) Department of Veterinary Medicine, University of Sassari, Via Vienna 2, Sassari, Italy.
(3) Swedish Forest Agency, Västra vägen 52 80324 Gävle, Sweden.
(4) Department of Botany, Ecology and Plant Physiology, Research Group on Education and Biodiversity Management (GESBIO), University of Cordoba, 14071, Cordoba, Spain.

* Correspondig author / Autor para correspondencia: Davide Carniato [carniato.davide95@gmail.com]

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The influence of snow cover, elevation, and latitude on fur colour in the mountain hare

Abstract: This study investigates the environmental factors, that influence the timing of winter fur change in the mountain hare (*Lepus timidus*). The transition from brown to white fur is a critical adaptive strategy that allows hares to remain camouflaged in snowy environments. Using data collected with camera traps from various elevations and latitudes, we analysed the influence of environmental factors, including snow presence, altitude, and latitude, on fur colour change. Our findings reveal that snow presence is the most significant determinant, with a strong correlation between snow cover and the transition to white fur. Latitude also significantly influences fur colour, likely reflecting the environmental gradients that vary with geographic location. In contrast, altitude did not have a significant effect on fur colour, nor did it interact with latitude in any meaningful way. However, seasonal altitudinal movements, driven by the availability of food and shelter, appear to influence the hare's habitat choice, with hares moving to lower elevations during winter to access food and higher elevations in summer. This seasonal behaviour may account for the lack of a direct correlation between altitude and fur colour. These results underscore the importance of snow cover and latitude as primary drivers of fur colour change, while altitude plays a secondary role. The findings highlight the need for conservation strategies that consider the potential impacts of climate change on snow cover dynamics, which could disrupt the synchronization between fur colour change and the environment, increasing hares' vulnerability to predation.

Keywords: environmental cues; fur colour transition; *Lepus timidus*; photoperiod; seasonal adaptation; snow cover

Influencia de la capa de nieve, la altitud y la latitud en el color de la piel de la liebre de montaña

Resumen: Este estudio investiga los factores ambientales, que influyen en el momento del cambio de pelaje invernal en la liebre de montaña (*Lepus timidus*). La transición del pelaje marrón al blanco es una estrategia adaptativa crucial que permite a las liebres permanecer camufladas en entornos nevados. Utilizando datos recopilados con cámaras trampa de diversas altitudes y latitudes, analizamos la influencia de factores ambientales, como la presencia de nieve, la altitud y la latitud, en el cambio de color del pelaje. Nuestros hallazgos revelan que la presencia de nieve es el determinante más significativo, con una fuerte correlación entre la cobertura de nieve y la transición al pelaje blanco. La latitud también influye significativamente en el color del pelaje, probablemente reflejando los gradientes ambientales que varían según la ubicación geográfica. En contraste, la altitud no tuvo un efecto significativo en el color del pelaje, ni interactuó de manera significativa con la latitud. Sin embargo, los movimientos altitudinales estacionales, impulsados por la disponibilidad de alimento y refugio, parecen influir en la elección de hábitat de la liebre, moviéndose a elevaciones más bajas durante el invierno para acceder a alimentos y a mayores elevaciones en verano. Este comportamiento estacional podría explicar la falta de una correlación directa entre la altitud y el color del pelaje. Estos resultados subrayan la importancia de la cobertura de nieve y la latitud como los principales impulsores del cambio de color del pelaje, mientras que la altitud juega un papel secundario. Los hallazgos destacan la necesidad de estrategias de conservación que consideren los posibles impactos del cambio climático en la dinámica de la cobertura de nieve, lo que podría alterar la sincronización entre el cambio de color del pelaje y el entorno, aumentando la vulnerabilidad de las liebres a la depredación.

Palabras clave: señales ambientales; transición del color del pelaje; *Lepus timidus*; fotoperiodo; adaptación estacional; cobertura de nieve

Introduction

Understanding how wildlife adapts to seasonal changes is crucial for predicting their responses to environmental fluctuations and for developing effective conservation strategies (Fuller et al. 2010; Beever et al. 2017). This study focuses on the mountain hare (*Lepus timidus*), a species that exhibits a remarkable adaptation to its environment through seasonal fur colour changes

(Flux 1970; Stoner et al. 2003). The transition from brown summer fur to white winter fur is an essential survival strategy that provides camouflage against predators in snowy landscapes (Zimova et al. 2020a). However, the timing of this fur change can be influenced by various environmental factors, and mismatches between fur colour and the surrounding environment can increase predation risk and impact population dynamics (Mills et al. 2013; Atmeh et al. 2018).

The timing of fur change in the mountain hare is primarily driven by environmental cues that signal the approach of winter (Stokes et al. 2023). Elevation and latitude are two critical factors that influence the onset and duration of winter conditions, and consequently, the timing of fur change. At higher elevations, temperatures drop earlier in the season, and snow cover persists longer, necessitating an earlier fur change in the autumn, but later fur change in the spring. Similarly, higher latitudes experience more pronounced seasonal changes, which can also affect the timing of fur colour transition.

Temperature is a key determinant of the timing of fur change (Jackes and Watson 1975; Stokes et al. 2023). As temperatures drop, physiological changes in the mountain hare trigger the growth of white fur, which is better suited to snowy environments (Zimova et al. 2018). Photoperiod, or daylength, is a key parameter influencing the timing of seasonal fur changes in mountain hares, either alone or alongside other variables like snow cover (Watson 1963; Flux 1970; Hofman 2004). Shortening days signal the approach of winter, triggering hormonal changes that start the moulting process (Ferreira et al. 2020). Additionally, snow cover serves as a direct environmental cue, with its presence and duration affecting the timing and extent of fur color change, ensuring effective camouflage throughout winter (Zimova et al. 2016).

In addition to these primary factors, other environmental variables can play a role in the timing of fur change. Vegetation type and cover can influence microclimates, affecting local temperatures and snow retention (Peltier et al. 2023). Wind patterns and precipitation can also impact snow cover dynamics, further influencing the hare's camouflage needs (Jones et al. 2020). Moreover, the interaction between these factors can create complex environmental conditions that affect the timing of fur change in different ways (Zimova et al. 2016).

Understanding the interplay of these factors is crucial, especially in the context of climate change. Rising global temperatures and altered precipitation patterns are leading to changes in snow cover dynamics (Brown and Mote 2009). In many regions, snow arrives later and melts earlier, potentially disrupting the synchronization between fur change and snow cover (Semenchuk et al. 2013). This asynchrony can leave hares vulnerable to predation during periods when their white fur stands out against a snowless background (Zimova et al. 2014). Such changes not only impact individual hares but can also have broader implications for population dynamics and ecosystem health (Mills et al. 2013).

In addition, it is important to consider the genetic factors that may influence the timing of fur change. Genetic variation within and between populations can result in different adaptive strategies to local environmental conditions (Boursot et al. 1993; Feder et al. 2012). This genetic diversity can be a crucial element in the resilience of species to rapidly changing climates.

Recent advances in research tools, such as camera traps, have significantly enhanced our ability to monitor wildlife behaviour and ecological processes across diverse habitats (O'Connell et al. 2011). In the context of this study, camera traps represent a valuable tool for documenting the timing of winter fur change in mountain hares (Bison et al. 2024). By providing non-invasive, time-stamped visual records, camera traps enable researchers to track seasonal changes in fur colouration in relation to environmental variables, offering critical insights into the spatiotemporal dynamics of this adaptation. As this study is part of a special issue on camera traps, it highlights the potential of this technology to support long-term monitoring efforts and inform conservation strategies.

While the seasonal fur colour change of mountain hares has been widely studied, the influence of elevation and latitude on this adaptation remains underexplored. Previous research has largely focused on factors such as snow cover or photoperiod, often without accounting for their geographic variation or the potential interplay between these variables. This study contributes to filling this gap by examining how fur colour transitions are influenced by snow presence, latitude, and altitude across different regions, using detailed records obtained through camera traps. By integrating these environmental variables, this work aims to provide insights into the drivers of phenological adaptations in mountain hares.

In this context, the primary objectives of this study are i) to analyse the timing of winter fur change in the mountain hare across different elevations and latitudes, and ii) to assess the relationship between fur change timing and various environmental factors, including snow presence, latitude, and altitude. By gathering and analysing data from diverse habitats, this study aims to provide a comprehensive understanding of the factors driving fur change. Through detailed examination of the mountain hare's adaptive strategies, this research seeks to contribute valuable insights into the broader field of phenology and species adaptation. The findings will be essential for informing conservation efforts aimed at preserving mountain hare populations and maintaining ecosystem balance in the face of ongoing and future climate change.

Material and methods

Study area

The study was conducted using images from camera traps that were deployed by the University of Gävle in two different areas of the county of Gävleborg in Sweden (**Fig. 1**), to monitor ungulate populations. The Ockelbo region in central Sweden is characterised by extensive forests that form part of the dominant landscape. The forests in this area are mainly composed of coniferous trees, such as Scots pine (*Pinus silvestris*) and Norway spruce (*Picea abies*), although some areas of mixed forest with deciduous trees such as birch (*Betula spp.*) can also be found. The second area, Kårböle, is situated in a more mountainous and rugged region, giving it a more uneven forested landscape with hills covered by dense forests. These forests tend to be more continuous and less fragmented, providing a more isolated habitat for wildlife. There was a widespread forest fire in this area in 2018. The size of the Ockelbo study area was 24 650 hectares, and the size of the Kårböle study area was 12 750 hectares, with camera traps deployed in each area at a density of one camera per 850 hectares. The total area covered by the cameras was 9 106 m^2 in Ockelbo and 4710 m^2 in Kårböle.

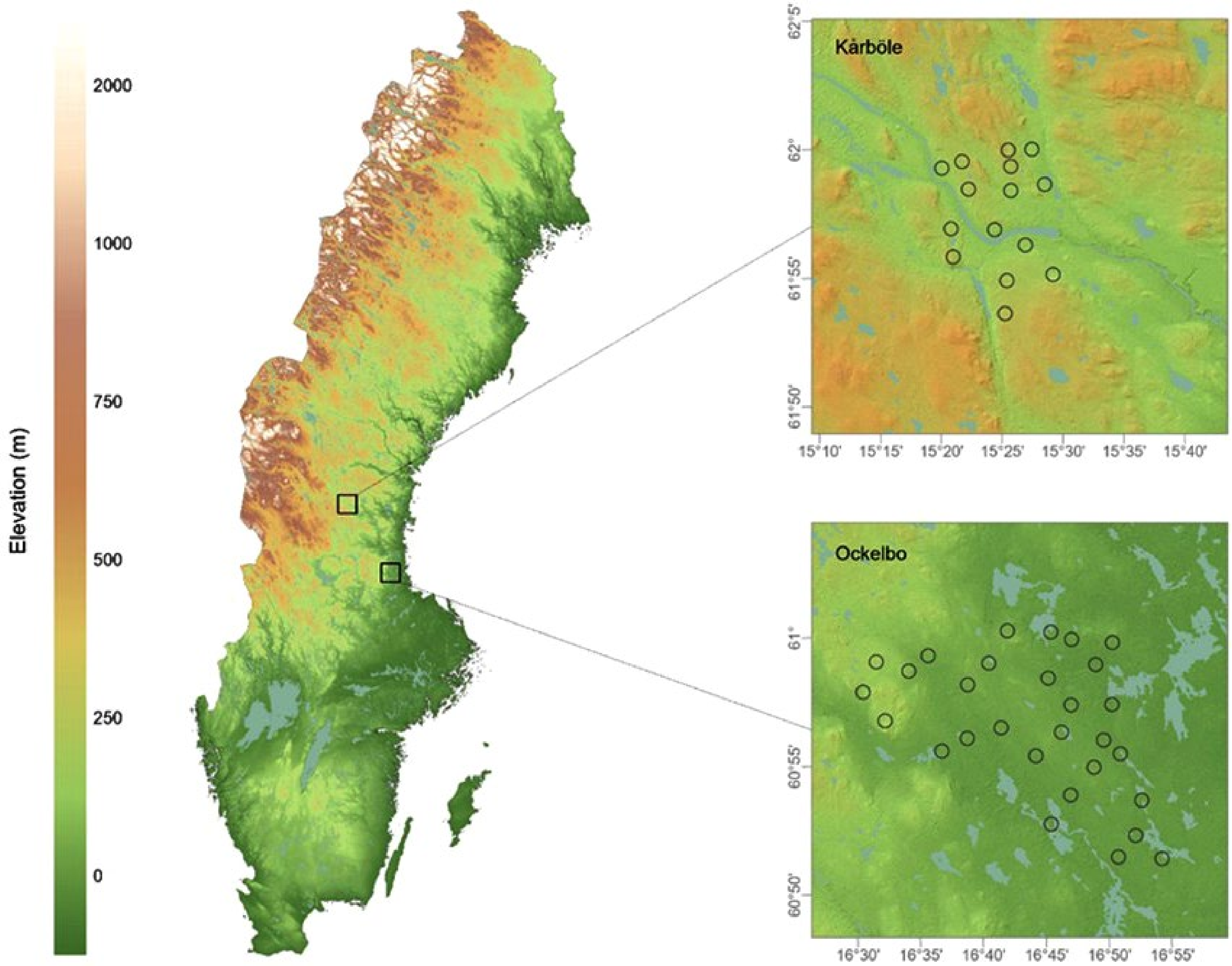

Figure 1. Map of Sweden (left) with inserts showing the two study areas (right) and the location of the cameras (black circles), as well as the latitude and altitude of each camera. Elevation data was obtained from Markhöjdmodell Nedladdning, grid 1+ ©Lantmäteriet (2021).

Figura 1. Mapa de Suecia (izquierda) con las dos áreas de estudio (derecha) que muestra la ubicación de las cámaras (los círculos negros), así como la latitud y altitud de cada cámara. Los datos de elevación se obtuvieron de Markhöjdmodell Nedladdning, cuadrícula 1+ ©Lantmäteriet (2021).

Sampling design

Images of mountain hares were collected from 44 Reconyx HyperFire 2 HF2X cameras (29 in Ockelbo and 15 in Kårböle) between June 2020 and October 2022, with the earliest image captured on 20 June 2020 and the latest on 31 October 2022, resulting in 1948 observations of mountain hares from the two areas. (25 cameras in Ockelbo, with an efficiency of 0.057 observation/day and 15 cameras in Kårböle with an efficiency of 0.089 observation/day). The camera traps effort was 25 504 days in Ockelbo and 11 213 in Kårböle.

The cameras were placed at salt lick stones near a water source. The cameras were mounted facing north approximately 1.5 meters above ground (± 20 cm) at an average distance of 10 meters from the pole holding the salt lick stone. The capturing angle of the HF2X is 40º and the maximum reliable detection range of the PIR sensor is 30 meters, providing a total theoretical capturing area of 314 m^2/camera (1/9th of the area of a circle with the radius of 30 meters). ** The range of altitude for the camera trap locations was 63-260 m above sea level in Ockelbo, and 228-353 m above sea level in Kårböle.

To trigger the camera, two criteria have to be fulfilled. The first is that the object must have a temperature different from the surrounding environment. The second is that the object with a temperature difference has to move horizontally within the active zone of the camera, approximately 1/8th of the distance across the field of view.

All cameras were configured to take a set of 4 pictures (one per second) when triggered, followed by a 1-hour delay before they could be triggered again.

When an individual animal appeared in multiple pictures, consecutive images were considered a single observation unless more than an hour had elapsed between captures. Observations where the images did not provide sufficient detail to assess fur colour were discarded, resulting in 1,656 observations for the study.

For each mountain hare observation, we made a record of fur colour by estimating the proportion of the animal's coat that was white (excluding the legs and belly), and classifying moulting stage into three categories, modified from Zimova et al. (2020b) and Stokes et al. (2023). Hares with ≥90% white fur were classified as 'white', hares with ≤10% white fur were classified as 'brown', and all other hares were classified as 'moulting' (**Figure A1** of the Annex).

Environmental cues

We classified ground snow cover into three categories, based on the amount of snow visible in the images: 'Full snow cover', 'partial snow cover', and 'no snow'. 'Full snow cover' if there were no patches of visible lower vegetation, 'no snow' if there was no snow whatsoever, and 'partial snow cover' for everything in between. Altitude and latitude were extracted based on camera trap positions, with altitude, specifically, obtained from a digital terrain model (DTM) with a resolution of 1x1 meter (Lantmäteriet 2021), using ArcGIS Pro 3.2.2 (Esri 2024).

Statistical analysis

Prior to building the models, collinear variables with Variation Inflation Factors (VIF) > 3 were removed (Zuur et al. 2009; Zuur et al. 2007), which were study area, temperature and day of the year (photoperiod) due to their strong collinearity with snow cover, a variable that we prioritized as the most direct and ecologically relevant predictor for fur colour change.

The statistical analysis was performed to evaluate the effects of environmental factors, including snow presence, altitude, and latitude, on the fur colour of the studied species. The analysis also considered the potential interaction between altitude and latitude. A multinomial generalized linear model (GLM) was fitted to the data with fur colour as the response variable (three levels; white, brown and moulting), implemented via the "multinom" function from the "nnet" package in R (Venables and Ripley 2002).

The predictors included in the model were snow presence (a categorical variable with three levels: no snow, partial and full snow cover), altitude (a continuous variable), and latitude (a continuous variable). The interaction between altitude and latitude was also included to assess whether the effect of latitude on fur colour varied with changes in altitude. Given the potential for unequal group sizes and unbalanced data, Type III sum of squares was employed in the analysis. This method is appropriate when the design is not fully balanced, allowing for the assessment of each predictor's effect while accounting for the presence of other variables in the model. The significance of the main effects and the interaction term was tested using Type III ANOVA followed by a post-hoc Tukey's HSD test to identify significant pairwise differences between seasons, implemented via the "Anova" function from the "car" package in R (Fox and Weisberg 2019). The likelihood ratio chi-square test was used to determine the statistical significance of each factor. The model's fit was assessed, and p-values were reported for each predictor to determine its influence on fur colour. A significance level of α=0.05 was used for all statistical tests. Results were considered statistically significant if the p-value was less than 0.05. The statistical analysis was conducted using R software, version [R version 4.4.0 (2024-04-24)] (R Core Team 2024). We evaluated spatial and temporal autocorrelation in the data to ensure the robustness of the model's inferences. Moran's I was used to test for spatial autocorrelation in the residuals, and no significant patterns were detected. Similarly, temporal autocorrelation was assessed using the autocorrelation function (ACF), which showed no significant dependency over time. These findings suggest that spatial and temporal autocorrelation are unlikely to have influenced the results.

Results

Descriptive results

In total, we obtained 1656 records of mountain hares (849 in Ockelbo and 807 in Kårböle), with 699 observations of white hares, 720 of brown hares, and 327 of moulting hares. The frequency of colour distribution in the two study areas was similar (chi-square= 1.71, p=0.42) (**Fig. 2**).

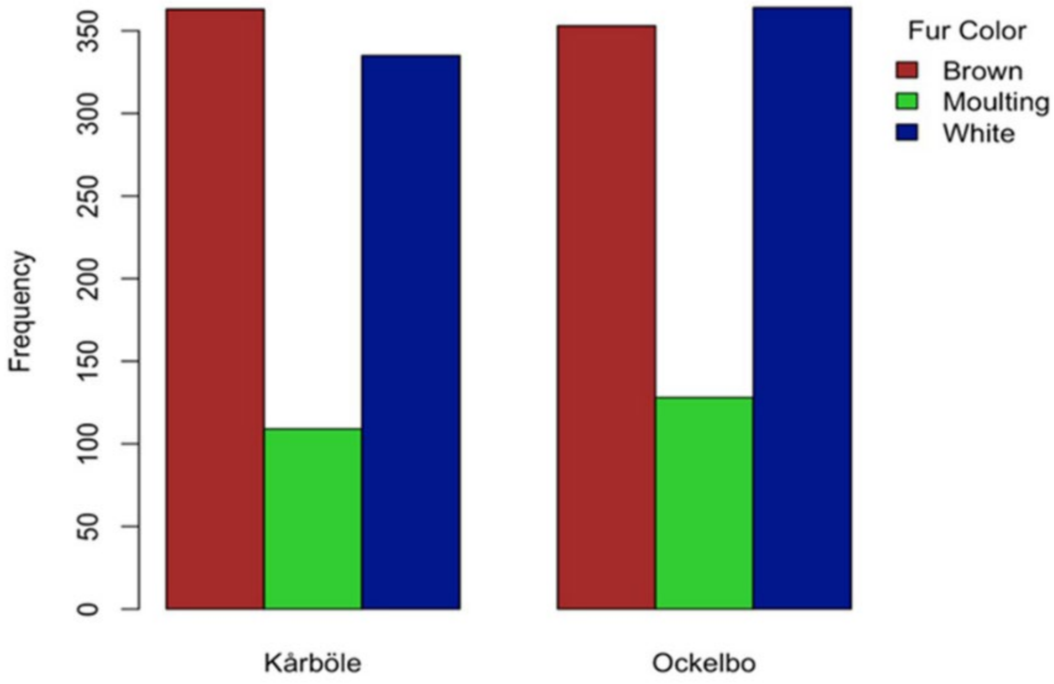

Figure 2. Colour frequency according to the study area (not significant p>0.05).

Figura 2. Frecuencia de color según zona de estudio (no significativo p>0.05).

Factors that determine colour change

The analysis revealed a highly significant effect of snow on fur colour. This suggests that snow presence plays a critical role in determining the fur colour (**Figure A2** of the Annex), likely as an adaptive response to camouflage in snowy environments (**Fig. 3**). Latitude also showed a statistically significant effect on fur colour (**Table 1**). This finding indicates that fur colour varies with latitude, possibly reflecting environmental or climatic gradients that influence selective pressures on fur pigmentation (**Fig. 4**).

Table 1. Chi square and p value of the multinomial model.

Tabla 1. Chi cuadrado y valor p del modelo multinomial.

Predictor	Chi square	p-value
Snow	1632.51	< 0.001
Altitude	2.22	0.32
Latitude	9.08	0.01
Altitude*Latitude	2.32	0.31

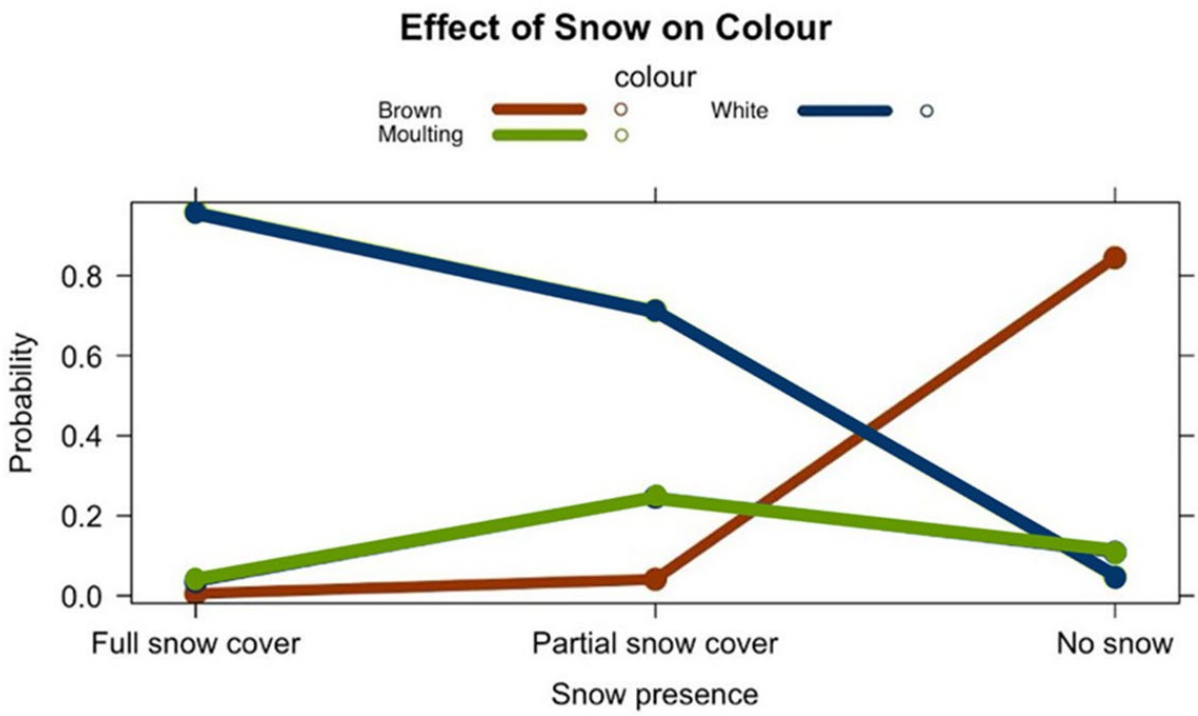

Figure 3. Probability of frequency of each colour (0 to 1) according to snow cover.
Figura 3. Probabilidad de frecuencia de cada color (0 a 1) según la cobertura de nieve.

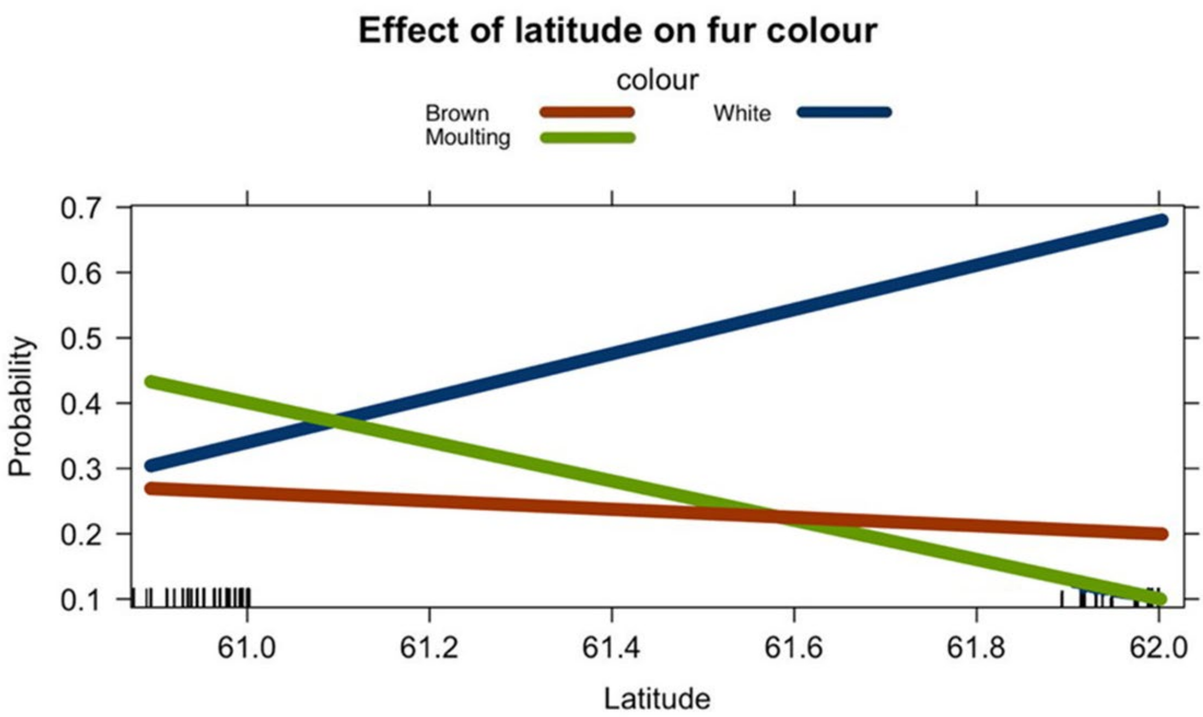

Figure 4. Relationship between the probability of each colour and latitude.
Figura 4. Relación entre la probabilidad de cada color y la latitud.

In contrast, altitude did not have a significant main effect on fur colour. Similarly, the interaction between altitude and latitude was not significant, suggesting that the effects of latitude and altitude on fur colour are independent and do not interact in a meaningful way. However, we found that the altitude at which hares are found depends on the season, being at a higher altitude in summer and autumn, followed by a lower altitude in spring and finally the lowest altitude in winter (**Fig. 5**). This seasonal altitudinal pattern coincides with the variation in colour of hares according to seasonality (**Fig. 6**).

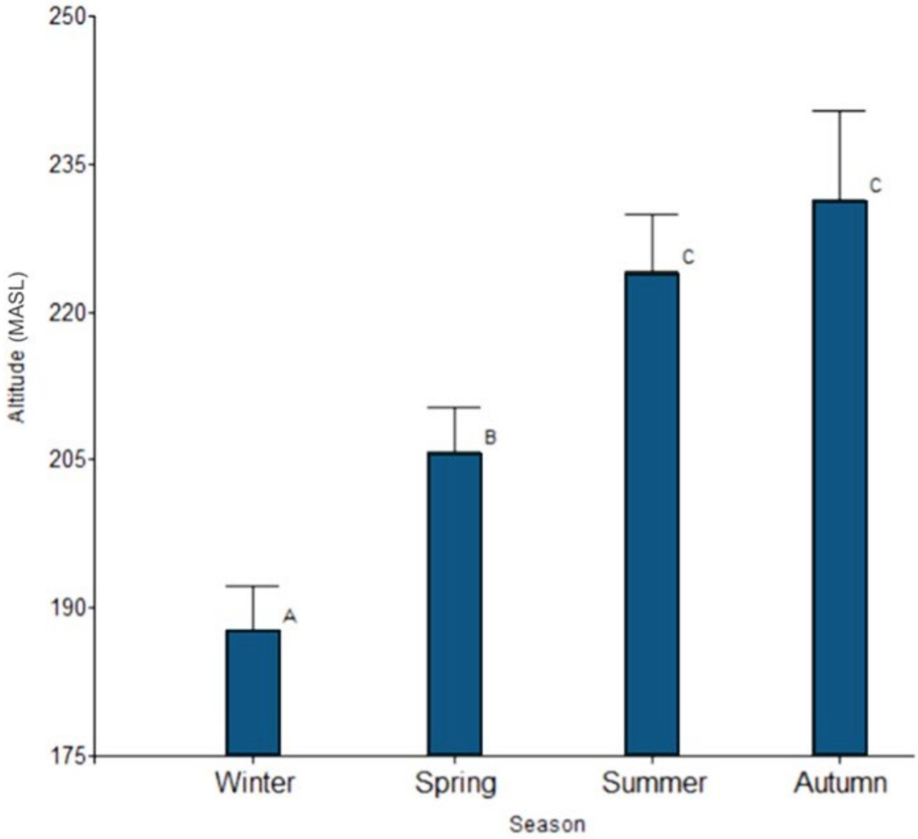

Figure 5. Changes in altitude according to season. Different letters indicate significant differences (p<0.05) based on a post-hoc Tukey's HSD test following a one-way ANOVA.

Figura 5. Cambios en la altitud según la estación. Letras diferentes indican diferencias significativas (p<0,05) según un análisis post-hoc Tukey's HSD realizado después de un ANOVA de una vía.

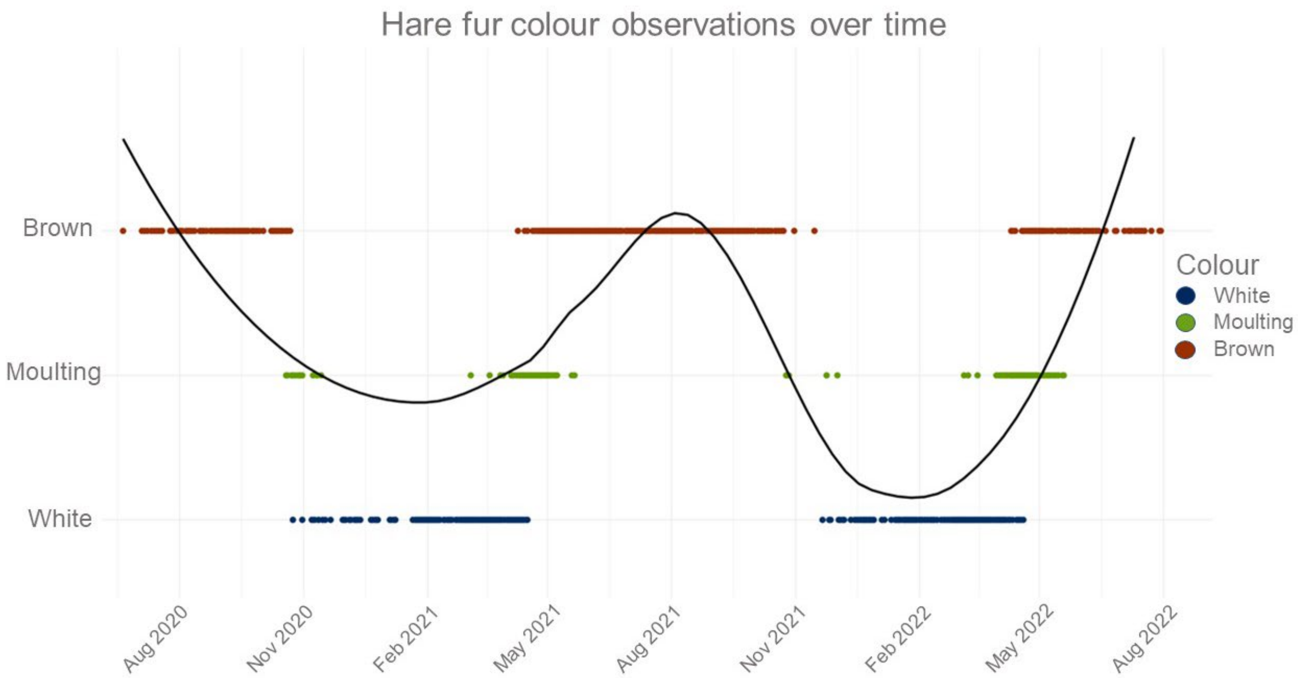

Figure 6. Changes in the colour of the hare's fur according to seasonality. The black line represents the seasonal trend in fur colour, based on fitted values from the statistical model.

Figura 6. Cambios en el color del pelaje de la liebre según la estacionalidad. La línea negra representa la tendencia estacional en el color del pelaje, basada en los valores ajustados del modelo estadístico.

Discussion

This study provides a comprehensive understanding of how key environmental factors —snow cover, latitude, and altitude— drive fur colour changes in the mountain hare (*Lepus timidus*) – a critical adaptation for survival in environments with pronounced seasonal fluctuations (Mills et al. 2013; Zimova et al. 2014). The results reveal the crucial importance of snow presence and latitude as determinants of fur colour within the studied range, while altitude did not show a significant effect. The lack of interaction between altitude and latitude further suggests that these factors operate independently in shaping the observed patterns of fur colour.

The statistical analysis demonstrated that snow presence is the most influential factor in determining fur colour. This finding is consistent with previous studies suggesting that snow acts as a powerful environmental cue, prompting the transition to white fur for camouflage in snowy landscapes (Mills et al. 2013; Zimova et al. 2014). The strong correlation between snow cover and fur colour highlights the hare's adaptation to its environment, where the ability to blend into the snow is critical for avoiding predators (Zimova et al. 2016; Kennah 2022; Oli et al. 2023).

Latitude exhibited a statistically significant effect on fur colour, indicating that fur colour variation is influenced by latitudinal gradients (Stokes et al. 2023). This finding suggests that geographic differences, as determined by latitude, play a crucial role in shaping fur pigmentation. Latitudinal gradients often correlate with variations in environmental or climatic conditions, such as changes in photoperiod (Ferreira et al. 2017), temperature, and (Zimova et al. 2014) seasonal weather patterns, which can impose different selective pressures on fur colour (Peltier et al. 2023).

In higher latitudes, where winter conditions are more severe and snow cover is more persistent, animals typically exhibit a shift to lighter fur colours to enhance camouflage and avoid predation. Conversely, in lower latitudes, where snow cover is less frequent or shorter in duration, the transition to a white winter coat may be less pronounced or even absent. This variation can be attributed to differences in photoperiod, where longer winter nights in higher latitudes may signal the need for a seasonal colour change. Additionally, temperature fluctuations and snowfall patterns can directly influence the timing and extent of the fur colour transition.

In contrast, altitude did not have a significant main effect on fur colour, nor did the interaction between altitude and latitude. This lack of significance suggests that the effects of latitude and altitude on fur colour operate independently and do not interact in a meaningful way within the studied population. While higher altitudes generally lead to earlier onset of winter conditions, this factor alone does not appear to drive the fur colour change as strongly as snow presence or latitude. Flux (1970) found that colours showed no definite correlation with altitude. However, Stokes et al. (2023) found that mountain hare moult timing is strongly correlated with altitude and latitude with hares that live at higher latitudes and altitudes keeping their winter white coats for longer than their conspecifics that inhabit lower latitudes and altitudes. However, these authors had a much broader altitude range (0–841 m). The altitudinal range in this study (63–353 m above sea level) represents a subset of the broader altitudinal distribution of mountain hares in Sweden, which extends to the upper reaches of the Caledonian Mountains. This limited range may partially explain the lack of a significant effect of altitude on fur colour change observed in our results. In higher altitudes, where snow cover tends to persist longer and winter conditions are harsher, the relationship between altitude and fur colour may become more pronounced. Future studies incorporating a broader altitudinal gradient could provide additional insights into how this factor influences seasonal adaptations in mountain hares.

Seasonal altitudinal movements may be responsible for the lack of differences. At the microniche scale (as in this study), the availability of food and shelter drives the altitudinal movement of hares according to the seasons (Bison et al. 2024). During the winter, hares may descend to lower areas where food is more accessible (Rehnus and Bollmann 2020). These lower regions tend to have less snow accumulation or offer more shelter and food sources, such as branches and bushes that protrude from the snow. By contrast, during the summer and autumn months, when hares change to their brown coat, they may migrate to higher altitudes where fresh and abundant vegetation is available. Higher altitudes provide new grasses and herbaceous plants that hares prefer during the growing season (Rehnus and Bollmann 2020). This pattern of seasonal movement, related to foraging, is common in many species inhabiting mountainous regions. Additionally, shifting locations with the seasons not only maximizes food availability but may also help hares reduce predator exposure by taking advantage of seasonal camouflage provided by their fur.

Understanding the interplay of these environmental factors is particularly important in the context of climate change. As global temperatures rise and snow cover patterns shift, the synchronization between fur colour change and the environment may become disrupted. Such mismatches could increase the vulnerability of hares to predation, potentially leading to declines in population numbers. Conservation strategies should therefore consider the potential impacts of changing snow cover dynamics and aim to preserve habitats that support the natural camouflage and survival of mountain hares.

Conclusion

In conclusion, our results show that camera traps provide detailed information on mountain hare ecology and confirm the importance of working at different scales. Overall, this study emphasizes the dominant role of snow cover and latitude in driving fur colour change in mountain hares, while highlighting the relatively minor role of altitude, since it is at a microniche scale, it is related to seasonal altitudinal movements. These findings contribute to a broader understanding of phenological adaptations in wildlife and underscore the importance of monitoring environmental changes that could threaten these adaptive traits.

Authors' contribution

Anna Göransson: Data curation, Visualization, Methodology, Writing – Review and editing. Davide Carniato: Research, formal analysis, Writing – initial draft. Lars Hillstrom: Funding acquisition, Resources, Writing – Review and editing. Petter Hillborg: Data curation, Methodology. Marcus Larsson: Resources, Writing – Review and editing. Antonio J. Carpio: Conceptualization, Supervision, Writing – Review and editing.

Data availability

Data of this study is available on the repository https://doi.org/10.5281/zenodo.14912867

Financing, required permits, potential conflicts of interest and acknowledgments

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The authors declare that they have no conflicts of interest.

References

Atmeh, K., Andruszkiewicz, A., Zub, K. 2018. Climate change is affecting mortality of weasels due to camouflage mismatch. *Scientific Reports* 8(1), 7648. https://doi.org/10.1038/s41598-018-26057-5

Beever, E.A., Hall, L.E., Varner, J., Loosen, A.E., Dunham, J. B., Gahl, M.K., et al. 2017. Behavioral flexibility as a mechanism for coping with climate change. *Frontiers in Ecology and the Environment* 15(6), 299-308. https://doi.org/10.1002/fee.1502

Bison, M., Yoccoz, N.G., Carlson, B.Z., Bayle, A., Delestrade, A. 2024. Camera traps reveal seasonal variation in activity and occupancy of the Alpine Mountain hare *Lepus timidus* varronis. *Wildlife Biology* e01186. https://doi.org/10.1002/wlb3.01186

Boursot, P., Auffray, J.C., Britton-Davidian, J., Bonhomme, F. 1993. The evolution of house mice. *Annual Review of Ecology and Systematics* 24,119-152. https://doi.org/10.1146/annurev.es.24.110193.001003

Brown, R.D., Mote, P.W. 2009. The response of Northern Hemisphere snow cover to a changing climate. *Journal of Climate* 22(8), 2124-2145. https://doi.org/10.1175/2008JCLI2665.1

Esri. 2024. ArcGIS Pro (Version 3.2.2) [Computer software]. https://www.esri.com/

Feder, J.L., Egan, S.P., Nosil, P. 2012. The genomics of speciation-with-gene-flow. *Trends in Genetics* 28(7), 342-350. https://doi.org/10.1016/j.tig.2012.03.009

Ferreira, M.S., Alves, P.C., Callahan, C.M., Marques, J.P., Mills, L.S., Good, J.M., Melo-Ferreira, J. 2017. The transcriptional landscape of seasonal coat colour moult in the snowshoe hare. *Molecular Ecology* 26(16), 4173-4185. https://doi.org/10.1111/mec.14177

Ferreira, M.S., Alves, P.C., Callahan, C.M., Giska, I., Farelo, L., Jenny, H., et al. 2020. Transcriptomic regulation of seasonal coat color change in hares. *Ecology and Evolution* 10(3), 1180-1192. https://doi.org/10.1002/ece3.5956

Fuller, A., Dawson, T., Helmuth, B., Hetem, R.S., Mitchell, D., Maloney, S.K. 2010. Physiological mechanisms in coping with climate change. *Physiological and Biochemical Zoology* 83(5), 713-720. https://doi.org/10.1086/652242

Flux, J.E. 1970. Colour change of Mountain hares (*Lepus timidus scoticus*) in north-east Scotland. *Journal of Zoology* 162(3), 345-358. https://doi.org/10.1111/j.1469-7998.1970.tb01270.x

Fox, J, Weisberg. S. 2019. *An R Companion to Applied Regression*, Third edition. Sage, Thousand Oaks CA. https://www.john-fox.ca/Companion/

Hofman, M.A. 2004. The brain's calendar: Neural mechanisms of seasonal timing. *Biological Reviews of the Cambridge Philosophical Society* 79, 61–77. https://doi.org/10.1017/S1464793103006250

Jackes, A.D., Watson, A. 1975. Winter whitening of Scottish Mountain hares (*Lepus timidus scoficus*) in relation to daylength, temperature and snow-lie. *Journal of Zoology* 176, 403–409. https://doi.org/10.1111/j.1469-7998.1975.tb03211.x

Jones, M.R., Mills, L.S., Jensen, J.D., Good, J.M. 2020. Convergent evolution of seasonal camouflage in response to reduced snow cover across the snowshoe hare range. *Evolution* 74(9), 2033-2045. https://doi.org/10.1111/evo.13976

Kennah, J. 2022. *An evaluation of the costs and responses of coat colour mismatch in snowshoe hares*. Masters thesis, Memorial University of Newfoundland. https://doi.org/10.48336/MXSP-H118

Lantmäteriet 2021. *Markhöjdmodell Nedladdning, grid 1+*. [GeoTIFF]. https://www.lantmateriet.se/sv/geodata/vara-produkter/produktlista/markhojdmodell-nedladdning-grid-1/

Mills, L.S., Zimova, M., Oyler, J., Running, S., Abatzoglou, J.T., Lukacs, P.M. 2013. Camouflage mismatch in seasonal coat color due to decreased snow duration. *Proceedings of the National Academy of Sciences* 110(18), 7360-7365. https://doi.org/10.1073/pnas.1222724110

O'Connell, A.F., Nichols, J.D., Karanth, K.U. 2011. *Camera Traps in Animal Ecology: Methods and Analyses*. Springer. https://doi.org/10.1007/978-4-431-99495-4

Oli, M.K., Kenney, A.J., Boonstra, R., Boutin, S., Murray, D.L., Peers, M.J., et al. 2023. Does coat colour influence survival? A test in a cyclic population of snowshoe hares. *Proceedings of the Royal Society B* 290(1996), 20221421. https://doi.org/10.1098/rspb.2022.1421

Peltier, T.R., Shiratsuru, S., Zuckerberg, B., Romanski, M., Potvin, L., Edwards, A., et al. 2023. Phenotypic variation in the molt characteristics of a seasonal coat color-changing species reveals limited resilience to climate change. *Oecologia* 202(1), 69-82. https://doi.org/10.1007/s00442-023-05371-4

R Core Team. 2024. *R: A language and environment for statistical computing,* version 4.4.0 (2024-04-24). [Software]. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org

Rehnus, M., Bollmann, K. 2020. Mountain hares Lepus timidus follow the green-up wave in the pursuit of high-quality food. *Wildlife Biology* 2020(3), 1-5. https://doi.org/10.2981/wlb.00720

Semenchuk, P.R., Elberling, B., Cooper, E.J. 2013. Snow cover and extreme winter warming events control flower abundance of some, but not all species in high arctic S valbard. *Ecology and Evolution* 3(8), 2586-2599. https://doi.org/10.1002/ece3.648

Stokes, A.W., Hofmeester, T.R., Thorsen, N.H., Odden, J., Linnell, J.D., Pedersen, S. 2023. Altitude, latitude and climate zone as determinants of mountain hare (Lepus timidus) coat colour change. *Ecology and Evolution* 13(10), e10548. https://doi.org/10.1002/ece3.10548

Stoner, C.J., Bininda-Emonds, O.R., Caro, T.I.M. 2003. The adaptive significance of coloration in lagomorphs. *Biological Journal of the Linnean Society* 79(2), 309-328. https://doi.org/10.1046/j.1095-8312.2003.00190.x

Venables, W.N. Ripley, B.D. 2002. *Modern Applied Statistics with S.,* Fourth Edition. Springer, New York. ISBN 0-387-95457-0. https://doi.org/10.1007/978-0-387-21706-2_14

Watson, A. 1963. The effect of climate on the colour changes of mountain hares in Scotland. *Proceedings of the Zoological Society of London* 141, 823–835. https://doi.org/10.1111/j.1469-7998.1963.tb01629.x

Zimova, M., Mills, L.S., Lukacs, P.M., Mitchell, M.S. 2014. Snowshoe hares display limited phenotypic plasticity to mismatch in seasonal camouflage. *Proceedings of the Royal Society B: Biological Sciences* 281(1782), 20140029. https://doi.org/10.1098/rspb.2014.0029

Zimova, M., Mills, L.S., Nowak, J.J. 2016. High fitness costs of climate change-induced camouflage mismatch. *Ecology letters* 19(3), 299-307. https://doi.org/10.1111/ele.12568

Zimova, M., Hackländer, K., Good, J.M., Melo-Ferreira, J., Alves, P.C., Mills, L.S. 2018. Function and underlying mechanisms of seasonal colour moulting in mammals and birds: what keeps them changing in a warming world?. *Biological Reviews* 93(3), 1478-1498. https://doi.org/10.1111/brv.12405

Zimova, M., Giery, S.T., Newey, S., Nowak, J.J., Spencer, M., Mills, L.S. 2020a. Lack of phenological shift leads to increased camouflage mismatch in mountain hares. *Proceedings of the Royal Society B* 287(1941), 20201786. https://doi.org/10.1098/rspb.2020.1786

Zimova, M., Barnard, L.S., Davis, B.M., Kumar, A.V., Lafferty, D.J.R., Mills, L.S. 2020b. Using remote cameras to measure seasonal molts. *Ecosphere* 11, e03084. https://doi.org/10.1002/ecs2.3084

Zuur, A., Ieno, E.N., Smith, G.M. 2007. *Analyzing ecological data*. Springer. https://doi.org/10.1007/978-0-387-45972-1

Zuur, A., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M. 2009. *Mixed effects models and extensions in ecology with R*. Springer Science & Business Media. https://doi.org/10.1007/978-0-387-87458-6

Annex / Anexo

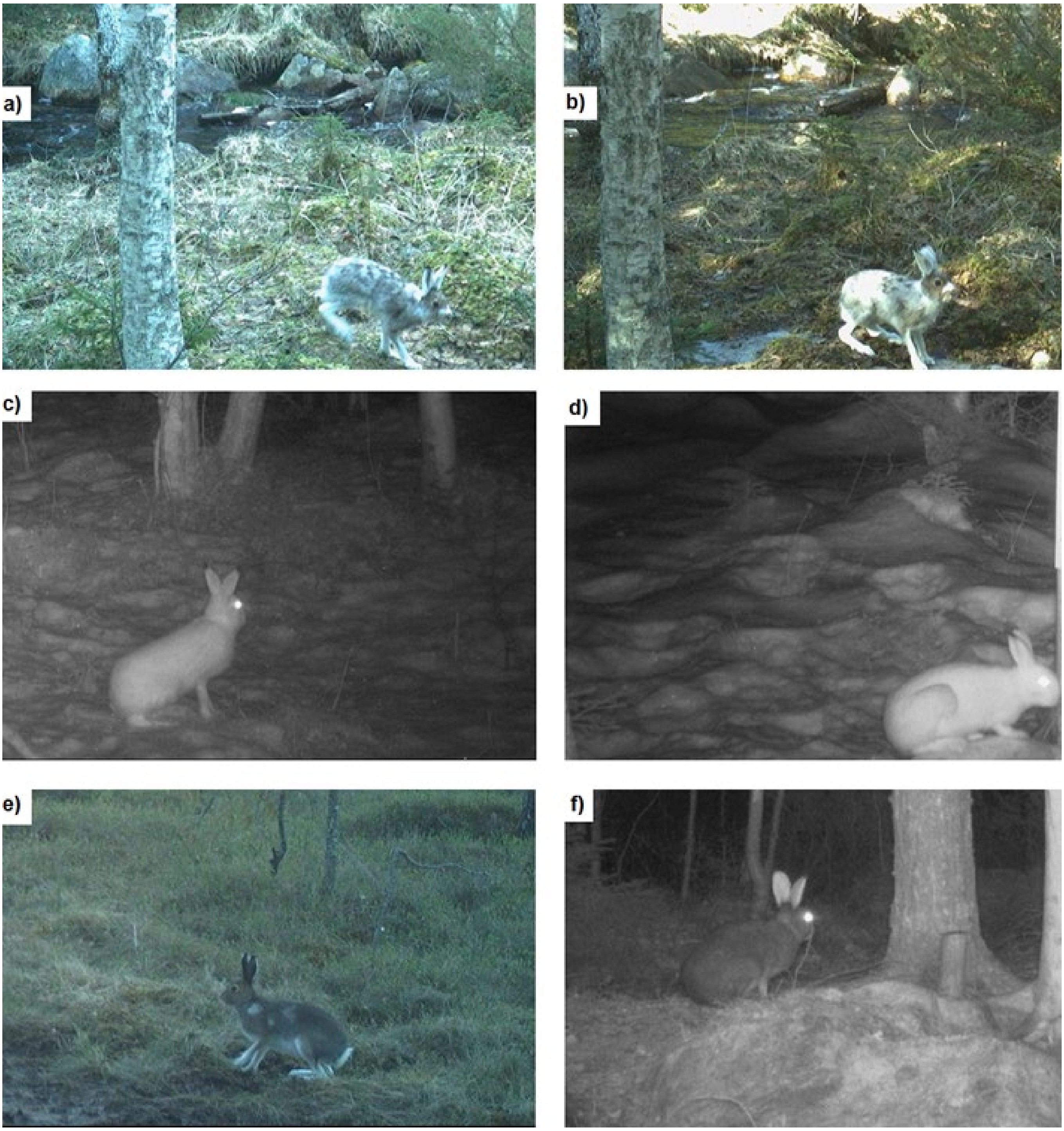

Figure A1. Images of the hares with the 3 fur colours: a) and b) moulting, c) and d) white and e) and f) brown.

Figura A1. Imágenes de las liebres con los 3 colores de pelaje. a) y b) mudando, c) y d) blanco y e) y f) marrón.

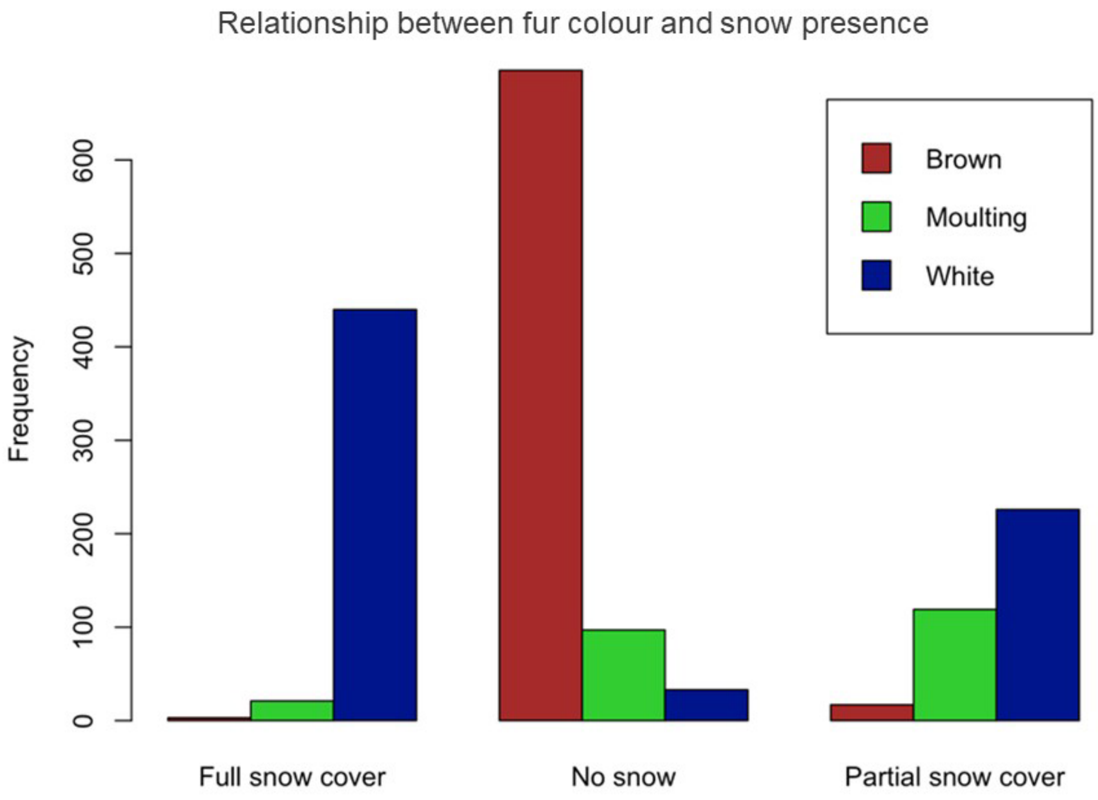

Figure A2. Relationship between fur color and snow presence.

Figura A2. Relaciòn entre color del pelaje y presencia de nieve.