Mountain hares Lepus timidus follow the green-up wave in the pursuit of high-quality food

Authors: Rehnus, Maik, and Bollmann, Kurt

Source: Wildlife Biology, 2020(3)

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/wlb.00720

Communications

Wildlife Biology 2020: wlb.00720
doi: 10.2981/wlb.00720

Subject Editor: Luca Corlatti. Editor-in-Chief: Ilse Storch. Accepted 31 July 2020

Communications

Mountain hares *Lepus timidus* follow the green-up wave in the pursuit of high-quality food

Maik Rehnus and Kurt Bollmann

M. Rehnus (https://orcid.org/0000-0002-1973-4878) ✉ (maik.rehnus@wsl.ch) and K. Bollmann (https://orcid.org/0000-0002-4690-7121), Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Zürcherstrasse 111, CH-8903 Birmensdorf, Switzerland.

Spatial patterns in animal behavior can provide insight into habitat quality and the distribution of resources. Understanding how, when, and why animals use certain areas is critical to their conservation and management. We investigated the distribution of pellets of mountain hares *Lepus timidus* in the Swiss Alps and compared differences between spring and autumn. 1515 pellet locations from 119 individuals (70 males, 49 females) were used. Pellets were collected from 2014 to 2019; individuals were determined using an established, non-invasive genetic technique. We found evidence of an altitudinal shift in the occurrence of pellets from lower elevations in spring to higher elevations in autumn. This seasonal pattern is also supported by altitudinal shifts of three individual core activity areas (2 males, 1 females) and by higher hare activities at the high plateau in autumn. We conclude that the annual 'wave' of greening from lower to higher elevations, which correlates with forage availability and quality, explains this shift.

Keywords: Alps, altitudinal shift, home range, non-invasive genetic sampling, pellets, season, vegetation

Spatial patterns in habitat use by animals can provide insight into habitat productivity and resource distribution (Phillips et al. 1998, Bennetts and Kitchens 2000). For example, in landscapes where high-quality habitats are available and resources are predictable, individuals can develop a high site fidelity and range over relatively small areas (Switzer 1993). Understanding how animals use different habitats due to seasonal changes in food quantity and quality helps to explain how these resources influence individual life-history trajectories (Larter and Nagy 2001).

Diet composition in terrestrial mammals like leporids differs greatly from season to season because they eat many types of grasses, shrubs and forbs (Chapman and Flux 1990). This flexibility allows arctic-alpine species like mountain hares *Lepus timidus* to cope with changing environmental conditions and the corresponding changes in food quantity and quality (Thulin and Flux 2003). For example, a study by Rehnus (2013) showed that fewer graminoids and forbs are consumed during the snow season as compared to the rest of the year. At the same time, hares consume more gymnosperms during the winter months than in snow-free times. Many studies on the dietary requirements of leporids during the snow-free season have observed that animals tend to select inflorescences and forbs which are known to have a higher nutritive value (Chapuis 1990, Johannessen and Samset 1994, Paupério and Alves 2008, Seccombe-Hett and Turkington 2008). However, during flowering and seed production, plants produce fewer leaves and more stems. This increases the fiber content and reduces the protein content, thereby reducing the forage quality (Albon and Langvatn 1992, Duru 1997, Bumb et al. 2016). To take advantage of plants' high nutritive state, herbivore species should follow the green-up wave along an altitudinal gradient. For example, red deer *Cervus elaphus* are found at high altitudes in the Alps during summer due to food quality (Luccarini et al. 2006, Zweifel-Schielly et al. 2009). However, it is still under discussion as to whether elusive and difficult-to-spot leporids from arctic–alpine environments also undertake seasonal shifts in mountainous habitats. According to Bisi et al. (2011) mountain hares do not completely shift their home ranges in relation to resource distribution from one season to the next in the Alps (but see Slotta-Bachmayr 1998), whereas the same species used distinct seasonal areas depending on resource distribution in the boreal forest (Dahl 2005).

Mountain hare populations of the Alps are highly suitable for analysing altitudinal shifts because this genuine species

---

lives at high elevations in isolated glacial relict populations (Thulin and Flux 2003, Rehnus 2013). Climate habitat model, however, show a decreasing population trend in the Alps (Rehnus et al. 2018).

In this study, we investigated the occurrence of altitudinal shifts in pellet locations from spring to autumn based on non-invasive genetic population monitoring data (Rehnus and Bollmann 2016) from six years (2014–2019). We also used multiple locations of the same individuals in both seasons from the same year to investigate altitudinal shifts in core activity areas of mountain hares as further support of seasonal distribution patterns.

Material and methods

Study area

The study area comprises 3.5 km² and is situated along the Ofenpass in the Swiss National Park in southeastern Switzerland (46°39′N, 10°11′E; Fig. 1). The study area was selected to represent the ecological range occupied by the mountain hare in the Swiss National Park and is accessible under different snow conditions with a minimal risk of avalanches. The Swiss National Park is designated by the International Union for the Conservation of Nature (IUCN 2016) as a Category Ia nature reserve (strict nature reserve/wilderness area). It is closed to the public in spring; and open in summer and autumn when hiking is limited to pre-defined walking routes. There is no grazing by domestic animals in the National Park.

The study's elevational range was from 1693 to 2587 m a.s.l. Its topography is characterised by mountain slopes with a typical vegetation zoning consisting of subalpine coniferous forests, alpine meadows and rock and scree in the uppermost part of the mountain, which is shaped as a high plateau. Habitats within the study area were classified according to the habitat categories of HABITALP, a standardized habitat classification system for protected areas in the Alps (Lotz 2006). The study area encompasses seven main habitat types: meadows (29%; with diverse grasses, including *Nardus stricta*, *Festuca* sp., *Poa* sp., *Agrostis* sp., *Luzula* sp. and sedges), timber stands (24%), scree slopes (16%), storeyed stands (12%; mixed *Larix decidua*, *Pinus cembra*, *P. sylvestris*, *P. mugo* spp., *Picea abies*), sapling stands (6%; dominated by *P. mugo* spp.), pole timber (5%) and mature stands (5%). Residual habitats cover 3% of the area. The climate in the Swiss National Park is continental, with mean January and July temperatures of −9°C and 11°C, respectively (Haller et al. 2013). The mean monthly precipitation measured at 1970 m a.s.l. is 34 mm in January and 108 mm in July (Haller et al. 2013).

Species data

We collected fresh pellets over six consecutive years (2014–2019) in spring (end of March until first half of April) and autumn (October). Samples were collected both systematically and opportunistically, as described in detail by Rehnus and Bollmann (2016). Systematic sampling was conducted on 91 plots that were pre-selected on a 200-m square grid; all hare pellets within each trial plot were collected during each visit. For the opportunistic sampling, we collected pellets as we moved from one systematic plot to the next. Only fresh fecal pellets were collected because amplification success rates were significantly lower for pellets older than five days (Rehnus and Bollmann 2016). Samples were collected and stored in separate plastic

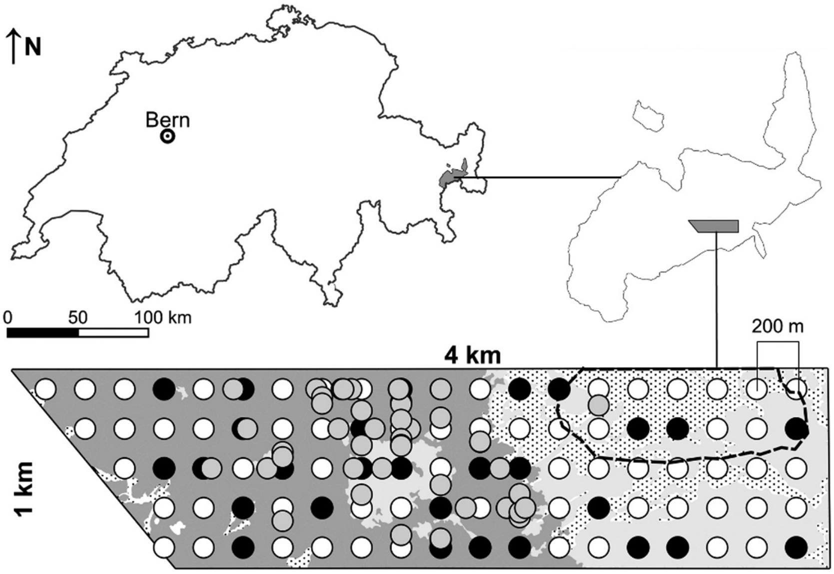

Figure 1. Location of the study area (3.5 km²) with sampling locations (circles) in the Swiss National Park (grey region) in Switzerland. Background colours illustrate forests (dark grey), meadows (light grey) and scree and rocks (black stipples). To demonstrate the sampling strategy, we present sampling results from spring 2014. White circles indicate the absence of mountain hare pellets during systematic sampling; black (grey) circles indicate the presence of faeces during systematic (opportunistic) sampling (Rehnus and Bollmann 2016, adapted). The uppermost part of the mountain (≥ 2500 m a.s.l.) is shaped as a high plateau (dashed line among sampling locations) and is composed by 39% of alpine meadows and 61% of rock and scree.

tubes without skin contact to minimize DNA contamination (Sloan et al. 2000). After collection in the field, samples were frozen and stored until they were analysed in the lab.

We used nine nuclear microsatellites (Lsa1, Lsa3 (Kryger 2002), Sat 2, Sat5, Sat8, Sat12 (Mougel et al. 1997), Sol30, Sol8 (Rico et al. 1994), Sol33 (Surridge et al. 1997)) and a sex marker (SRY; Wallner et al. 2001) to identify individuals and assign them to the collected feces samples. DNA samples were genotyped in three independent replicates and consensus homozygote genotypes were accepted if all three replicates were consistent. Consensus heterozygote genotypes were accepted if at least two replicates were consistent and no more than two alleles were found across all three replicates (Schenkerz et al. 2020).

Statistical analysis

We evaluated altitudinal shifts from spring to autumn as indicated by individual pellet locations and individual core activity areas. Pellet locations are good indicators of feeding sites and core activity areas of mountain hare (Angerbjörn 1983, Krebs et al. 2001, Hiltunen 2003, Rehnus et al. 2016).

Our dataset contains 1001 pellet locations during the early breeding season and 514 pellet locations during the post-reproductive period from 70 males and 49 females. We tested altitudinal shifts for systematic and opportunistic sampling using linear models with altitude as the response variable, season as the predictor variables and individual ID and year as a random factors. We also analysed the number of used systematic plots at the high plateau and samples found opportunistically in alpine meadows at the high plateau (≥ 2500 m a.s.l.) in our study area and compared them between spring and autumn with a Mann–Whitney U-test.

To support the hypothesis of a potential seasonal shifts, we calculated the area of minimum convex polygons 95% (MCP95) for seasonal locations of unique individuals in the R-package 'reproducible core activity area analysis' (Signer and Balkenhol 2015). Core activity areas are part of the individual home ranges that depend on seasonal ecological conditions (Hiltunen et al. 2004, Bisi et al. 2011). We used a dataset of six activity core areas from three unique individuals (2 males, 1 females) which fulfilled the criteria of a minimum of 10 observations at unique locations per season within the same year. We assume that this minimum adequately represents the core activity areas of mountain hares in our study area because of the species' site fidelity (Bisi et al. 2011). Altitudinal shifts of core activity areas were calculated as the difference of the centroids of seasonal MCP95-polygons. Further, we estimated the number of unique individuals at the high plateau in our study area and tested for seasonal differences.

All statistical tests were conducted using R ver. 3.6.3 (<www.r-project.org>) and full-model table is supplemented (Supplementary material Appendix 1 Table A1). Analyses were not separated by sex because between male and female mountain hares is a weak habitat segregation in both seasons (Rehnus and Bollmann 2020).

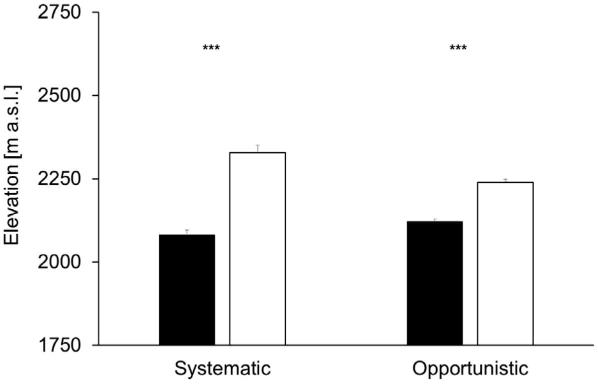

Figure 2. Elevations (mean ± SE) of pellet locations in spring (black) and autumn (white) during systematic and opportunistic sampling in the Swiss National Park between 2014 and 2019. Analyses were conducted for systematic ($F_{1,135} = 55.1$, $p < 0.001$) and opportunistic ($F_{1,1055} = 166.3$, $p < 0.001$) sampling with altitude as the response variable and season as the predictor variables, and individual ID and year as random factors to account for individual clustering in samples and to consider effects of year.

Results

Mountain hare pellets were found at higher altitudes in autumn as compared to spring for both systematic (mean ± SE: 2328.0 ± 22.9 m a.s.l. versus 2082.2 ± 14.0 m a.s.l.; $F_{1,135} = 55.1$, $p < 0.001$) and opportunistic sampling (2238.4 ± 9.4 m a.s.l. versus 2122.5 ± 6.0 m a.s.l.; $F_{1,1055} = 166.3$, $p < 0.001$; Fig. 2). Differences in altitude between years varied from 160 to 361 m for systematic and 11 to 210 m for opportunistic sampling (Supplementary material Appendix 1 Fig. A1). The number of used systematic plots at the high plateau was higher in autumn (3.3 ± 0.2) than in spring (1.2 ± 0.4; $F_{1,5} = 22.8$, $p < 0.001$; Fig. 3). This corresponds with the finding that the number of opportunistic samples found in meadows at the high plateau (≥ 2500 m a.s.l.) was also higher in autumn (7.8 ± 1.3) than in spring (1.3 ± 0.8; $F_{1,5} = 24.6$, $p = 0.004$; Fig. 3).

On average, mountain hares had core activity areas that were 2- to 4-times larger in spring than in autumn (Table 1). The centers of these area are found at higher altitudes

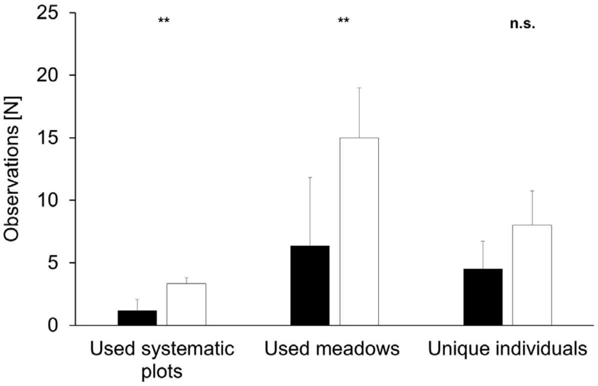

Figure 3. Average number (mean ± SE) of used systematic plots and opportunistic samples found in meadows at and unique individuals per year assigned to the highest zone (mountain plateau, ≥ 2500 m a.s.l.) in our study area in spring (black) and autumn (white) between 2014 and 2019 in the Swiss National Park.

Table 1. Altitudinal shifts in individual core activity areas from spring to autumn in the Swiss National Park. Altitudinal shifts were calculated as the difference in the altitude of the core activity area in autumn and spring for unique individuals (2 males, 1 female) with a minimum of 10 observations at unique locations per season within the same year from 2014 to 2019.

Individuals	Sex	Year	Observations		Core activity area [ha]		Seasonal overlaps [%]	Altitudinal shifts to autumn [m]
			Spring	Autumn	Spring	Autumn		
70	Female	2017	12	11	9.2	4.6	0.5	119.6
81	Male	2018	16	11	19.9	5.5	0.0	328.3
97	Male	2019	15	10	30.0	12.4	1.2	115.3

in autumn compared to spring while seasonal overlaps were below 1.8% between areas (Table 1). The number of unique individuals at the high plateau was slightly higher in autumn (8.0 ± 1.2) than in spring (4.5 ± 1.0; $F_{1,5} = 4.9$, $p = 0.079$; Fig. 3).

Discussion

We found clear evidence of an altitudinal shift in pellet locations from lower elevations in spring to higher elevations in autumn. This finding is supported by a shift of individual core activity areas. The use of higher amounts of alpine meadow habitat later in the vegetation period is in line with these results.

Upward altitudinal shifts of mountain hares from spring to autumn have also been recorded by Slotta-Bachmayr (1998) in the Austrian Alps. He noted that altitudinal shifts may be driven by snow cover, which influences food availability. Accordingly, upward shifts start in spring and follow the receding snow line until early winter, when snow cover begins to reduce food availability again (Slotta-Bachmayr 1998). The length of this vegetation pattern depends on the inter-annual variability of winter conditions and duration and could influence the between year difference in the altitudinal shift of activity areas. Altitudinal shifts to higher altitudes after snow melting have also been shown in other herbivores living in mountain habitats, such as red deer, Alpine ibex (*Apra ibex* and chamois *Rupicapra rupicapra* (Grignolio et al. 2003, Zweifel-Schielly et al. 2009, Darmon et al. 2012). Mason et al. (2017) showed that the shifting pattern of Alpine ibex is caused by a tradeoff between behavioral thermoregulation and foraging. During warmer periods, ibex utilize areas that are less productive and therefore consume lower quality forage (Mason et al. 2017). We cannot rule out such a mechanisms for the mountain hare as the species has been shown to be sensitive to warmer temperatures (Rehnus et al. 2018). The average ambient temperature over the study period is 3.0°C in autumn and as such 4°C higher than in spring, but 8°C lower than in summer (Rehus and Bollman unpubl.). Accordingly, mountain hares would be expected to occur much higher in the summer season. However, this is not possible due to topographic limitations. As mountain hares also stay in the area in summer, we assume that they move upward to co-benefit from more comfortable ambient temperatures and mainly form higher quality food which is linked to the higher proportions of meadows above the timber line. Similarly, it has been shown that altitudinal shifts by red deer are driven by food quality and the maximal protein concentrations of graminoids and herbs (Albon and Langvatn 1992, Zweifel-Schielly et al. 2009). If high-quality food is not available, mountain hares are likely to use an intermediate feeding strategy in which they switch from grazing to browsing (Hulbert et al. 2001). Only minor altitudinal shifts of mountain hares have been observed in the Italian Alps (Bisi et al. 2011). This is likely due to differences in resource distribution and availability between study areas.

The use of higher-elevation habitat increases the risk of predation (e.g. eagle owl *Bubo bubo*) because meadows offer limited cover during hares' nocturnal activities (Rehnus 2013). However, it has been observed that large herbivores often favor improved forage options over predator avoidance (Fryxell and Sinclair 1988). Similarly, the high site fidelity of mountain hares (Bisi et al. 2011) is likely due to the increased benefits of familiarity: the more familiar an animal is with an area's distribution of its conspecifics, predators and resources, the greater advantage it has (Nathan et al. 2008, van Moorter et al. 2009).

Our study presents details about altitudinal shifts in the feeding sites and activity areas of mountain hares in the Alps. However, further research is needed on how these shifts are affected by climate change (Rehnus et al. 2018) and how they interact with nutritional needs and thermoregulatory mechanisms.

Acknowledgements – We thank the Swiss National Park for granting permission to conduct this study, S. Brodbeck, F. Gugerli and L. Schenker (WSL) for conducting the genetic analyses, and E. Gleeson (SciencEdit.CH) for assistance with language editing.
Author contributions – Both authors contributed equally to this paper.
Conflicts of interest – No conflicts of interest

References

Albon, S. D. and Langvatn, R. 1992. Plant phenology and the benefits of migration in a temperate ungulate. – Oikos 65: 502–513.

Angerbjörn, A. 1983. Reliability of pellet counts as density estimates of mountain hares. – Finn. Game Res. 41: 13–20.

Bennetts, R. E. and Kitchens, W. M. 2000. Factors influencing movement probabilities of a nomadic food specialist: proximate foraging benefits or ultimate gains from exploration? – Oikos 91: 459–467.

Bisi, F. et al. 2011. Space use patterns of mountain hare (*Lepus timidus*) on the Alps. – Eur. J. Wildl. Res. 57: 305–312.

Bumb, I. et al. 2016. Influence of management regime and harvest date on the forage quality of rangelands plants: the importance of dry matter content. – AoB Plants 8: plw045.

Chapman, J. A. and Flux, J. E. C. 1990. Rabbits, hares and pikas. Status survey and conservation action plan. – IUCN, Gland.

Chapuis, J. L. 1990. Comparison of the diets of two sympatric lagomorphs, *Lepus europaeus* (Pallas) and *Oryctolagus cuniculus*

(L.) in an agroecosystem of the Ile-de-France. – Z. Säugetierkunde 55: 176–185.

Dahl, F. 2005. Distinct seasonal habitat selection by annually sedentary mountain hares (*Lepus timidus*) in the boreal forest of Sweden. – Eur. J. Wildl. Res. 51: 163–169.

Darmon, G. et al. 2012. Spatial distribution and habitat selection in coexisting species of mountain ungulates. – Ecography 35: 44–53.

Duru, M. 1997. Leaf and stem in vitro digestibility for grasses and dicotyledons of meadow plant communities in spring. – J. Sci. Food Agric. 74: 175–185.

Fryxell, J. M. and Sinclair, A. R. E. 1988. Causes and consequences of migration by large herbivores. – Trends Ecol. Evol. 3: 237–241.

Grignolio, S. et al. 2003. Habitat selection in adult males of Alpine ibex, *Capra ibex ibex*. – Fol. Zool. 52: 113–120.

Haller, H. et al. 2013. Atlas des Schweizerischen Nationalparks. Die ersten 100 Jahre. – Haupt, Bern.

Hiltunen, M. 2003. Feeding intensity of mountain hares (*Lepus timidus*) during winter in Finland. – Mamm. Biol. 68: 48–52.

Hiltunen, M. et al. 2004. Habitat use of the mountain hare *Lepus timidus* in summer: the importance of different vegetation layers. – Acta Theriol. 49: 479–490.

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

IUCN 2016. Protected areas category Ia. – <www.iucn.org/about/work/programmes/gpap_home/gpap_quality/gpap_pacategories/gpap_cat1a/>. 19 October 2016>.

Johannessen, V. and Samset, E. 1994. Summer diet of the mountain hare (*Lepus timidus* L.) in a low-alpine area in southern Norway. – Can. J. Zool. 72: 652–657.

Krebs, C. J. et al. 2001. Estimating snowshoe hare population density from pellet plots: a further evaluation. – Can. J. Zool. 79: 1–4.

Kryger, U. et al. 2002. Isolation and characterization of six polymorphic microsatellite loci in South African hares (*Lepus saxatilis* F. Cuvier, 1823 and *Lepus capensis* Linnaeus, 1758). – Mol. Ecol. Not. 2: 422–424.

Larter, N. C. and Nagy, J. A. 2001. Seasonal and annual variability in the quality of important forage plants on Banks Island, Canadian High Arctic. – Appl. Veg. Sci. 4: 115–128.

Lotz, A. (ed.) 2006. Alpine habitat diversity – HABITALP – project report 2002–2006. – Nationalpark Berchtesgaden, Berchtesgaden.

Luccarini, S. et al. 2006. Red deer (*Cervus elaphus*) spatial use in the Italian Alps: home range patterns, seasonal migrations and effects of snow and winter feeding. – Ethol. Ecol. Evol. 18: 127–145.

Mason, T. et al. 2017. The behavioral tradeoff between thermoregulation and foraging in a heat-sensitive species. – Behav. Ecol. 28: 908–918.

Mougel, F. et al. 1997. Nine polymorphic microsatellite loci in the rabbit, *Oryctolagus cuniculus*.– Anim. Gen. 28: 58.

Nathan, R. et al. 2008. A movement ecology paradigm for unifying organismal movement research. – Proc. Natl Acad. Sci. USA 105: 19052–19059.

Paupério, J. and Alves, P. C. 2008. Diet of the Iberian hare (*Lepus granatensis*) in a mountain ecosystem. – Eur. J. Wildl. Res. 54: 571–579.

Phillips, D. M. et al. 1998. Seasonal changes in home-range area and fidelity of martens. – J. Mammal. 79: 180–190.

Rehnus, M. 2013. Der Schneehase in den Alpen. Ein Überlebenskünstler mit ungewisser Zukunft. – Haupt Verlag, Bern, Stuttgart, Wien.

Rehnus, M. and Bollmann, K. 2016. Non-invasive genetic population density estimation of mountainhares (*Lepus timidus*) in the Alps: systematicor opportunistic sampling? – Eur. J. Wildl. Res. 62: 737–747.

Rehnus, M. and Bollmann, K. 2020. Weak habitat segregation between male and female mountain hares (*Lepus timidus*). – Ann. Zool. Fenn. 57: 129–135.

Rehnus, M. et al. 2016. The seasonal tradeoff between food and cover in the Alpine mountain hare (*Lepus timidus*). – Eur. J. Wildl. Res. 62: 11–21.

Rehnus, M. et al. 2018. Alpine glacial relict species losing out to climate change: the case of the fragmented mountain hare population (*Lepus timidus*) in the Alps. – Global Change Biol. 24: 3236–3253.

Rico, C. et al. 1994. Four polymorphic microsatellite loci for the European wild rabbit, *Oryctolagus cuniculus*. – Anim. Gen. 25: 367.

Schenker, L. et al. 2020. Hare's affairs: lessons learnt from a non-invasive genetic monitoring for tracking mountain hare individuals.– Ecol. Evol. in press.

Seccombe-Hett, P. and Turkington, R. 2008. Summer diet selection of snowshoe hares: a test of nutritional hypotheses. – Oikos 117: 1874–1884.

Signer, J. and Balkenhol, N. 2015. Reproducible home ranges (rhr): a new, user-friendly R package for analyses of wildlife telemetry data. – Wildl. Soc. Bull. 39: 358–363.

Sloan, M. A. et al. 2000. Highly reliable genetic identification of individual northern hairy-nosed wombats from single remotely collected hairs: a feasible censusing method. – Mol. Ecol. 9: 1233–1240.

Slotta-Bachmayr, L. 1998. Biologie und Ökologie des Alpenschneehasen (*Lepus timidus varronis* Miller 1901). Verbreitung, Raumnutzung, Aktivität und Habitatwahl in den Hohen Tauern. – Faculty of Natural Sciences, Paris London Univ. Salzburg, p 116.

Surridge, A. K. et al. 1997. Polymorphic microsatellite loci in the European rabbit (*Oryctolagus cuniculus*) are also amplified in other lagomorph species.– Anim. Genet. 28: 302–305.

Switzer, P. V. 1993. Site fidelity in predictable and unpredictable habitats. – Evol. Ecol. 7: 533–555.

Thulin, C.-G. and Flux, J. E. C. 2003. *Lepus timidus* Linnaeus, 1758 – Schneehase. – In: Krapp, F. (ed.), Handbuch der Säugetiere Europas Band, 3/II: Hasenartige Lagomorpha. Aula Publisher, Wiebelsheim, pp. 155–185.

van Moorter, B. et al. 2009. Memory keeps you at home: a mechanistic model for home range emergence. – Oikos 118: 641–652.

Wallner, B. et al. 2001. Non-invasive PCR sexing of rabbits (*Oryctolagus cuniculus*) and hares (*Lepus europeaus*). – Mammal. Biol. 66: 190–192.

Zweifel-Schielly, B. et al. 2009. Habitat selection by an Alpine ungulate: the significance of forage characteristics varies with scale and season. – Ecography 32: 103–113.

Supplementary material (available online as Appendix wlb-00720 at <www.wildlifebiology.org/appendix/wlb-00720>). Appendix 1.