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SHORT COMMUNICATION

Diet niches of the Alpine mountain hare (*Lepus timidus varronis*) and European hare (*Lepus europaeus*) living in coexistence in the Alps

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Abstract
A species' diet niche is shaped by the evolutionary processes of adaptation to the available food resources in its habitat and by competition with ecologically similar species. In the European Alps, Alpine mountain hares (*Lepus timidus varronis*) and European hares (*Lepus europaeus*) occur parapatrically along the elevation gradient and hybridise with each other in overlapping areas. Evidence that the areas of overlap are not stable suggests that interspecific competition between the two congeneric hare species is strong. Competitive exclusion might take place at a fine spatial scale and influence the feeding behaviour of the two hare species. In this study, we investigated diet ecology of Alpine mountain hares, European hares and their hybrids in the Alps in the middle and at the end of the plant vegetation growth period by collecting hare faeces along the altitudinal gradient in Grisons (Switzerland). We performed genetic analysis to identify the hare species and analysed the faeces microscopically to determine dietary composition. Plant components at the level of dicotyledons/monocotyledons, plant family and plant species in faeces of 49 European hares, 16 Alpine mountain hares and 22 hybrids (with discordant nuclear and mitochondrial genetic backgrounds) were identified. Alpine mountain hares used significantly more Ericaceae as food plants than European hares and hybrids. As mountain hares support phenolics in the nutrition better than European hares, our results suggest that the diet of the two lagomorph species are affected by phenolics content in the Alpine ecosystem. Our findings underline the Alpine mountain hare's adaptation to the Alpine ecosystem by using characteristic Alpine vegetation as food plants. The phenolics tolerance and specialist feeding strategy might be a decisive advantage of the Alpine mountain hare in the competition between the two lagomorph species in the Alps.

Keywords Feeding ecology · Brown hare · Lagomorpha · Mitochondrial introgression · Resource partitioning · Epidermal plant fragments

Introduction

Diet might describe a predominant characteristic of the ecological niche of a species (Simberloff and Dayan 1991). Species specialize optimally through adaptation to the food resources available in their habitat (Root 1967; Begon et al. 1999). In addition, competition with ecologically similar species also has an influence on the shaping of the diet niche during evolution (Root 1967; Begon et al. 1999). In the Alps, Alpine mountain hares (*Lepus timidus varronis*) and European hares (*Lepus europaeus*) occur parapatrically along the elevation gradient (Angerbjörn and Schai-Braun 2023; Hackländer 2023). Hybridisation followed by introgression is common in these two lagomorph species in the Alps (Zachos et al. 2010; Schai-Braun et al. 2023). Evidence that the areas of overlap in northern Europe (Thulin 2003; Jansson and Pehrson 2007) and the Alps (Schai-Braun et al. 2021; La Morgia et al. 2023) are not stable indicates that interspecific competition between the two congeneric hare species is strong. Ecological niche theory predicts that two similar and closely related species in sympatry must reduce interspecific competition by partitioning at least one resource (Hutchinson 1959). A spatial separation of the two hare species along the elevation gradient in the Alps has been demonstrated (Schai-Braun et al. 2023). However, competitive exclusion might take place at a fine spatial scale and influence the feeding behaviour of the two hare species. Moreover, hybrids can shape evolutionary processes

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by contributing to both the loss of species or the origin of species (Allendorf et al. 2001; Sakai et al. 2001; Laikre et al. 2010). Studies of food preferences show that Irish mountain hares (*L. t. hibernicus*) living in allopatry with European hares use more grasses and herbs (Wolfe et al. 1996; Dingerkus and Montgomery 2001) than Scottish mountain hares (*L. t. scoticus*) living in sympatry with European hares (Hewson 1962; Hulbert et al. 1996). Wolfe et al. (1996) argued that competitive exclusion by the European hare restricts mountain hare distribution in Ireland. Mountain hares are grazers in summer and browsers in winter (Hulbert et al. 1996). The plant groups used by the Alpine mountain hare are 47.0% gymnosperms, 32.5% graminoids, dwarf shrubs (8.5%), forbs (2.8%) and bryophytes (0.6%) (Rehnus et al. 2013). Alpine mountain hares prefer ligneous plants, whereas grasses are neutrally or negatively selected (Schai-Braun et al. 2020). The European hare selects its food for high-energy content (fat and protein), and avoids fibre (Schai-Braun et al. 2015; Santilli et al. 2024). The diet of European hares inhabiting the alpine zone in Australia is dominated by grasses, herbs and shrubs (Green et al. 2013). About the diet of Alpine mountain hares and European hares living in coexistence along the elevation gradient in the Alps nothing is known. Hence, it is unclear whether competition between both hare species might cause differentiation of diet niches. Moreover, hybrids may influence competition between the two congeneric species by their feeding behaviour, too. The goal of this study was to investigate diet ecology of Alpine mountain hares, European hares and their hybrids in the Alps with particular interest in used plant families and plant species. Our hypotheses were: (1) in the Alps, forage used by Alpine mountain hares and European hares differ in the level of dicotyledons/monocotyledons, with respect to plant family and plant species; (2) hybrids of both hare species use forage similar to both parent species. To test these hypotheses, we collected hare faeces on five transects along the altitudinal gradient in the Alpine canton of Grisons (Switzerland) in the middle and at the end of the plant vegetation growth period. We performed genetic analysis and microscoped hare faecal samples to investigate foraging ecology of the two hare species and their hybrids. The results are relevant to gain insights into the competition between Alpine mountain hares and European hares influencing their feeding behaviour.

Materials and methods

Study area and data collection

The study area comprised five transects between the villages of Susch and Ramosch in Grisons, Switzerland (Susch 46°44′N, 10°4′E, Ramosch 46°49′N, 10°23′E, Supporting Information 1). The study area consisted of forest (39%), grassland (35%), shrubs (19%), Alpine habitat types (4%), watercourse (3%), residential area (< 1%), and agricultural crop land (< 1%). These cover an altitude range between 1,000 and 2,600 m a.s.l. Fresh faecal samples were collected in the year 2019 along the altitudinal gradient. Each transect was searched twice in the middle (1.-13.7.2019) and at the end (2.-11.9.2019) of the plant vegetation growth period. A minimum of two faecal pellets per sample location was placed in a 50-ml bottle filled with ethanol (96%) to distinguish between the two hare species by further genetic analysis. The faeces were collected with gloves to avoid contamination with human DNA. Each sample location was recorded with a GPS device (Garmin GPSMAP 60Cx).

Genetic analysis

DNA was extracted from the faecal pellets using the QIAamp DNA Stool Mini Kit (Qiagen, Valencia, California, USA). A molecular marker (219 bp) of the mitochondrial control region (mtDNA) was amplified using the primers Lmtof1 and LmtNr1 (Palumbi et al. 2002), and sequencing was performed after purification of the amplified samples using the Lmtof1 primer. Short nuclear DNA markers (nDNA) containing species-specific nuclear SNPs were then amplified only in samples for which the mtDNA marker had been successfully amplified. Fragments of SMCX and Albumin nuclear genes were amplified following the procedures described by Melo-Ferreira et al. (2009). Sanger sequencing was performed after purification of amplified products (176 bp for SMCX and 137 bp for Albumin). These fragments of nuclear genes have been shown to present fixed species-specific SNPs in both species (Melo-Ferreira et al. 2009), and thus allow the species diagnosis and detection of hybridization. This analysis, together with the inspection of the mtDNA lineage, also allowed to determine whether there is a discordance between the nuclear and mitochondrial genetic background indicating mtDNA introgression, i.e., hybridisation. Samples of hares with discordance between the nuclear and mitochondrial genetic information were considered as hybrids in our analysis. We also genotyped microsatellites in those samples with successful mtDNA amplification. We used a battery of 16 hare microsatellites (Le2, Le3, Le4, Le6, Le15, Le17, Le19, Le23, Le28, Le30, Le43, Le45, Le46, Le47, Le48 and Le51) developed in the CIBIO/CONCEN laboratory, which revealed to be highly polymorphic and informative for identifying both species and hybrids (Costa et al. 2024). These markers were amplified in three multiplex PCR reactions. The first screening was done with one multiplex, and only those samples that amplified for this first multiplex, were genotyped for the remaining two multiplexes (for a more detailed description of the genetic analysis see Schai-Braun et al. 2024).

Ground vegetation inventory and reference collection

As hares have a potential feeding area during 24 h of about 25 ha (Smith et al. 2004), we took an inventory of all plant species present at the time of faecal sample collection (1.-13.7. and 2.-11.9.2019) within a 282 m buffer around the transects (282 m is the radius of an area of 25 ha). Plant species of the ground vegetation (from 0 to 1 m height) were identified according to Fischer et al. (2008), with plant nomenclature following Lauber et al. (2018a). In the field, the Flora Helvetica App (Version 1.4.6 for Android) was used for species determination (Lauber et al. 2018b). Contemporaneously, a collection of identified epidermal fragments was compiled as reference collection (see Holechek et al. 1982).

Dietary composition

To determine dietary composition, we identified epidermal fragments within the faecal pellets using a microscope (Chapuis 1990; Reichlin et al. 2006) and the previously compiled reference collection of epidermis fragments (Schai-Braun et al. 2020). 1–2 pellets of each sample were dissolved in the sample bag. Samples then were heated in a beaker with a glycerine-water mixture (1:1, 10 ml) for 5–10 min with constant stirring at 80 °C until the sample was semi-homogeneously dissolved. From each sample solution, 5 random aliquots of around 100 µl (~ 2 drops with a 3 ml Pasteur pipette) were pipetted onto a microscope slide and covered with a coverslip. The method for locating epidermal fragments involved systematically traversing the microscope slide. A 20x-40x magnification was suitable for photographing and identifying the vascular plant fragments.

Statistical analyses

All statistical analyses were carried out with the software R 4.3.2 (R Core Team 2023). We used Pearson's chi-squared test to examine the association between the vascular plant fragments of monocotyledons and dicotyledons in the faeces of European hares, Alpine mountain hares and their hybrids ($n = 87$). We used Fisher's exact test to examine the associations between the plant families or plant species identified in the faeces of European hares, Alpine mountain hares and their hybrids ($n = 85$ and $n = 10$, resp.) as expected frequencies were lower than five.

Results

We recorded 65 monocotyledon and 208 dicotyledon plant species in our vegetation inventory of the study area (for further information see Supporting Information 2). A total of 229 faecal pellet samples were collected. From the initially tested faecal pellet samples, a total of 201 (88%) amplified for Cytochrome b. From these 201 samples, 100 (50%) amplified successfully for the SMCX and/or Albumin nuclear genes and/or for the microsatellites. Hence, 55 samples were assigned to the European hare, 19 to the Alpine mountain hare, and 26 samples showed signs of mtDNA introgression (discordance between nuclear and mitochondrial genetic background) indicating signs of hybridisation. Twenty-five faecal samples of introgressed hares had mtDNA of the Alpine mountain hare and nDNA of the European hare and were, accordingly, from backcrossed European hares. One faecal sample of an introgressed hare had mtDNA of the European hare and nDNA of the Alpine mountain hare and was from a backcrossed Alpine mountain hare. None of the hybrids of our study were F1 or F2 hybrids, hence, all hybrids resulted from older hybridisation events. European hare faecal pellets were collected within an altitudinal range of 1225–2281 m a.s.l. (on average 1,600 m +/− 48 SE), Alpine mountain hare within 1941–2270 m a.s.l. (on average 2,149 m +/− 23 SE), and hybrids within 1,140–2,106 m a.s.l. (on average 1,413 m +/− 49 SD, for an overview of the elevation ranges see Supporting Information 3). Plant components in faeces of 49 European hares, 16 Alpine mountain hares and 22 hybrids were successfully analysed (see Supporting Information 4).

Diet composition

Relative magnitude of the plants' epidermis fragments identified in the faeces of Alpine mountain hares, European hares and their hybrids showed different use in a hares' diet (Fig. 1). As an example, we identified more Poaceae in the hares' faeces than other plant families (see Fig. 1c). Both dicotyledon/monocotyledon components ($X^2 = 0.010$, $df = 2$, $p = 0.994$) and plant species components (Fisher's exact test, $p = 1.000$) in the faeces of Alpine mountain hare, European hare and their hybrids were independently associated (Fig. 2a, c). That is, both hare species and their hybrids used dicotyledons and monocotyledons, and *Picea abies* and *Larix decidua* similarly as food, and no significant differences were found. In contrast, plant family components in the faeces of Alpine mountain hare, European hare and their hybrids were dependently associated (Fisher's exact test, $p = 0.012$, Fig. 2b). That means, Alpine mountain hares used significantly more Ericaceae as food plants than European hares and hybrids. Representative species of the family Ericaceae in the study area were common heather (*Calluna vulgaris*), winter heath (*Erica carnea*), rusty-leaved alpenrose (*Rhododendron ferrugineum*), European blueberry (*Vaccinium myrtillus*), bog blueberry (*Vaccinium uliginosum*), and lingonberry (*Vaccinium vitis-idaea*).

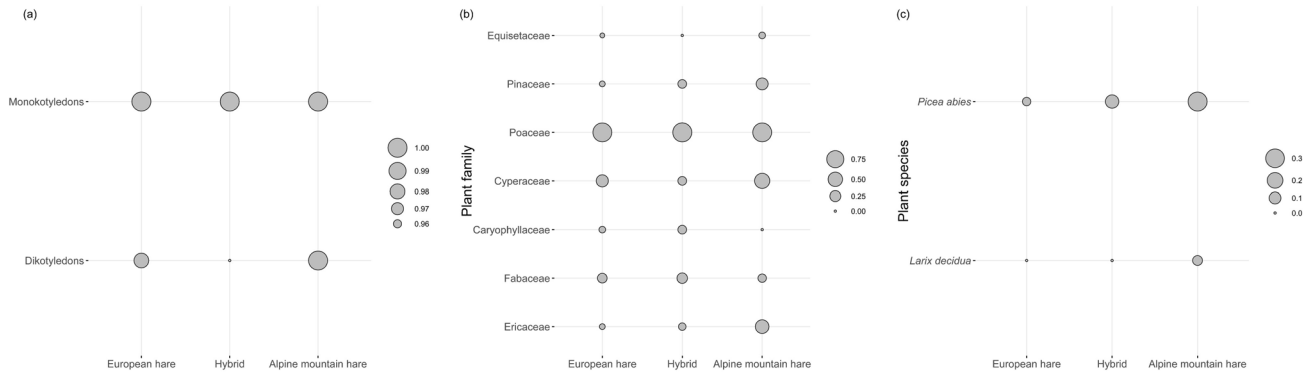

Fig. 1 Contingency table of relative frequencies of **a** dicotyledons and monocotyledons, **b** plant family and **c** plant species components in the faeces of European hares ($n=49$), Alpine mountain hares ($n=16$) and hybrids ($n=22$). The dot size reflects the relative magnitude of the corresponding component. Data was collected in the European Alpine region in Grisons, Switzerland, in the year 2019 within an altitudinal range of 1000–2600 m a.s.l

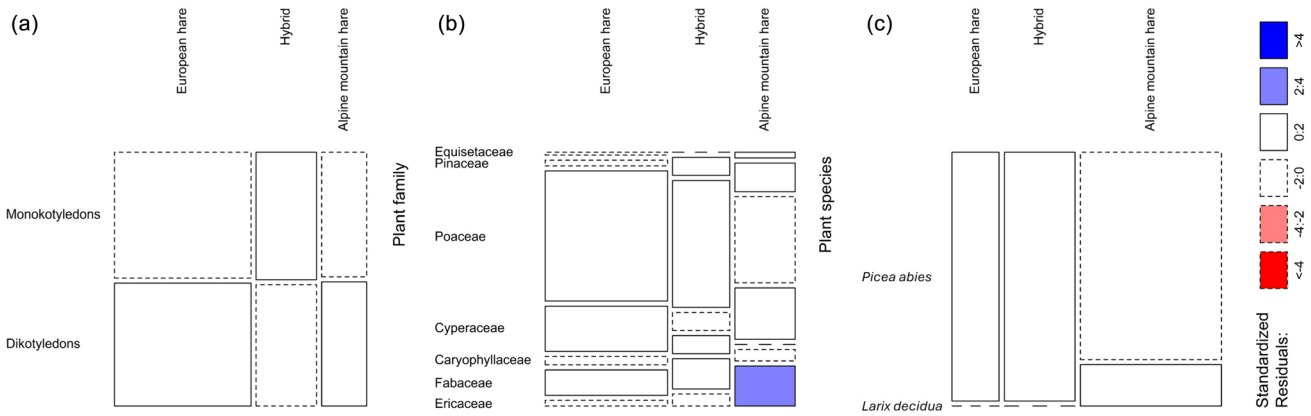

Fig. 2 Contingency table of **a** dicotyledons and monocotyledons, **b** plant family and **c** plant species components in the faeces of European hares ($n=49$), Alpine mountain hares ($n=16$) and hybrids ($n=22$). Blue color indicates that the observed value is higher than the expected value if the data were random, i.e. a significant difference in use as food plant existed. Data was collected in the European Alpine region in Grisons, Switzerland, in the year 2019 within an altitudinal range of 1000–2600 m a.s.l. See text for statistical details Supporting Information

Discussion

Alpine mountain hares in our study used significantly more Ericaceae as food plants than European hares and hybrids, which is in line with the results on Alpine mountain hares in the Austrian Alps selecting the order Ericales (Schai-Braun et al. 2020) as diet. The birch, a plant rich in phenolics, is an important food source in winter to mountain hares (Hyytinen 1974; Rousi et al. 1989; Tahvanainen et al. 1991; Hiltunen 2003) but not European hares (Rödel et al. 2004). Mountain hares sustain phenolics in the nutrition better than European hares (Iason and Palo 1991). Negative effects in herbivores after ingestion of phenolics, e.g. tannins, are caused by their high affinity to proteins. This reduces the digestibility and nutritional quality of the diets (Tahvanainen et al. 1991). Some mammalian species are thought to counteract tannins by secreting tannin-binding salivary proteins (TBSPs) acting as a defence against tannins (Shimada 2006). TBSPs tend to be present in browsing herbivores such as mountain hares, but not in grazing herbivores (Austin et al. 1989; Mole et al. 1990). The lower digestibility of tannin-rich plants could lead to an overestimation of these plants in the diet (Rothman et al. 2009). This might affect the estimation of food selection in ecological studies. It has been argued that this phenolics tolerance is the reason for the mountain hare's distinct use of birch as forage. Both fruits and leaves of plants of the Ericaceae family comprise a high content of phenolic compounds (Ștefănescu et al. 2019).

Hence, our results suggest that the diet of the two lagomorph species are affected by phenolics content also in the Alpine ecosystem. Additionally, our findings underline the Alpine mountain hare's adaptation to the Alpine ecosystem by using characteristic Alpine vegetation as food plants, in comparison to the more generalist feeding strategy of the European hare. The phenolics tolerance and specialist feeding strategy might be a decisive advantage of the Alpine mountain hare in the competition between the two lagomorph species in the Alps. The hybrids' similar diet use to European hares regarding Ericaceae as forage can be well explained that almost all hybrids were backcrossed European hares. This result might be related to the fact that those hybrids have the nuclear background of the European hare, but capture the mitochondria of the mountain hare due to ancestral hybridization as reported in other hare populations and species (e.g., Alves et al. 2008; Melo-Ferreira et al. 2014). We used the same methods for the identification of diet composition, i.e., using a microscope to detect plant species in faeces and comparing the results with a compiled reference collection of plant epidermis of the study area, in the Alps in Grisons, Switzerland, and Vorarlberg, Austria (Schai-Braun et al. 2020). However, in Grisons we were not able to identify plant epidermal fragments to the lower taxonomic rank, i.e., genus and species, as in the study conducted in Vorarlberg. The much lower success of identifying plant fragments in Grisons than in Vorarlberg was due to alterations in ground vegetation sampling methods. In Vorarlberg, the locations where faeces were discovered varied greatly in habitat type, making it easier to apply visual microscopy methods than in Grisons. We strongly recommend using other methods for future studies, e.g., eDNA with microscopy serving as a complementary approach to identify the composition of plant parts (such as seeds, bark, and leaf cells) or DNA metabarcoding analysis to identify diet plants in faeces.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s42991-024-00455-x.

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Author contributions SS and KH conceived the ideas and designed methodology. SS helped collecting data. SS, JQ, and PCA analysed the data. SS led the writing of the manuscript. SS, FF, HJ, KL, PCA, JQ and KH contributed critically to the drafts and gave final approval for publication.

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Declarations

Conflict of interest SS is a subject editor for Mammalian Biology.

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References

Allendorf FW, Leary RF, Spruell P, Wenburg JK (2001) The problems with hybrids: setting conservation guidelines. Trends Ecol Evol 16:613–622. https://doi.org/10.1016/S0169-5347(01)02290-X

Alves PC, Melo-Ferreira J, Freitas H, Boursot P (2008) The ubiquitous mountain hare mitochondria: multiple introgressive hybridization in hares, genus *Lepus*. Philos Trans R Soc Lond B Biol Sci 363:2831–2839. https://doi.org/10.1098/rstb.2008.0053

Angerbjörn A, Schai-Braun SC (2023) Mountain hare *Lepus timidus* Linnaeus, 1758. In: Hackländer K, Zachos FE (eds) Handbook of the mammals of Europe. Springer International Publishing, Cham, pp 1–29. https://doi.org/10.1007/978-3-319-65038-8_12-1

Austin PJ, Suchar LA, Robbins CT, Hagerman AE (1989) Tannin-binding proteins in saliva of deer and their absence in saliva of sheep and cattle. J Chem Ecol 15:1335–1347. https://doi.org/10.1007/BF01014834

Begon M, Harper J, Townsend C (1999) Ecology: individuals, populations and communities. Blackwell Science, Oxford

Chapuis JL (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 Säugetierkd 55:176–185

Costa J, Queirós J, Ballesteros F, Mucci N, Souto J, Silva E, Melo-Ferreira J, Alves PC (2024) Low genetic diversity and shallow population structure in the broom hare, *Lepus castroviejoi* (Lagomorpha: Leporidae). Biol J Linn Soc 141:148–167. https://doi.org/10.1093/biolinnean/blad061

Dingerkus SK, Montgomery W (2001) The diet and landclass affinities of the Irish hare *Lepus timidus hibernicus*. J Zool 253:233–240. https://doi.org/10.1017/S0952836901000206

Fischer M, Oswald K, Adler W (2008) Exkursionsflora für Österreich, Liechtenstein, Südtirol, 3rd edn. Biologiezentrum des Oberösterreichischen Landesmuseums, Linz

Green K, Davis N, Robinson W, McAuliffe J, Good R (2013) Diet selection by European hares (*Lepus europaeus*) in the alpine zone of the Snowy Mountains, Australia. Eur J Wildl Res 59:693–703

Hackländer K (2023) European hare *Lepus europaeus* Pallas, 1778. In: Hackländer K, Zachos FE (eds) Handbook of the mammals

of Europe. Springer International Publishing, Cham, pp 1–36. https://doi.org/10.1007/978-3-319-65038-8_9-1
Hewson R (1962) Food and feeding habits of the mountain hare *Lepus timidus scoticus*, Hilzheimer. Proc Zool Soc Lond 139:515–526
Hiltunen M (2003) Feeding intensity of mountain hares (*Lepus timidus*) during winter in Finland. Mamm Biol 68:48–52. https://doi.org/10.1078/1616-5047-00061
Holechek J, Vavra M, Pieper R (1982) Botanical composition determination of range herbivore diets: a review. J Range Manage 35:309–315
Hulbert IAR, Iason G, Racey PA (1996) Habitat utilization in a stratified upland landscape by two Lagomorphs with different feeding strategies. J Appl Ecol 33:315–324
Hutchinson GE (1959) Homage to Santa Rosalia or why are there so many kinds of animals? Am Nat 93:145–159. https://doi.org/10.1086/282070
Hyytinen T (1974) Winter nutrition of the brown hare (*Lepus europaeus* Pallas) in western central Finland. Suomen Riista 25:42–49
Iason G, Palo R (1991) Effects of birch phenolics on a grazing and a browsing mammal: a comparison of hares. J Chem Ecol 17:1733–1743
Jansson G, Pehrson Å (2007) The recent expansion of the brown hare (*Lepus europaeus*) in Sweden with possible implications to the mountain hare (*L. timidus*). Eur J Wildl Res 53:125–130. https://doi.org/10.1007/s10344-007-0086-2
La Morgia V, Martini I, Tosatto E, Mazza E, Bertolino S, Santovito A (2023) Global warming is promoting the rapid invasion of the mountain hare range by the European hare in the Alps. Biodivers Conserv 32:3875–3891. https://doi.org/10.1007/s10531-023-02664-1
Laikre L, Schwartz MK, Waples RS, Ryman N (2010) Compromising genetic diversity in the wild: unmonitored large-scale release of plants and animals. Trends Ecol Evol 25:520–529. https://doi.org/10.1016/j.tree.2010.06.013
Lauber K, Wagner G, Gygax A (2018a) Flora helvetica. Haupt, Berne
Lauber K, Wagner G, Gygax A (2018b) Flora helvetica app (iOS and android). Haupt, Berne. www.flora-helvetica.ch
Melo-Ferreira J, Alves PC, Freitas H, Ferrand N, Boursot P (2009) The genomic legacy from the extinct *Lepus timidus* to the three hare species of Iberia: contrast between mtDNA, sex chromosomes and autosomes. Mol Ecol 18:2643–2658. https://doi.org/10.1111/j.1365-294x.2009.04221.x
Melo-Ferreira J, Farelo L, Freitas H, Suchentrunk F, Boursot P, Alves PC (2014) Home-loving boreal hare mitochondria survived several invasions in Iberia: the relative roles of recurrent hybridisation and allele surfing. Heredity 112:265–273. https://doi.org/10.1038/hdy.2013.102
Mole S, Butler LG, Iason G (1990) Defense against dietary tannin in herbivores: a survey for proline rich salivary proteins in mammals. Biochem Syst Ecol 18:287–293. https://doi.org/10.1016/0305-1978(90)90073-O
Palumbi S, Martin A, Romano S, McMillan W, Stice L, Grabowski G (2002) The simple fool's guide to PCR, Honolulu
R Core Team (2023) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.R-project.org
Rehnus M, Marconi L, Hackländer K, Filli F (2013) Seasonal changes in habitat use and feeding strategy of the mountain hare (*Lepus timidus*) in the Central Alps. Hystrix 24:161–165. https://doi.org/10.4404/hystrix-24.2-4703
Reichlin T, Klansek E, Hackländer K (2006) Diet selection by hares (*Lepus europaeus*) in arable land and its implications for habitat management. Eur J Wildl Res 52:109–118. https://doi.org/10.1007/s10344-013-0723-x
Rödel HG, Völkl W, Kilias H (2004) Winter browsing of brown hares: evidence for diet breadth expansion. Mamm Biol 69:410–419. https://doi.org/10.1078/1616-5047-00163
Root RB (1967) The niche exploitation pattern of the blue-gray gnatcatcher. Ecol Monogr 37:317–350. https://doi.org/10.2307/1942327
Rothman JM, Dusinberre K, Pell AN (2009) Condensed tannins in the diets of primates: a matter of methods? Am J Primatol 71:70–76. https://doi.org/10.1002/ajp.20623
Rousi M, Tahvanainen J, Uotila I (1989) Inter- and intraspecific variation in the resistance of winter-dormant birch (*Betula* spp.) against browsing by the mountain hare. Ecography 12:187–192. https://doi.org/10.1111/j.1600-0587.1989.tb00837.x
Sakai AK, Allendorf FW, Holt JS, Lodge DM, Molofsky J, With KA, Baughman S, Cabin RJ, Cohen JE, Ellstrand NC, McCauley DE, O'Neil P, Parker IM, Thompson JN, Weller SG (2001) The population biology of invasive species. Annu Rev Ecol Syst 32:305–332. https://doi.org/10.1146/annurev.ecolsys.32.081501.114037
Santilli F, Viviano A, Mori E (2024) Dietary habits of the European brown hare: summary of knowledge and management relapses. Ethol Ecol Evol 36:21–40. https://doi.org/10.1080/03949370.2023.2213200
Schai-Braun SC, Reichlin T, Ruf T, Klansek E, Tataruch F, Arnold W, Hackländer K (2015) The European hare (*Lepus europaeus*): A picky herbivore searching for plant parts rich in fat. PLoS ONE 10:e0134278. https://doi.org/10.1371/journal.pone.0134278
Schai-Braun SC, Lapin K, Bernhardt KG, Alves PC, Hackländer K (2020) Effect of landscape type, elevation, vegetation period, and taxonomic plant identification level on diet preferences of Alpine mountain hares (*Lepus timidus varronis*). Eur J Wildl Res 66:57. https://doi.org/10.1007/s10344-020-01398-7
Schai-Braun SC, Jenny H, Ruf T, Hackländer K (2021) Temperature increase and frost decrease driving upslope elevational range shifts in Alpine grouse and hares. Glob Change Biol 27:6602–6614. https://doi.org/10.1111/gcb.15909
Schai-Braun SC, Schwienbacher S, Smith S, Hackländer K (2023) Coexistence of European hares and Alpine mountain hares in the Alps: what drives the occurrence and frequency of their hybrids? J Zool 320:214–225. https://doi.org/10.1111/jzo.13067
Schai-Braun SC, Cybulska N, Filli F, Jenny H, Queirós J, Alves PC, Hackländer K (2024) Competition between sympatric hare species in the Alps is boostered by climate change and hybridisation. Eur J Wildl Res 70:83. https://doi.org/10.1007/s10344-024-01830-2
Shimada T (2006) Salivary proteins as a defense against dietary tannins. J Chem Ecol 32:1149–1163. https://doi.org/10.1007/s10886-006-9077-0
Simberloff D, Dayan T (1991) The guild concept and the structure of ecological communities. Annu Rev Ecol Syst 22:115–143. https://doi.org/10.1146/annurev.es.22.110191.000555
Smith RK, Jennings NV, Robinson A, Harris S (2004) Conservation of European hares *Lepus europaeus* in Britain: is increasing habitat heterogeneity in farmland the answer? J Appl Ecol 41:1092–1102. https://doi.org/10.1111/j.0021-8901.2004.00976.x
Ștefănescu BE, Szabo K, Mocan A, Crişan G (2019) Phenolic compounds from five Ericaceae species leaves and their related bioavailability and health benefits. Molecules 24:2046. https://doi.org/10.3390/molecules24112046
Tahvanainen J, Niemelä P, Henttonen H (1991) Chemical aspects of herbivory in boreal forest - feeding by small rodents, hares, and cervids. In: Palo T, Robbins C (eds) Plant defenses against mammalian herbivory. CRC, Boca Raton, pp 115–131
Thulin CG (2003) The distribution of mountain hares *Lepus timidus* in Europe: a challenge from brown hares *L. europaeus*? Mammal Rev 33:29–42. https://doi.org/10.1046/j.1365-2907.2003.00008.x

Wolfe A, Whelan J, Hayden TJ (1996) The diet of the mountain hare (*Lepus timidus hibernicus*) on coastal grassland. J Zool 240:804–810. https://doi.org/10.1111/j.1469-7998.1996.tb05327.x

Zachos FE, Slimen HB, Hackländer K, Giacometti M, Suchentrunk F (2010) Regional genetic in situ differentiation despite phylogenetic heterogeneity in Alpine mountain hares. J Zool 282:47–53. https://doi.org/10.1111/j.1469-7998.2010.00710.x

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