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ORIGINAL ARTICLE

Foraging ecology of Alpine mountain hares and European hares in the Alps: is competition about food a driving force in overlapping elevations?

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Abstract

The Alpine mountain hare (*Lepus timidus varronis*) and the European hare (*Lepus europaeus*) live parapatrically along the elevation gradient in the Alps with areas of overlap. Indications suggest competition between the two lagomorph species in overlapping areas. Resource partitioning in form of feeding niche differentiation may reduce competition and enable coexistence. The two hare species hybridise and produce fertile hybrids. To examine foraging behaviour of Alpine mountain hares, European hares and their hybrids in the Alps with particular interest in indications of competition between the two lagomorph species, we performed genetic analysis of hare faecal samples collected on five transects along the altitudinal gradient in the Alps in Grisons (Switzerland) at the middle and the end of the vegetation growth period in the year 2021. We then investigated visually foraging ecology using Fourier-Transform Infrared Spectroscopy (FTIRS). We recorded 32 European hares, 50 Alpine mountain hares, and 18 hybrids. Foraging behaviour of the Alpine mountain hares was different from foraging behaviour of European hares and hybrids. Alpine mountain hares displayed a specialist's foraging behaviour, whereas European hares and hybrids a generalist's foraging behaviour. Some Alpine mountain hares inhabiting overlapping elevations with European hares showed feeding niche differentiation, whereas others showed similar feeding behaviour as European hares suggesting competition between the two species about food. Our study underlines that European hares living in the Alps might be a competitor to the Alpine mountain hare. As a specialist, the Alpine mountain hare will be susceptible to future environmental change due to climate change.

Keywords Brown hare · Congeneric · Diet breadth · Foraging ecology · Spectral signals · Lagomorpha

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Introduction

Stable coexistence of species requires that species possess ecologically different niches, to that they can avoid or reduce interspecific competition for essential resources (Hardin 1960). Two related and resembling species in sympatry should minimize interspecific competition by partitioning resources according to the ecological niche theory (Hutchinson 1959). Spatial separation (birds: Holmes & Robinson 1988; mammals: Rakotondranary et al. 2011) or temporal separation (mammals: Thorén et al. 2011) may explain the coexistence of different taxa. As observed in various sympatric species, feeding niche differentiation may enable the coexistence of these taxa (e.g.: reptiles: Pianka 1973; birds: Holmes & Robinson 1988; mammals: Thorén et al. 2011). Diet and habitat designate a dominant aspect of a species' ecological niche (Simberloff and Dayan 1991). Diet can be responsible for species evolution (Price et al. 2012; Cantalapiedra et al. 2014) and distribution range (Kissling et al. 2009, 2012). The European hare (*Lepus europaeus*) and the Alpine mountain hare (*Lepus timidus varronis*) occur parapatrically in the Alps along the elevation gradient with areas of overlap (Schai-Braun et al. 2021). The Alpine mountain hare inhabits elevations between 800 and 4,000 m above sea level (a.s.l.) (Angerbjörn and Schai-Braun 2023), whereas the European hare has been observed up to 2,800 m a.s.l. (Hackländer 2023). Evidence that areas of overlap in northern Europe (Thulin 2003; Jansson and Pehrson 2007) and in the Alps (Schai-Braun et al. 2021, 2023) are not stable suggests that interspecific competition between the two congeneric hare species may be strong. Although the congeneric European hare and Alpine mountain hare are ecologically similar, the two lagomorph species have evolved distinctly different ecological traits. European hares are generalists inhabiting various habitats generally in lowland areas (Hackländer 2023), whereas Alpine mountain hares are well adapted to Alpine environments with cold and snowy winters (Angerbjörn and Schai-Braun 2023). Accordingly, also the feeding ecology of the two lagomorph species differ. The European hare preferers weeds and grasses (Reichlin et al. 2006), and selects its food for high-energy content (fat and protein), and avoids fibre (Schai-Braun et al. 2015). Mountain hares are grazers in summer and browsers in winter (Hulbert et al. 1996), and prefer ligneous plants, whereas grasses are neutrally or negatively selected (Schai-Braun et al. 2020). Allopatric mountain hares in Ireland eat much more grasses and herbs (Wolfe et al. 1996; Dingerkus and Montgomery 2001) than mountain hares that live in sympatry with European hares (Hewson 1962; Hulbert et al. 1996). Consequently, Wolfe et al. (1996) argued that the mountain hare is primarily a grazing animal and competitive exclusion by the European hare may restrict mountain hare feeding behaviour and distribution.

Plant composition changes along the elevation gradient (Körner 2003; Sundqvist et al. 2013) and plant diversity decreases with increasing elevation in the Alps (Theurillat et al. 2003). Thus, availability of food plants for hares changes along the elevation gradient. Accordingly, we expect foraging ecology of the two lagomorph species in the Alps to differ as, firstly, they inhabit different elevation ranges with different available plant species along the elevation gradient and, secondly, due to their dissimilar adaptation to the Alpine environment. However, in overlapping areas foraging ecology of the two lagomorph species is not easily predictable. Plant availability is the same for the two hare species at the same elevation. Hence, the two lagomorph species might feed similarly on available plant species and display a similar foraging behaviour at the same elevation. On the other hand, foraging behaviour might show differences between the two lagomorph species in overlapping areas (i.e., at the same elevation) in order to reduce strong interspecific competition by feeding niche differentiation. Accordingly, foraging ecology of the two lagomorph species may differ in areas of overlapping distribution.

As the European hare is a generalist and the Alpine mountain hare a specialist, diet breadth is predicted to be larger in European hares than in Alpine mountain hares. European hares and mountain hares hybridise with each other and fertile hybrids result from hybridisation events (Lönnberg 1905). In general, hybrids are morphologically and ecologically intermediates of their parent species (Grant and Grant 1996; Hatfield and Schluter 1999; Lönnberg 1905). Thus, diet breadth of hybrids is assumed to be in between of the European hare's and the Alpine mountain hare's diet breadth. The vegetation growth period in the Alps is much shorter than in lowland areas (Calanca and Holzkämper 2010). Diet breadth of Alpine mountain hare was greater at the beginning than at the end of the vegetation growth period (Schai-Braun et al. 2020), whereas about the diet breadth of European hares living in the Alps nothing is known. As a generalist, the European hare is probably poorly adapted to the short Alpine vegetation growth period and might have larger diet breadths than Alpine mountain hares in order to meet daily energetic requirements at the end of the vegetation growth period.

Fourier-transform infrared spectroscopy (FTIRS) is used to obtain an infrared spectrum of absorption or emission of a material by collecting high-resolution spectral data over a wide spectral range. FTIRS is a promising approach to explore variation in food choice of wildlife species by means of non-invasively gained faecal samples. On the one hand, FTIRS yields characteristic spectral fingerprints for various food plants and plant parts (Nopp-Mayr et al. 2020). On the

other hand, diverse foraging regime of wild-living animals are reflected by spectral signals and, thus, can be compared to each other using FTIRS (Nopp-Mayr et al. 2020).

The goal of this study was to investigate foraging ecology of Alpine mountain hares, European hares and their hybrids in the Alps with particular interest in indications of competition between the two lagomorph species. Our hypotheses were: (1) foraging behaviour of the Alpine mountain hare is different of foraging behaviour of the European hare in the Alps, whereas foraging behaviour of hybrids shows similar aspects to both parent species; (2) both hare species display a differing foraging behaviour in overlapping areas in order to reduce interspecific competition by feeding niche differentiation; (3) the European hare, a generalist, exhibits a greater diet breadth than hybrids, and hybrids a greater diet breadth than the Alpine mountain hare, a specialist; (4) diet breadth of European hares at the end of the vegetation growth period is greater than diet breadth of Alpine mountain hares. To test these hypotheses, we performed genetic analysis of hare faecal samples collected on five transects along the altitudinal gradient in the Alps in Grisons (Switzerland) at the middle and the end of the vegetation growth period in the year 2021 to identify whether pellets derived from European hares, Alpine mountain hares, or their hybrids. We then investigated visually foraging ecology of the two hare species and their hybrids using FTIRS.

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, Supplementary Information Fig. 1). The study area consisted of grassland (57%), forest (31%), shrubs (5%), rock (3%) residential area (2%), watercourse (1%), ruderal sites (1%), agricultural crop land (< 1%), and wetlands (< 1%) (Price et al. 2021). The transects cover an altitude range between 1,000 and 2,600 m a.s.l. Faecal samples were collected in the year 2021 along the altitudinal gradient. Each transect was searched twice at the middle of the vegetation growth period (3-11.7.2021) and at the end of the vegetation growth period (20-27.8.2021). Faeces were placed in a 50-ml bottle filled with Silica for the genetic analysis. Each sample location was recorded with a GPS device (Garmin GPSMAP 60Cx) and consisted of a minimum of two pellets. The faeces were collected with gloves to avoid contamination with human DNA.

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

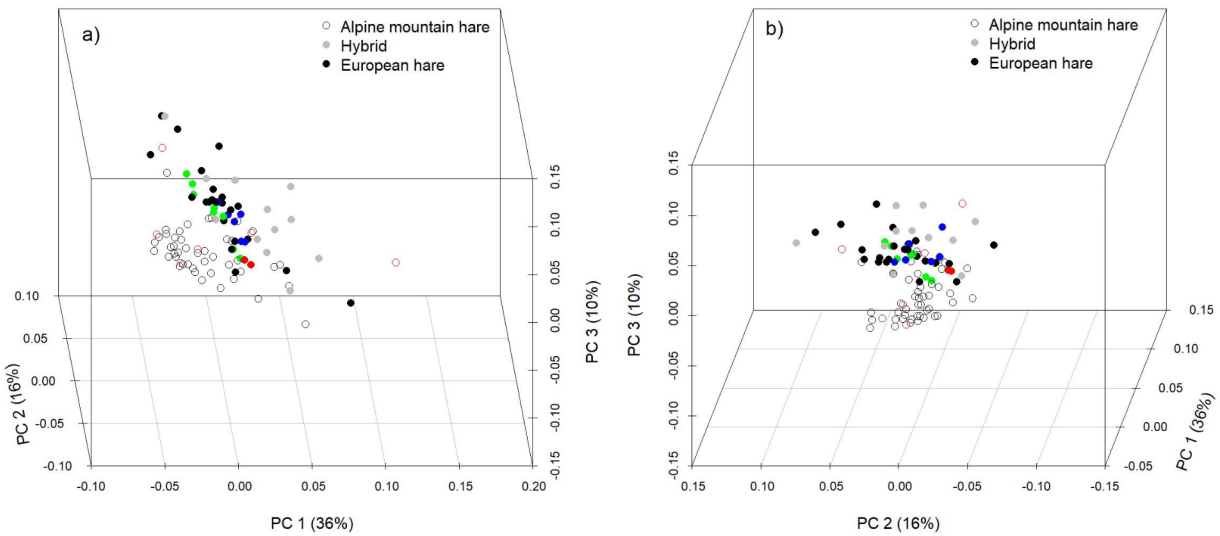

Fig. 1 Scores' plots Scores' plots of a PCA based on FTIR spectra of hare faeces (European hares: $n = 32$, Alpine mountain hares: $n = 50$, hybrids: $n = 18$) rotated with angles of (**a**) 100° and (**b**) 250°. Coloured points indicate faeces collected in overlapping areas (red = European hares at especially high elevations, i.e. 2,340 and 2,345 m a.s.l., green = European hares, blue = hybrids, white with red border = Alpine mountain hares). Numbers in brackets represent the amount of explained variability in spectra on the first three PCA axes

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 speciesspecific 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 determination of mtDNA introgression, i.e., hybridisation. Samples of hares with detected hybridisation respectively introgression are referred to as hybrids in the following. 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. 2023). 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.

Table 1 Elevation The elevation range of faeces of the Alpine mountain hare ($n = 50$), the European hare ($n = 32$) and their hybrids ($n = 18$) collected along the altitudinal gradient in Grisons in the year 2021

Elevation range (m a.s.l.)	Alpine mountain hare	Hybrid	European hare
2,500	1	-	-
2,400	1	-	-
2,300	11	-	2
2,200	6	-	-
2,100	14	-	-
2,000	11	1	-
1,900	4	2	2
1,800	2	3	6
1,700	-	-	4
1,600	-	1	7
1,500	-	3	4
1,400	-	1	4
1,300	-	7	3
Sum	50	18	32

Sample preparation

Of each sample 1–3 (mean: 1.47) pellets were dried in a drying oven at 80 °C for 24 h, a method proven not to influence spectral characteristics (Duboc et al. 2016). The dried samples were ground with a vibratory disc mill (Fritsch® Pulverisette 9) for 60–80 s and 1000 rotations per minute. In case of very low quantities, the samples were manually ground with a mortar, yielding a homogenous powder that allowed for reliable measurements of Fourier-Transform Infrared (FTIR) spectra.

FTIR spectroscopy

FTIR spectra were recorded on a Bruker ® FTIR spectrometer (Tensor 27) in the Attenuated Total Reflectance (ATR) mode. At a spectral resolution of 4 cm^{-1}, 32 scans were collected. Five to ten replicates of each sample were performed. The replications were vector-normalized and averaged with the integrated software OPUS ® 7.2. That means, for each faecal sample we got a FTIR spectrum that was the results of the average of several replica.

Statistical analyses

Principal Component Analysis (PCA) was performed to compare the spectra of the different faecal samples with The Unscrambler ® X 10.1 software. Graphical display was carried out using the software R 4.3.1 (R Core Team 2023) using the R package scatterplot3d (Ligges and Mächler 2003) to show the influencing factors (i.e., European hare vs. Alpine mountain hare vs. hybrids; Esbensen 2012). Three dimensions (3D) graphs were rotated using different angles to investigate differences between European hare, Alpine mountain hare, and hybrids.

Results

A total of 243 faecal pellet samples were collected in the year 2021. Of these, 159 were collected at the middle, and 84 at the end of the vegetation growth period. From the initially tested faecal pellet samples, a total of 227 (93%) amplified for Cytochrome b. From these 227 samples, 100 (44%) amplified successfully for the SMCX and/or Albumin nuclear genes and/or for the microsatellites (see Supplementary Information Table 1). Hence, 32 samples were assigned to the European hare, 50 to the Alpine mountain hare, and 18 samples showed signs of mtDNA introgression, respectively hybridisation. All introgressed individuals had mtDNA of the Alpine mountain hare and nDNA of the European hare and were, accordingly, backcrossed

European hares. European hare faecal pellets were collected within an altitudinal range of 1,372–2,345 m a.s.l. (mean = 1,704.31 m a.s.l., SE = 42.17 m a.s.l.), Alpine mountain hare within 1,806–2,570 m a.s.l. (mean = 2,159.82 m a.s.l., SE = 22.61 m a.s.l.), and hybrids within 1,352–2,004 m a.s.l. (mean = 1,605.06 m a.s.l., SD = 57.64 m a.s.l., for an overview of the elevation ranges see Table 1).

Foraging behaviour

The first three principal components captured most of the variation (PC1 36%, PC2 16%, PC3 10%). Results of the PCA displayed with a 3D plot and rotated with angles of 100° and 250° revealed a distinct separation of Alpine mountain hare from European hare and hybrid regarding FTIR patterns of faecal pellets (Fig. 1). European hare and hybrid faeces in the plot were intermingled without discernible separation. Note that also some single Alpine mountain hare faeces were positioned within the hybrid and European hare point cloud.

Feeding niche in overlapping elevations

In overlapping elevations with the Alpine mountain hare, all European hare faeces including the two samples collected at a very high elevation (2,340 m a.s.l. and 2,345 m a.s.l.) and all hybrid faeces were within the hybrid and European hare point cloud. Half of the Alpine mountain hare faeces collected in the overlapping elevations with the European hare were within their point cloud (1,873 m a.s.l., 1920 m a.s.l., and 1963 m a.s.l.), whereas the other half was in the European and hybrid point cloud (1,806 m a.s.l., 1907 m a.s.l., and 1968 m a.s.l.).

Diet breadth

The position of Alpine mountain hare faeces was visually closer together within a small heap than the position of hybrid and European hare faeces.

Effect of the vegetation growth period

When visually investigating data separated by season, the same separation was discernible but point clouds at the middle were more compact than at the end of the vegetation growth period (Figs. 2 and 3). At the end of the vegetation growth period, the Alpine mountain hare point cloud and the European hare and hybrid point cloud exhibited a similar loose distribution. Note that sample size was quite low at the end of the vegetation growth period ($n = 31$).

Discussion

The distribution of faeces along the altitudinal gradient showed that single European hares are inhabiting high elevations in the Alps but most are inhabiting elevations below 2,000 m a.s.l. This is in line with the findings of a

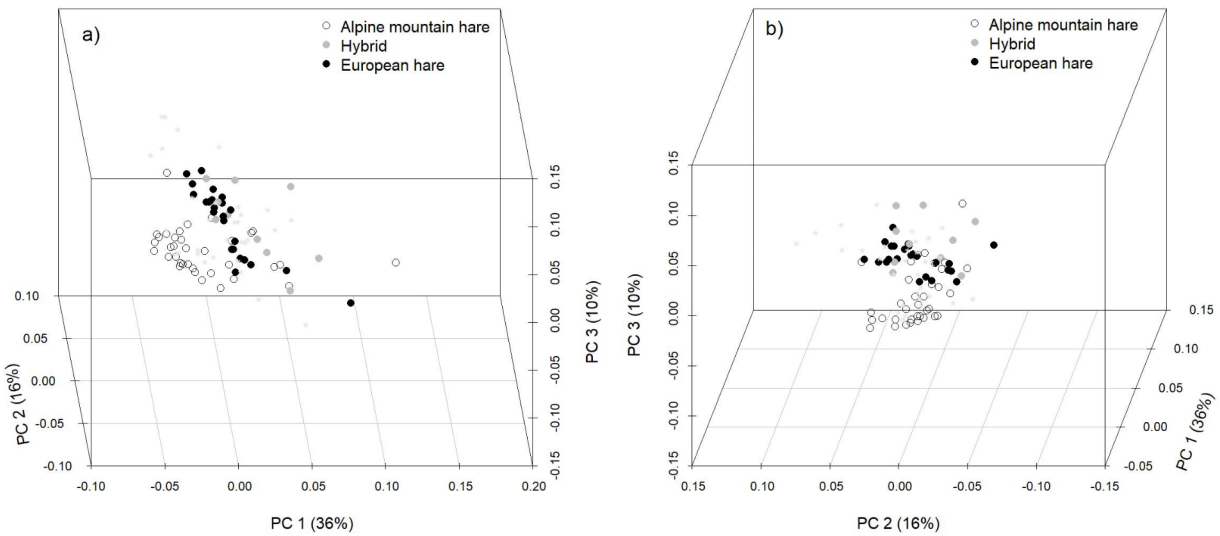

Fig. 2 PCA Scores' plot middle of the vegetation growth period Scores' plots of a PCA based on FTIR spectra of hare faeces (European hares: $n = 24$, Alpine mountain hares: $n = 35$, hybrids: $n = 10$) rotated with angles of **a**) 100° and **b**) 250° collected at the middle of the vegetation growth period. Small light grey asterisks represent the scores' plots of hare faeces collected at the end of the vegetation growth period ($n = 31$). Numbers in brackets represent the amount of explained variability in spectra on the first three PCA axes

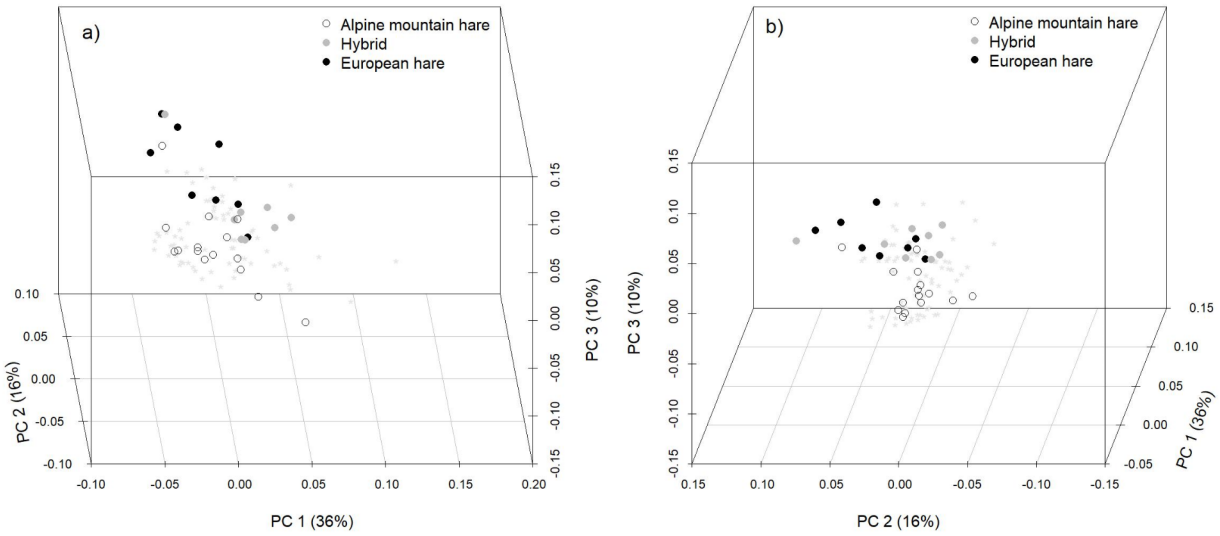

Fig. 3 PCA Scores' plot end of the vegetation growth period Scores' plots of a PCA based on FTIR spectra of hare faeces (European hares: $n=8$, Alpine mountain hares: $n=15$, hybrids: $n=8$) rotated with angles of **a**) 100° and **b**) 250° collected at the end of the vegetation growth period. Small light grey asterisks represent the scores' plots of hare faeces collected at the middle of the vegetation growth period ($n=69$). Numbers in brackets represent the amount of explained variability in spectra on the first three PCA axes

study conducted in the Swiss National Park (Schenker et al. 2020). None of the hybrids of our study were F1 or F2 hybrids, hence, all hybrids resulted from older hybridisation events. As both hare species live parapatrically in the study area, we hypothesise that the hybridisation events of our hybrids might have taken place in the last decades and might represent contemporary hybridisation. Hybrids were not recorded only in an altitudinal range between the range of Alpine mountain hares and European hares but most numerously at low elevations together with European hares. We explained our results of FTIR spectra by the hares' diet composition. It might be possible that also differences in digestion processes between the two species influenced the spectra.

Foraging behaviour

The distinct separation in chemical composition and thus in spectral signals of Alpine mountain hare faeces from European hare and hybrid faeces indicates differences in foraging behaviour between Alpine mountain hares and European hares/hybrids inhabiting the Alps. The similarities between European hares and hybrids may be explained by the fact that hybrids were all backcrossed European hares and from older hybridisation events. Dietary overlap in lagomorph species has been shown to be higher than expected in specialist and generalist species (Crowell et al. 2018). Dietary overlap was also discernible in single Alpine mountain hare faeces of our study. This might indicate that resource competition is going on between the two species. Resource competition may be caused in areas where availability of specific food plants of the specialist is low (Crowell et al. 2018) or in unstable areas of overlap.

Feeding niche differentiation in overlapping elevations

All European hares in overlapping elevations with Alpine mountain hares expressed foraging behaviour of the own species and not of the species competing with. This might indicate that European hares in the Alps reduced interspecific competition by feeding niche differentiation. However, the foraging behaviour of half of the Alpine mountain hares in overlapping elevations with the European hare displayed feeding niche differentiation, whereas the other half showed similar feeding behaviour as European hares. We interpret our results that some Alpine mountain hares seemed to reduce potential interspecific competition but others' feeding behaviour suggested potential competition going on with European hares about food. Furthermore, our results may indicate that the plant composition of the elevation has less impact on the foraging behaviour in the two lagomorph species than interspecific competition. In case of feeding niche differentiation, resource partitioning might take place based on consumption of different parts of the same food (e.g., leaves, stems) or based on chemical characteristics of

food plants. Food selection of the two hare species might respond to chemical properties of food plants. As an example, it is known that mountain hares support phenolics in the nutrition better than European hares (Iason and Palo 1991) and, thus, diet of the two lagomorph species might differ in phenolics content. The hybrids as backcrossed European hares fitted well into the European hares' foraging behaviour including feeding niche differentiation with Alpine mountain hares. Note that we recorded hybrids in three out of five transects and Alpine mountain hares in four out of five transects (see Supplementary Information Table 1). However, we were not able to divide the data by transect due to faecal sample size.

Diet breadth

A more diverse feeding regime of European hares and hybrids compared to Alpine mountain hares became visually evident. Accordingly, our results show that Alpine mountain hares are specialists in their foraging behaviour, whereas European hares are generalists in their foraging behaviour. This is in line with a study on diet niche partitioning of a specialist and generalist lizard species living in sympatry (Vitt and Carvalho 1995). Hybrids being backcrossed European hares had a similar diet breadth to European hares. Consequently, hybrids' diet breadth was not in between European hares and Alpine mountain hares as predicted in hypothesis (3).

Effect of the vegetation growth period

Season, i.e., the phenology of availability of distinct plant species, did not affect the different foraging behaviour of Alpine mountain hares and of European hares and hybrids as the distinct separation was still clearly visible on the graphs when dividing the data in middle and end of vegetation growth period. Dry conditions in summer might affect diet quality for hares inhabiting the Alps. Hence, competition about food between the two hare species may also be going on during the vegetation growth period. Especially, female hares nursing leverets are depending on high quality food (Hackländer et al. 2002). In contradiction to hypothesis (4), the loose distribution of the point clouds at the end of the vegetation growth period suggests that all hares had to enlarge their diet breadth in order to meet daily energetic requirements at the end of the vegetation growth period and not only European hares. As a conclusion, the European hare, a generalist, seems not to be less well adapted to the short Alpine vegetation growth period than the Alpine mountain hare, a specialist during the vegetation growth period. Nevertheless, the situation of competition between the two hare species might be different when snow is impeding foraging. Moreover, snow occurrence will have an influence on the competition by having most probably a distinct effect on predation on these two lagomorph species in the Alps.

Conclusion and future prospects

As a conclusion, our study underlines that European hares living in the Alps might be a strong competitor to the Alpine mountain hare due to its generalist feeding strategy which enables this species to adapt well also to the Alpine environment. As a specialist with limited feeding regime, the Alpine mountain hare will be highly susceptible to future environmental change due to climate change (Acevedo et al. 2012; Verde Arregoitia et al. 2015). Moreover, climate change may compromise specialists such as the Alpine mountain hare adapted to cold conditions, by competitive interactions with the European hare (Acevedo et al. 2012). This means that for the Alpine mountain hare, climate change might reinforce competition with the European hare.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s13364-024-00765-y.

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

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Data availability Data is available as Supplementary Information.

Declarations

Ethical approval The study complies with the current laws of Switzerland.

Conflict of interest The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this manuscript.

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