Weak habitat segregation between male and female mountain hares (*Lepus timidus*)

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Sexual habitat segregation affects animal distribution and can lead to different life-histories across sexes. We investigated sex-related habitat segregation in the mountain hare (*Lepus timidus*) during the early-breeding and post-reproductive periods at the macro- (home range) and microscale (pellet location) by using pellet data sets from a non-invasive genetic population monitoring in the Swiss Alps. The data sets comprise six years (2014–2019) of sampling and include 119 individuals (70 males, 49 females). At the macroscale, the sex-related habitat segregation was weak in both periods but higher in the early-breeding period as compared with that in the post-reproductive period. Home ranges of females contained a higher proportion of forest stands in the early-breeding period. At the microscale, the sex-related habitat segregation for habitat characteristics was low in both periods. We conclude that habitat segregation between male and female mountain hares is weak during the early-breeding and post-reproductive periods.

Introduction

Sexual differences in habitat use are omnipresent in vertebrates and affect animal distribution and survival (Ruckstuhl *et al.* 2000, Isaac 2005) as well as life histories (Ostfeld 1990, Wauters *et al.* 1992, Hoffman *et al.* 2008). Sex-related habitat segregation is frequently observed in species with sexual dimorphism such as e.g., many ungulates in which males are clearly larger than females (Mysterud 2000, Ruckstuhl *et al.* 2000). Hypotheses on sexual segregation exist in polygynous, dimorphic ungulates including sexual differences in predator avoidance strategies, nutrient requirements, scramble competition, and social preferences (Main *et al.* 1996) that can

lead to different habitat use of males and females (Mysterud 2000). Sexual habitat segregation is not well understood in solitary, monomorphic species like the *Lepus* species. It can, however, be expected in these species because sexes show different behaviour during the mating season (Litvaitis 1990). Since females are dominant (Graf 1985) they use habitats with higher food availability (Litvaitis 1990). Both sexes also differ in diet composition, especially during the high-breeding period (Hulbert *et al.* 2001). However, both sexes have similar ecological needs regarding cover and protection in the early-breeding period (Zaccaroni *et al.* 2009).

The mountain hare (*Lepus timidus*) is a suitable model species to study the effects of sex-

related differences in physiological requirements on the habitat segregation of a monomorphic *Lepus* species: Male and female mountain hares are mostly solitary and have similar body sizes with an average weight between 2.2 and 2.8 kg in the Alps (Thulin *et al.* 2003, Rehnus 2013). During the early-breeding period, glucocorticoid metabolite levels are higher in females than in males, which can lead to their higher energy demand (Rehnus *et al.* 2017). As a result, during the early-breeding period females consume more food of higher nutritive value (e.g., graminoids) than males (Rehnus *et al.* 2020).

In this study, during six years (2014–2019), we investigated the occurrence of sex-related habitat segregation at the macro- (home range) and the microscale (pellet locations) by means of permanent non-invasive genetic population monitoring (Rehnus *et al.* 2016a) during the early-breeding and post-reproductive periods.

Material and methods

Study area

The study area comprised 3.5 km² and was situated along the Ofenpass in the Swiss National Park in SE Switzerland (46°39'N, 10°11'E; elev. 1693–2587 m a.s.l.). The area was selected to represent the ecological range occupied by the mountain hare in the Swiss National Park. It was also 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 as a nature reserve/wilderness area (Category Ia; see <https://www.iucn.org/theme/protected-areas/about/protected-areas-categories/category-ia-strict-nature-reserve>) and is closed to the public in winter. Thus, mountain hares can be studied during winter under natural conditions without human disturbance.

Habitats within the study area were delimited and classified according to the habitat categories of HABITALP, a standardized habitat classification project for protected areas in the Alps (Lotz 2006). The following seven main habitat types were encountered: meadows (29%; with diverse grasses, including *Nardus stricta*, *Festuca* sp.,

Poa sp., *Agrostis* sp., *Luzula* sp., and sedges), timber stands (24%), scree and rocks (18%), 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 covered 1% 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).

Data collection

We collected fresh pellets during six consecutive years (2014–2019) during the early-breeding period (end of March until first half of April) and the post-reproductive period (October). Only fresh faecal pellets were collected because amplification success rates were significantly lower for pellets older than five days (Rehnus *et al.* 2016a). Samples were stored in separate plastic tubes without touching by hand to minimize DNA contamination (Sloan *et al.* 2000). After collection in the field, samples were frozen (at −20 °C) and stored until they were analysed in the laboratory.

We used nine nuclear microsatellites Lsa1, Lsa3 (Kryger 2002), Sat2, Sat5, Sat8, Sat12 (Mougel *et al.* 1997), Sol30, Sol8 (Rico *et al.* 1994), Sol33 (Surrige *et al.* 1997), and a sex marker (SRY; Wallner *et al.* 2001) to identify individuals and assign them to the collected faeces 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 (L. Schürz unpubl. data).

Habitat data

To evaluate sexual habitat segregation in mountain hares at the macroscale, we estimated habitat

composition of individual home ranges by calculating the area of minimum convex polygons 95% (MCP95) using the R package “reproducible home range analysis” (Signer *et al.* 2015). We used a data set of 11 individuals (6 males, 5 females) for which we had a minimum of 15 observations from the early-breeding and the post-reproductive periods from six years (2014–2019). We assumed that a minimum of 15 observations should adequately represent home ranges of mountain hares in our study area because home-range sizes are saturated at about 20 fixes (Dahl *et al.* 2005). Similarly, mountain hares do not shift their home ranges completely from one season to the next or from one year to the next, i.e., their site fidelity remains high throughout seasons and years (Bisi *et al.* 2011). For the calculated home ranges we estimated proportions of the seven habitat types (meadows, scree and rocks, sapling stands, pole stands, timber stands, mature stands and storeyed stands; see ‘Study area’).

To estimate sex-related habitat segregation at the microscale, we estimated the average degree of cover of four habitat types (grass and herbs, scree and rocks, dwarf shrubs, trees; Lotz 2006) within a circle of 10-m radius around each pellet locations. Pellet locations are good indicators of activity centres and feeding sites (Angerbjörn 1983, Krebs *et al.* 2001, Hiltunen 2003, Rehnus *et al.* 2016b). A circle of 10-m radius around each pellet location was considered sufficient to represent characteristics of open habitats and mountain forest stands (Ott *et al.* 1997). Our data set contained 1001 pellet locations during the early-breeding period and 514 pellet locations during the post-reproductive period, and included 70 males and 49 females.

Statistical analysis

To study sex-related differences in habitat composition of individual home ranges we calculated Pianka’s niche overlap index for the estimated home ranges. In calculating the index, a resource utilization matrix is taken as input which returns the average pairwise Pianka’s niche overlap index for both sexes (see <https://cran.r-project.org/web/packages/EcoSimR/EcoSimR.pdf>). The index values range from 0 (exclusive use of

certain resource categories by one sex) to 1 (identical resource utilization by both sexes). We also tested for within-period habitat segregation between sexes per habitat type using linear models (*nlme* package in R; see <https://cran.r-project.org/web/packages/nlme/nlme.pdf>), with proportion of habitat type as the response variable, sex as the predictor variable, and individual ID as random factor.

At the microscale, we tested for sex-related differences in the use of cover layers by calculating Pianka’s niche overlap index for both sexes within the periods. We used linear models with habitat type as the response variable, sex as the predictor variable, and individual ID as a random factor.

Before modelling, we tested the response variables (habitat type, cover layer) for normality with Shapiro-Wilk’s test, and found they fulfilled the linear model assumptions. All statistical tests were conducted using R 3.6.3 (R Development Core Team 2020).

Results

In the early-breeding period, the mean home-range (MCP95) sizes for males and females were 57.7 ha (34.6 ± 7.1 mean $\pm$ SD observations per individual) and 28.4 ha (31.2 ± 20.4 observations per individual), respectively. In the post-reproductive period, the home ranges were smaller: 14.3 ha for males (21.2 ± 7.3 observations per individual) and 12.0 ha for females (28.2 ± 13.9 observations per individual). The home range sizes did not differ between sexes in both periods (Table 1).

At the macroscale (home range), the sex-related habitat segregation was low in both periods with Pianka’s niche overlap indexes of 0.64 and 0.85 in the early-breeding and post-reproductive periods, respectively. Home ranges of females and males were dominated by forest stands (Table 1). In the early-breeding period, females were most likely found in forest stands (92.5% vs. 61.5% for males) while males used more open areas (38.5% vs. 7.5% for females).

At the microscale (pellet location), there was no sex-related habitat segregation in the early-breeding and the post-reproductive periods

Fig. 1. Habitat characteristics (cover layers; mean + SD) of mountain hare pellet locations (radius = 10 m) during (A) the early-breeding and (B) post-reproductive periods in the Swiss National Park. Estimates of habitat composition are based on 1001 and 514 pellet locations from the early-breeding and post-reproductive periods between 2014 and 2019, respectively, which were assigned to 70 males (grey) and 51 females (white).

(Pianka's niche overlap indexes: 1.00 and 0.99, respectively). There were no significant differences in habitat characteristics around pellet locations between sexes in the early-breeding period (scree and rocks: $F_{1,906} = 0.3$, $p = 0.577$; grass and herbs: $F_{1,906} = 0.1$, $p = 0.778$; dwarf shrubs: $F_{1,906} = 0.2$, $p = 0.691$; trees: $F_{1,906} = 0$, $p = 0.904$) and the post-reproductive period (scree and rocks: $F_{1,440} = 0.1$, $p = 0.721$; grass and herbs: $F_{1,440} = 1.4$, $p = 0.230$; dwarf shrubs:

Table 1. Habitat type characteristics of mountain-hare home ranges (MCP95) in the Swiss National Park. The home-range (MCP95) estimates were based on 329 and 302 observations during the early-breeding and post-reproductive periods, respectively, for six males and five females, with a minimum of 15 observations per period between 2014 and 2019. Habitat types according to HABITALP (see Lotz 2006).

Habitat types	Males (mean ± SD)	Females (mean ± SD)	<i>F</i>	<i>p</i>	<i>R</i> ²
Early-breeding period					
Total area (ha)	57.7 ± 29.4	28.4 ± 14.1	3.4	0.098	0.27
Open habitats (%)	38.5	7.5	—	—	—
Meadows (%)	28.9 ± 14.0	7.1 ± 4.9	16.6	0.003	0.64
Scree and rocks (%)	9.7 ± 12.6	0.4 ± 0.9	1.8	0.211	0.17
Tree stands (%)	61.5	92.5	—	—	—
Sapling stands (%)	13.2 ± 9.1	7.9 ± 8.4	8.6	0.017	0.49
Pole stand (%)	5.4 ± 3.7	28.0 ± 21.0	0.1	0.745	0.01
Timber stands (%)	14.6 ± 17.8	27.8 ± 21.9	0	0.849	0
Mature stands (%)	9.6 ± 12.4	17.6 ± 11.3	0	0.905	0
Storeyed stands (%)	18.6 ± 7.3	11.1 ± 5.8	20.9	0.001	0.70
Post-reproductive period					
Total area (ha)	14.3 ± 9.1	12.0 ± 6.1	0.2	0.707	0.02
Open habitats (%)	29.8	27.1	—	—	—
Meadows (%)	12.7 ± 9.6	20.3 ± 16.9	0.1	0.775	0.01
Scree and rocks (%)	17.1 ± 23.0	6.8 ± 15.2	1.4	0.262	0.14
Tree stands (%)	70.2	72.9	—	—	—
Sapling stands (%)	16.9 ± 16.9	8.0 ± 11.1	1.0	0.343	0.10
Pole stand (%)	4.3 ± 6.3	20.4 ± 15.7	7.3	0.025	0.45
Timber stands (%)	23.0 ± 37.8	18.3 ± 22.4	1.1	0.330	0.11
Mature stands (%)	5.5 ± 13.6	3.5 ± 5.8	0	0.845	0
Storeyed stands (%)	20.4 ± 12.6	22.7 ± 20.9	0	0.864	0

$F_{1,440} = 0.3$, $p = 0.594$; trees: $F_{1,440} = 0.8$, $p = 0.358$; Fig. 1).

Discussion

We found only weak sex-related habitat segregation in the habitat composition of individual home ranges and around pellet locations during the mountain-hare early-breeding and post-reproductive periods.

At the macroscale, low segregation between males and females during both periods can be explained by a high home-range overlap between the sexes (Bisi *et al.* 2011). Home ranges of females and males were dominated by tree stands in all succession stages. Among them, timber and storeyed stands were most frequently represented. According to Litvaitis (1990), tree stands with good under- and overstory cover (e.g. sapling and storeyed stands) are also important habitat types for male snowshoe hares (*Lepus americanus*). Forest stands with heterogeneous cover offer more food resources, cover from predators, and suitable places to raise offspring for females mountain and snowshoe hares (Wolff 1980, Litvaitis *et al.* 1985, Litvaitis 1990, Bisi *et al.* 2011). Opposite to our expectation, sex-related habitat segregation in the early-breeding period was higher as compared with that in the post-reproductive period.

In the early-breeding period, males used open habitats more often than females which were detected more frequently in forest stands. We assume that females depend more on browse of woody species (Litvaitis 1990) to cover their higher demand for energy during this time of the year as their glucocorticoid metabolite levels are higher than in males (Rehnus & Palme 2017), whereas males are considered to have lower nutritional requirements (Litvaitis 1990, Hulbert *et al.* 2001). However, this and previous studies have shown that during the early-breeding period home ranges of males are greater than those of females (Hewson *et al.* 1990, Dahl 2005, Kauhala *et al.* 2005, Bisi *et al.* 2011). We hypothesize that males have to cross more open habitats to find several females which occur mainly in forest patches.

The lack of a sex-related habitat segregation at the microscale in both periods is in line with findings of Litvaitis (1990) regarding microhabi-

tat use of male and female snowshoe hares, as well as of Zaccaroni *et al.* (2009) on similar ecological needs for cover and food in both sexes of the European hare *L. europaeus*.

Rehnus *et al.* (2020) found that in the early-breeding period female mountain hares forage on graminoids at a higher rate than males. This could not be confirmed by a higher use of meadows by females in this study. Protein content and digestibility of graminoids is highest in the early phase of growth (Albon *et al.* 1992, Duru 1997, Bumb *et al.* 2016) but graminoids were inaccessible in our study area during the early-breeding period due to snow cover (Rehnus *et al.* 2013, Rehnus *et al.* 2016b). However, the weak sex-related segregation can be explained by the availability of feeding places (Angerbjörn 1983, Hiltunen 2003) limited by snow cover (Rehnus *et al.* 2016b). We assume that mountain hares cope with high spatio-temporal variability of resource availability by flexible, non-territorial behaviour which is evidenced by large and overlapping home ranges.

To date, studies on habitat use in hares concentrated on the reproduction period when females care for their offspring alone (Chapman *et al.* 1990). Our study, however, provides new insights into the sex-specific habitat use in the *Lepus* species outside the breeding period. Furthermore, the lack of sex-related habitat segregation found in our study indicates that both sexes benefit equally from habitat conservation measures for mountain hares (Rehnus *et al.* 2016b).

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