

Gastrointestinal parasite infestation in the alpine mountain hare (*Lepus timidus varronis*): Are abiotic environmental factors such as elevation, temperature and precipitation affecting prevalence of parasite species?

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ABSTRACT

Information concerning factors regulating Alpine mountain hare (*Lepus timidus varronis*) populations such as host-parasite interactions is missing as only a few parasitological surveys exist of this subspecies. Parasites are not only dependent on their host but also on suitable environmental conditions for infestation. Abiotic environmental factors have an important regulating role on parasites in mammals. It is estimated that the elevation range of parasites is likely to shift in response to alternate host movement and changes in climate. Here we assess the parasitic infestation in the Alpine mountain hare by analysing the parasites in faeces and comparing the parasite infestation at different elevation ranges and at varied weather conditions for two years in the Austrian Alps. Almost half of the faecal samples were free of parasites (46.2%, n = 52). Most frequent was the infection by Coccidia (46.2%), whereas stomach intestine strongylids, *Trichuris* spp, and Cestoda were only found in 9.6% of all faeces. Hence, only Coccidia may be prevalent enough to regulate Alpine mountain hare populations in the Austrian Alps. Elevation had a significant positive effect on the infection of animals by *Trichuris* spp, whereas temperature had a significant negative effect on the infection by any parasite traceable in faeces and, when looking at the parasite groups individually, on Coccidia.

1. Introduction

Existing knowledge of vertebrate population dynamics suggests that trophic interactions regarding predator-prey or host-parasite systems seem to be the main factor limiting populations and these interactions might lead to unstable dynamics (e.g. predation: Begon et al., 1999; Case, 2000; Krebs, 2009; parasitism: Scott and Dobson, 1989; Tompkins and Begon, 1999; Hudson et al., 2009). Evidence shows that predation or parasitism as the factor limiting populations may be variable within the same species (Newey et al., 2007). As an example, the nematode parasite *Trichostrongylus tenuis* has been demonstrated experimentally to cause red grouse (*Lagopus lagopus scoticus*) population cycles in northern England by influencing the host fecundity (Hudson et al., 1998), whereas in several other studies predation has been identified to

be the limiting factor for red grouse populations (Tharme et al., 2001; Baines et al., 2008; Fletcher et al., 2010). It is currently uncertain what factors prevent or enable parasites to be the limiting factor of host populations (Newey et al., 2007). The controversial impact of parasitism and predation on population dynamics has been recorded also in the mountain hare (*Lepus timidus*). Populations in Fennoscandia are limited by predation, whereas predation is unlikely to be important in mountain hare populations in Scotland (Newey et al., 2007). By contrast, some Scottish mountain hare populations are limited by parasites, whereas in Fennoscandia parasitism does not seem to be of any importance to mountain hare population dynamics (Newey et al., 2007). Current knowledge excludes information concerning the factors limiting and regulating mountain hare populations in the Alps of Central Europe. One reason is that no accurate population estimate of the

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Alpine mountain hare (*L. t. varronis*) exists due to the lack of a standardized census method. Moreover, only a few parasitological surveys provide some indications on the parasite fauna of this subspecies (Bouche, 1989; Meneguz and Rossi, 1990; Battisti et al., 2000; Tizzani et al., 2014). In the Alps, parasites infecting small or intermediate-sized mammals face particular conditions as valleys might act as a barrier to regular movements between host populations. Nevertheless, the two larger parasitological studies on Alpine mountain hares recorded both the tapeworm *Paranoplocephala wimerosa* to be the most frequent parasite in the French and Italian Alps (Bouche, 1989: 78%, n = 43; Meneguz and Rossi, 1990: 57%, n = 60). It is questionable whether Cestoda permeate the valleys' potential barrier effect and are also prevalent in Alpine mountain hares of the Austrian Alps and, accordingly, if tapeworms might be candidates for a parasite group regulating populations of this Alpine lagomorph subspecies.

Polyparasitism, i.e. coinfection of a host with several parasites, affects the immune response of the host and the pathogenic severity of the parasites (Keusch and Migasena, 1982; Graham, 2002; Supali et al., 2010). Yet, surveys assessing polyparasitism in mammals are contradictory in correlating coinfection with severity of manifestations (Liesenfeld et al., 2004; Nacher, 2011). The effects of polyparasitism are often unknown as parasitic interactions not always cause severe clinical symptoms (Liesenfeld et al., 2004; Schale et al., 2018). In some cases, combined infections may have synergistic effects and exacerbate manifestation (Buck et al., 1978; Graham, 2002; Gibson et al., 2011; Nacher, 2011). Whether the coexistence of multiple parasites affect the total parasite burden of the host has not been studied yet in medium-sized free-living mammals.

Parasites are not only dependent on their host or their alternate host but also on suitable environmental conditions for transmission and infestation. Free-living stages of many endoparasites such as eggs and larvae from gastrointestinal nematodes benefit from warm temperatures and moist conditions (Donald et al., 1982; Stromberg, 1997; O'Connor et al., 2006). Hence, optimal weather conditions for infective stages can enhance host exposure to parasitic infections substantially (Hernandez et al., 2013). Abiotic environmental factors having an important regulating role on distribution, transmission and developmental success of parasites in mammals include precipitation (e.g. Decker et al., 2001; Sacks et al., 2003; Miterpáková et al., 2006; Froeschke et al., 2010), temperature (e.g. Froeschke et al., 2010; Schares et al., 2016; Cadavid Restrepo et al., 2018; Fuentes-Vicente et al., 2018), and elevation (e.g. Akbar et al., 2012; Kramm et al., 2017). Because of the importance of environmental factors in host-parasite interactions and parasite life-history, it is estimated that not only the geographical but also the elevation range of most parasites is likely to shift in response to alternate host movement and a change in climate (Sutherst, 2001; Froeschke et al., 2010). As a species inhabiting the Alps, the Alpine mountain hare is comfortable in a wide elevational range. Hence, this lagomorph species is a perfect model to test whether elevation, precipitation and temperature influence parasitic prevalence in an alpine wildlife species.

The general goal of this study was to investigate parasitic infestation in the Alpine mountain hare. Our hypotheses were: (1) some parasites such as Cestoda are more common in Alpine mountain hares or infest this hare species more severe than others (2) animals infected by several parasite types also have a higher total parasite burden, and (3) elevation, precipitation and temperature have an effect on the parasitic infestation in Alpine mountain hares. We tested these hypotheses by analysing the parasites in mountain hare faeces and compared the parasite infestation at different elevation ranges and at varied weather conditions for two years in the Alps.

2. Material and methods

2.1. Study area

The survey was performed in two study areas situated in the Alps, near Dalaas (47°7'N, 10°0'E) in Vorarlberg, Austria, during the years 2014 and 2015. Study area A (900 ha, elevation range 1000 to 2000 m a.s.l.) encompassed subalpine spruce forest on acid soil (low plant species diversity), whereas study area B (1050 ha, elevation range 1600 to 2300 m a.s.l.) comprised of a species-rich limestone landscape with anthropogenic open areas (a vegetation mosaic). In both study areas, mountain hares live sympatrically with the European brown hare (*Lepus europaeus*) at lower elevations, whereas at higher elevations mountain hares live allopatrically. This information came from local hunters but was confirmed by own observations during the study years.

2.2. Data collection

To ascertain the species' parasites, faecal samples were collected twice a year at the beginning and end of the vegetation growth period (July and September) contemporaneously on 58 randomly selected 400 m² (20 × 20 m; 0.04 ha) plots along the elevation gradient in both study areas during the two years of the study. First, plots were emptied of all hare faeces. Plots were revisited three nights later and faeces were collected. Faeces were generally found in piles of several pellets produced by one individual hare. Each pile was split into two parts by a researcher wearing gloves. One part was placed in a 15-ml tube filled with 96% alcohol for the genetic analysis. The second part was put in a plastic bag for the parasitological analysis and kept in the refrigerator.

Weather data including daily accumulated precipitation and daily minimal, maximal and average temperature from the study region (weather station Sankt Anton am Arlberg, 47°7'53"N, 10°16'0"E) for the two study years were provided by the Austrian Central Institute for Meteorology and Geodynamics. As we were interested in fine scale weather effects and considered that some faeces were up to three days old, we averaged weather data for a time span of ten days. Time span was adjusted for the sample date of each faecal sample and included the ten days prior to the sample date.

2.3. Genetic species identification of faeces

All faeces were genetically analysed to determine the hare species. DNA extraction from faecal pellets was performed using the E.Z.N.A commercial kit. A fragment of the mitochondrial control region (219bp) was amplified using the primers Lmtof1 (5'-GAGGACAAATATCATTCT GAGG-3') and LmtNr1 (5'-AAACTGGCTCCAATAACCC-3') (Palumbi et al., 2002) and sequencing was carried out after purification of amplified products using the primer Lmtof1. For further analysis only faecal pellets from mountain hares were considered.

2.4. Parasitological analysis

84 faecal samples were examined for parasites by standard protocols (Foreyt, 2001). In short, a flotation and sedimentation analysis was performed using a saturated sugar solution (454 g sucrose mixed with 355 ml tap water). One gram faecal material was mixed in 10–12 ml water until faeces were in suspension. This suspension was sieved and centrifuged at 1700 rpm for 5 min. The tube was decanted and filled to one half with the flotation solution and again centrifuged at 1700 rpm for 5 min. The faecal counts of oocysts or eggs were categorised in scattered ((+); 1/visual field × 10 magnification), low (+; 2–3/visual field × 10 magnification), intermediate (++; 4–9/visual field × 10 magnification), and high (+++; > 9/visual field × 10 magnification). To avoid any analysis bias, samples were always analysed by the same person (AP).

2.5. Statistical analysis

All statistical analyses were carried out with the software R 3.5.3 (R Development Core Team, 2019). Different response variables (Cestoda, Coccidia, Stomach intestine strongylids, *Trichuris* spp) were analysed using cumulative link models with the package ordinal (Christensen, 2019). The models for the response variables included the covariates elevation, precipitation, temperature (minimal, maximal, and average) and their two-way interaction terms. When there were no significant interaction effects in our cumulative link models ($p > 0.10$), we omitted interactions from the models before re-calculation. We scaled covariates in these models as covariates were on different scales. Note that we tested in all models the covariates minimal, maximal, and average temperature separately. Additionally, the response variable severity of infestation was analysed using a cumulative link mixed model with the package ordinal (Christensen, 2019). The model included the covariate number of parasites (3 levels) and the variable individual as a random factor in order to allow paired testing as individuals suffering from several parasites occurred repeatedly in the analysis. For this model, the p -value was extracted by a likelihood ratio test (Faraway, 2006). The response variable parasite infestation was analysed using linear mixed-effects models with the package lme4 (Bates et al., 2015). The full model for the response variables included the covariates elevation, precipitation, temperature (minimal, maximal, and average) and their two-way interaction terms. Since there were never any significant interaction effects in our linear mixed-effects models ($p > 0.10$), we omitted interactions from the models before re-calculation. Note that we tested in all models the covariates minimal, maximal, and average temperature separately. The full models were used to create a set of models with all combinations of the independent variables using the package MuMIn (Bartoń, 2016). P -values and estimates (β) were extracted by model averaging (including all models with delta AIC < 10). The residuals of all models were checked for normal distribution by viewing QQ-plots and histograms. The homogeneity of variances and goodness of fit were examined by plotting residuals versus fitted values (Faraway, 2006).

3. Results

52 faecal samples could be genetically identified as Alpine mountain hares. The faeces were found on 11 plots within an altitudinal range of 1551–2073 m a.s.l. (median = 1650 m, SD = 175.2 m). Between 1 and 7 piles of several pellets with a median of 2 piles (SD = 1.875) were found on each of these plots. 16 were collected in July and 36 in September; 28 samples derived from area A and 24 from area B.

3.1. Parasitic infestation in alpine mountain hares

We did not find any parasites in the faecal samples of 24 of our Alpine mountain hare faecal samples (46.2%), whereas 28 samples (53.8%) were positive for parasites. Most frequently was the infection by Coccidia with 46.2% of all faecal samples infected (for an overview see Table 1). The faecal counts of Coccidia oocysts ranged between low and high. All other types of parasites affected only 9.6% of all faecal samples. The faecal counts of stomach intestine strongylid oocysts were

Table 1

Number and percent of Alpine mountain hares ($n = 52$) infested by a certain parasite type. The severity of infestation is indicated by negative (–), scattered ((+)), low (+), intermediate (++), and high (+++) infestation.

Parasite	–	%	(+)	%	+	%	++	%	+++	%	++++	%
Cestoda	47	90.4			4	7.7			1	1.9		
Coccidia	28	53.8	1	1.9	8	15.4	12	23.08	1	1.9	2	3.8
Stomach intestine strongylids	47	90.4	1	1.9	4	7.7						
<i>Trichuris</i> spp	47	90.4			5	9.6						

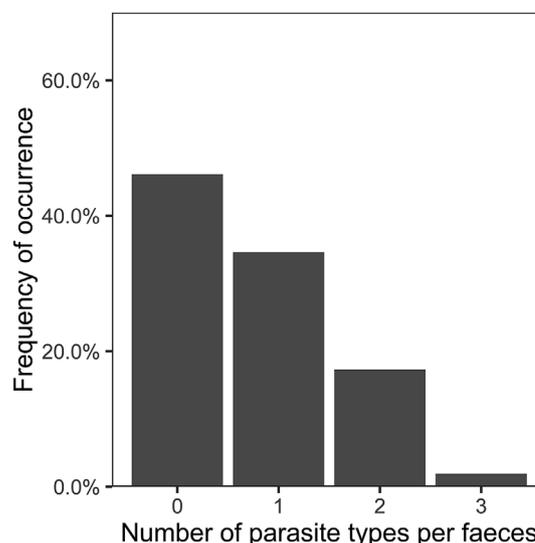


Fig. 1. Frequency of the number of parasite types. Frequency of the number of parasite types detected per Alpine mountain hare faeces in percent ($n = 52$) in Vorarlberg (Austria) during the years 2014 and 2015 within an altitudinal range of 1551–2073 m a.s.l.

either scattered or low. A low number of oocysts was counted in *Trichuris* spp, whereas in Cestoda the faecal counts of oocysts were variable. We found one type of parasite in a third of the mountain hare faeces (34.6%, Fig. 1), whereas 17.3% of the faecal samples were infested by two types of parasites. Only in one faecal sample (1.9%) three different types of parasites could be found. In nine out of ten times a double infestation consisted of Coccidia and either stomach intestine strongylids ($n = 3$), Cestoda ($n = 3$) or *Trichuris* spp ($n = 3$). One animal was only infected by Cestoda and stomach intestine strongylids, and another one by Coccidia, Cestoda and *Trichuris* spp. Moreover, we did not find any significant correlation between the number of parasite types per mountain hare faeces and the severity of parasitic infestation ($p > 0.10$; Fig. 2).

3.2. Effect of elevation, precipitation and temperature on the parasitic infestation of alpine mountain hares

Temperature (average temperature: $p = 0.041$; $\beta = -0.819$; minimal temperature: $p = 0.037$; $\beta = -0.926$; maximal temperature: $p = 0.043$; $\beta = -0.795$; Table 2) had a negative, whereas the interaction term temperature*precipitation (average temperature*precipitation: $p = 0.013$; $\beta = 1.267$; minimal temperature*precipitation: $p = 0.008$; $\beta = 1.536$; maximal temperature*precipitation: $p = 0.018$; $\beta = 1.166$) had a positive significant impact on Coccidia. The other parasite types were not significantly affected by precipitation nor temperature. Elevation had a significant positive effect on the incidence of *Trichuris* spp in faeces ($p = 0.043$; $\beta = 0.933$), whereas the prevalence of Cestoda, Coccidia, and stomach intestine strongylids in the faecal pellets was not significantly affected by elevation. Additionally, whether a faecal sample contained any parasite was influenced significantly and negatively by temperature (average temperature:

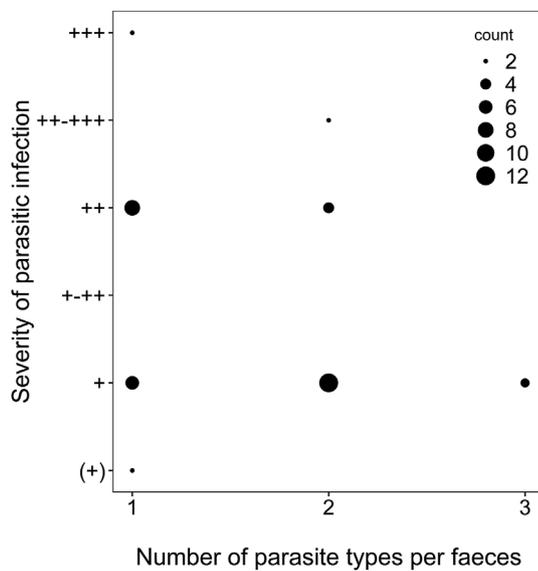


Fig. 2. Number of parasite types per faeces and severity of parasitic infestation. Correlation between number of parasite types per Alpine mountain hare faeces and severity of parasitic infestation (n = 28) found in Vorarlberg (Austria) during the years 2014 and 2015. Count visualises the number of faecal samples. The severity of infestation is indicated by scattered ((+)), low (+), intermediate (+++), and high (++++) infestation. See text for details on statistics.

Table 2

The statistical results of the effects of elevation, precipitation and temperature on the different parasite types and on whether an animal was infested by any parasitic disease traceable in faeces. The significant result is indicated in bold. See text for details on statistics.

Response variable	Covariate	β	SE	p
Cestoda	Elevation	-0.740	0.906	0.41
	Precipitation	0.198	0.536	0.71
	Average temperature	-1.347	1.092	0.22
	Minimal temperature	-1.733	1.108	0.12
	Maximal temperature	-1.148	1.014	0.26
Coccidia	Elevation	0.012	0.287	0.97
	Precipitation	-0.170	0.377	0.65
	Average temperature	-0.819	0.401	0.041
	Minimal temperature	-0.926	0.445	0.037
	Maximal temperature	-0.795	0.393	0.043
	Average temperature*precipitation	1.267	0.509	0.013
	Minimal temperature*precipitation	1.536	0.580	0.008
	Maximal temperature*precipitation	1.166	0.494	0.018
Stomach intestine strongylids	Elevation	-3.016	2.232	0.18
	Precipitation	0.121	0.711	0.86
	Average temperature	-2.420	1.923	0.21
	Minimal temperature	-1.662	1.247	0.18
	Maximal temperature	-3.115	2.523	0.22
Trichuris spp	Elevation	0.933	0.455	0.043
	Precipitation	-0.128	0.535	0.81
	Average temperature	-0.273	0.653	0.68
	Minimal temperature	-0.159	0.657	0.81
Parasite infestation	Maximal temperature	-0.313	0.653	0.63
	Elevation	0.001	0.002	0.64
	Precipitation	-0.412	0.395	0.30
	Average temperature	-0.455	0.159	0.005
	Minimal temperature	-0.673	0.272	0.024
	Maximal temperature	-0.324	0.108	0.003

p = 0.005; β = -0.455; minimal temperature: p = 0.024; β = -0.673; maximal temperature: p = 0.003; β = -0.324, Fig. 3) but neither by elevation nor precipitation.

4. Discussion

4.1. Parasitic infestation in alpine mountain hares

Almost half of our Alpine mountain hare faecal samples (46.2%) were free of parasites traceable in faeces. This is in contrast to other studies examining mountain hares (Irvin, 1970) or other mammals (e.g. Rengifo-Herrera et al., 2014; Moleón et al., 2015; Santana Lima et al., 2018) recording much higher parasitic incidence ($\geq 73\%$) in faecal samples. Perhaps, parasite prevalence is lower in faeces of this Alpine species because hare densities in the Alps are low (estimated 0.5–5 hares/km², Couturier, 1981; Bouche, 1989) and parasite load increases with higher host densities (Cremer et al., 2007; Kappeler et al., 2015). Another reason might be that only one sample was collected and some parasites are not constantly excreted (Xiao et al., 1994; Hinney et al., 2017; Joachim et al., 2018). Alternative, parasite infection of wild herbivores might be influenced by domestic herbivores grazing in the same areas (McKenzie and Davidson, 1989). In study area A no domestic herbivores were present, whereas in area B in some sites domestic herbivores (mostly cattle, some horses, a few goats and sheep) were present. 18 samples from our 52 faecal samples were collected in areas where domestic herbivores occurred. However, as only 3 of them were infected by parasites we consider the influence of domestic herbivores on parasite infection of the Alpine mountain hare in this region negligible. This is in line with Stancampiano et al. (2001) recording no influence of cattle presence on gastro-intestinal nematode egg output in Alpine chamois (*Rupicapra rupicapra rupicapra*) faeces. We differed between four parasite groups in our parasitological analysis: Coccidia, stomach intestine strongylids, Cestoda and *Trichuris* spp. When comparing the proportion of Coccidia infected Alpine mountain hares between studies, our animals were more frequently infected (46.2%) with this parasite than animals examined in the French (Bouche, 1989: 14%) and Italian Alps (Meneguz and Rossi, 1990: 34.5%; for an overview on the investigation methods used in the different Alpine mountain hare studies see Table 3). However, Coccidia have been reported to be even more commonly found in faeces of mountain hares inhabiting Britain (Irvin, 1970: 93%). In our study in the Austrian Alps, stomach intestine strongylids were only found in 9.6% of all Alpine mountain hare faeces. This is similar to the 6% of *Trichostrongylus retortaeformis* recorded in Alpine mountain hares in the French Alps (Bouche, 1989). In Scotland, more than 93% of Scottish mountain hares were infested by *T. retortaeformis* (Newey et al., 2005). This parasite affects body condition and fecundity of Scottish mountain hares and, hence, limits mountain hare populations (Newey et al., 2004, 2005, 2007; Newey and Thirgood, 2004). The Cestoda *Paranoplocephala wimerosa* has been reported to be the most frequent parasite in Alpine mountain hares inhabiting the French and Italian Alps (Bouche, 1989: 78%; Meneguz and Rossi, 1990: 57%). In our study, Cestoda were only found in 9.6% of all faeces. Also *Trichuris* spp were observed more frequently in other Alpine mountain hare surveys than in our study (Bouche, 1989: *Trichuris leporis* 33%; Meneguz and Rossi, 1990: *T. leporis* 32%; our study: *Trichuris* spp 9.6%). To conclude, we assume that probably only Coccidia may be sufficiently widespread to regulate populations of this lagomorph subspecies in the Austrian Alps. Nevertheless, it has to be kept in mind that parasite prevalence can be explained by several factors. Firstly, the examination method may partly be responsible for different parasite prevalences. As an example, Bouche (1989) recorded the liver fluke *Dicrocoelium lanceolatum* in 36% of the liver samples (n = 43), whereas only in 8% of his faecal samples (n = not declared). However, when comparing the parasitological results obtained by the same examination method in the different Alpine mountain hare studies, differences in parasite incidence are still considerable. Hence, differences in parasite prevalence between Alpine mountain hare populations inhabiting Italian, French and Austrian Alps cannot be explained completely by differing examination methods. Secondly, parasite prevalence might be explained by the availability of the intermediate host. Intermediate host

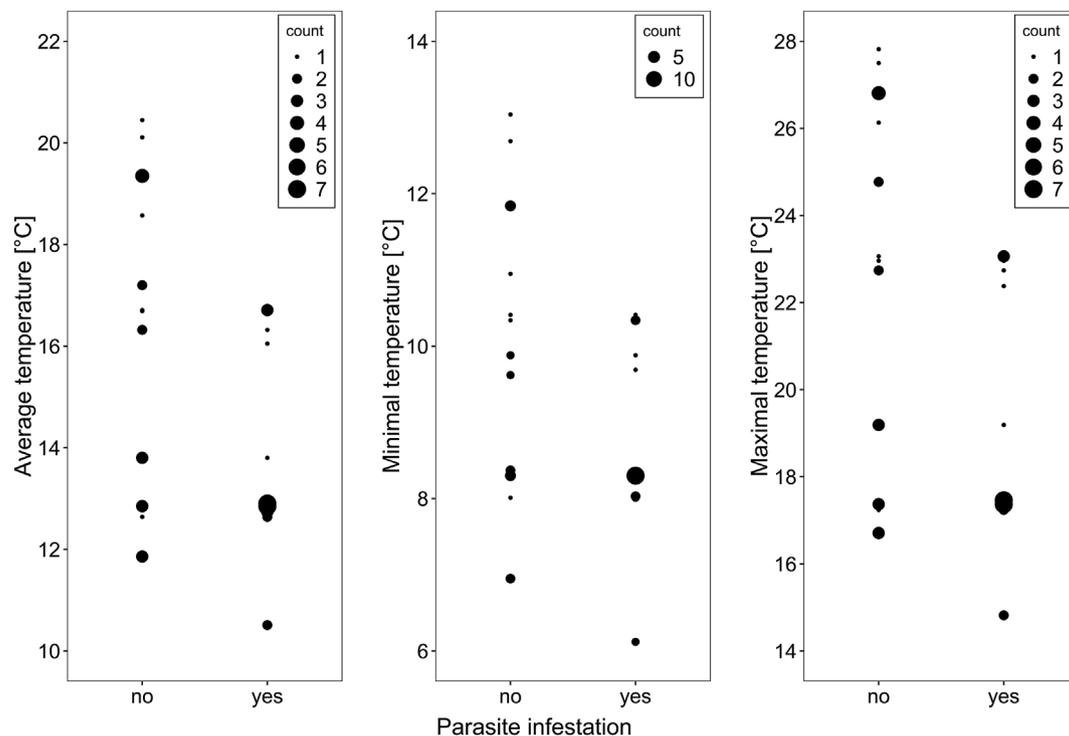


Fig. 3. Parasite infestation in faeces and ambient temperature. Correlation between parasite infestation in Alpine mountain hare faeces ($n = 52$) and average, minimal, and maximal temperature found in Vorarlberg (Austria) during the years 2014 and 2015. Count visualises the number of faecal samples. See text for details on statistics.

Table 3

The investigation methods of the different Alpine mountain hare studies conducted in the Italian, French and Austrian Alps.

Author(s)	Year	Examined sample(s)	n	Method
Bouche	1985	Lungs, digestive tract	43	Autopsy
		Faecal pellets	not declared	Coproscopy
Battisti et al.	2000	Lungs	1	Autopsy
Tizzani et al.	2014	Stomach, small intestine, and large intestine	7	Autopsy
Meneguz and Rossi	1990	Digestive tracts	60	Autopsy
This study		Faecal pellets	52	Coproscopy

of Cestoda species recorded to infest Alpine mountain hares are beetle mites (Oribatida) for *Mosgovoyia pectinata* and unknown for *Paranoplocephala wimerosa* (Denegri, 1993). As almost no information about these intermediate hosts are known, their influence in regulating tapeworm prevalence in the Alpine mountain hares cannot be finally clarified yet. Alpine mountain hares did not show an enhanced total parasite burden when afflicted by several parasite types. Hence, parasitic interactions between the four parasite groups Coccidia, stomach intestine strongylids, Cestoda and *Trichuris* spp may not present any increased severity of parasitic infestation in this medium-sized free-living mammal. This is in conformity with the described lack of counterregulatory effects between the helminth *Nippostrongylus brasiliensis* and the protozoan *Toxoplasma gondii* in laboratory mice (Liesenfeld et al., 2004).

4.2. Effect of elevation, precipitation and temperature on the parasitic infestation of alpine mountain hares

In our study, only *Trichuris* spp was affected by elevation. In line with our findings, elevation has been shown to be influencing *Trichuris trichiura* infections in humans (Steinmann et al., 2007; Manz et al., 2017). However, while *T. trichiura* infections in humans had an inverse

association with elevation, *Trichuris* spp infection in Alpine mountain hares was increased at higher elevations. Lower *T. trichiura* infections in humans at higher elevations are likely due to decreasing temperature at higher elevations, which might impede the development of *T. trichiura* eggs (Manz et al., 2017). Nevertheless, the increased *Trichuris* spp infections at higher elevations in Alpine mountain hares in our study was not related to temperature. According to our findings, infection of Coccidia was increased at lower temperatures. This is in contrast to several studies on Coccidia recording warm temperatures (28–37 °C) to favour the development and prolong the survival of oocysts (Perez et al., 1998; Om et al., 2010; Pyziel and Demiaszkiewicz, 2015; Makau et al., 2017). During our study, Coccidia infections were recorded most commonly at minimal temperatures of 8.0–8.4 °C, average temperatures of 12.6–12.9 °C and maximal temperatures of 17.2–17.5 °C. These ambient temperatures seem to be most suitable for Coccidia to infect the host Alpine mountain hare. No abiotic environmental factors had any effect on the parasitic groups Cestoda and stomach intestine strongylids. This is in contradiction to various other studies showing that precipitation and temperature have a regulating role on Cestoda and stomach intestine strongylid infections in mammals (e.g. Decker et al., 2001; Miterpáková et al., 2006; Froeschke et al., 2010). Nevertheless, it might be possible that some effects of abiotic environmental factors on parasite infections were missed as we examined only the temperature and precipitation within the 10 days before faecal samples were collected and not during earlier seasons. As an example, rainy weather conditions during the first weeks after emergence above ground has an effect on intestinal nematode loads in European rabbits (*Oryctolagus cuniculus*) during later life (Rödel and Starkloff, 2014). Our findings revealed also a negative relationship between the ambient temperature and the infection of Alpine mountain hares by any parasites traceable in faeces. This means that infection by any parasite traceable in faeces was increased at lower temperatures and, hence, lower temperatures seem to enhance the probability for Alpine mountain hares to be infected by any parasite traceable in faeces.

5. Conclusion

In conclusion, almost half of the Alpine mountain hare faecal samples were free of parasites. Our animals were more frequently infested (46.2%) with *Coccidia* than Alpine mountain hares examined in the French (14%) and Italian Alps (34.5%). Stomach intestine strongylids and Cestoda were only found in 9.6% of our samples. Hence, only *Coccidia* may be prevalent enough to regulate Alpine mountain hare populations in the Austrian Alps. Differences in parasite incidence between Alpine mountain hare populations inhabiting Italian, French and Austrian Alps seem to be large which cannot be explained solely by differing examination methods. Moreover, our findings showed a negative relationship between ambient temperature and infections by any parasite traceable in faeces and, when looking at the parasite groups individually, by *Coccidia*.

Conflicts of interest

The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, or in the decision to publish the results.

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