Gastrointestinal parasitic infestation in the Rock ptarmigan *Lagopus muta* in the French Alps and French Pyrenees based on long-term sampling (1987–2018)

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**Abstract**

Data presented in this work represents the first record of parasites from the Alpine and Pyrenean *Lagopus muta* subspecies, providing valuable information to consider for conservation management. From 1987 to 2018, 207 Rock ptarmigans were collected in the framework of a long-term sanitary monitoring in France. Eight parasites were found in the Alpine Rock ptarmigan, and one in the Pyrenean subspecies. Only two parasites occurred with high prevalence in the Alpine Rock ptarmigan: *Capillaria caudinflata* (38.9%) and *Eimeria* sp. (34.7%). Prevalence of the other parasites (*Ascaridia compar*, *Cestodes*, *Amphimerus*, and *Trichostrongylus tenuis*) was lower than 20%. *Dispharynx nasuta* was found with a prevalence of 52.9% in the Pyrenean Rock ptarmigan. Overall, we found a spatially aggregated distribution of parasites in the northern French Alps, probably due to both favourable climatic conditions for parasite cycle and high host density. Statistical analyses indicated a positive effect of altitude and latitude on *C. caudinflata* occurrence whereas risk factors for *Eimeria* sp. were the distance from urban areas and land cover. In addition, the majority of the infected birds came from areas close to ski-pistes, where human disturbance increases the susceptibility to diseases, causing stress to wildlife.

**Introduction**

The Rock ptarmigan *Lagopus muta* is a bird distributed with several subspecies in the arctic and alpine tundra of the Northern hemisphere. In contrast to the northern population, characterized by high density and occurring in wide and undisturbed habitats (Caizergues et al., 2003), the southernmost populations, which present a more fragmented distribution, have suffered a significant population reduction over the last decade. The decline may be explained by the climate change and human disturbance (Storch, 2000; Revermann et al., 2012; Imperio et al., 2013; Desmet, 2014; Novoa et al., 2014; Furrer et al., 2016), that are reducing even more the areas suitable for the presence of the species.

The Rock ptarmigan is classified as Least Concern (LC) by the International Union for the Conservation of Nature (IUCN, 2019), with no special conservation issues at the global level. However, National Red Data Books of several European countries, as well as the European Bird Directive (Council Directive 2009/147/EC) include it as a threatened species, pointing out the need for special conservation measures for its preservation (European Parliament and European Council, 2009).

Compared with other grouse species, scarce literature is currently available on the Rock ptarmigan (Zbinden and Hoerning, 1985), with most of the studies related to population dynamics, habitat and behaviour (Storch, 2000; Moss et al., 2010; Tizzani et al., 2020).

Specifically, few studies are available on the sanitary status of the species, and most of them have been carried out in the northern part of the species range, in Iceland (Skirnisson et al., 2012, 2016; Stenkewitz et al., 2016), Norway (Holmstad et al., 2005) and Japan (Murata et al., 2007; Matsubayashi et al., 2018). On the contrary, the health status of the Rock ptarmigan hasn’t been fully investigated in Southern Europe where two subspecies are present at the border of the distribution range: *L. m. helvetica* and *L. m. pyrenaica*.

To our knowledge, this is the first sanitary study carried out on the Pyrenean subspecies (*L. m. pyrenaica*). Moreover, it includes one of the few data currently published and available on the Alpine subspecies (*L. m. helvetica*), whose health evaluation is particularly difficult due to the fragmented distribution of the Alpine population, and to the difficulties to reach and sample the animals at high altitude areas. This is also one of the reasons why the studies on this species are usually limited to a very few number of samples.

Only Zbinden and Hoerning (1985) and more recently Fanelli et al. (2020), have carried out a study on the parasite community of wild Galliformes in the Alps, comparing the parasite diversity of the different host species. While the second study found no parasite affecting the Rock ptarmigan, the first found 13% of the birds infested by (in order of importance) *Capillaria*, *Coccidia*, *Hymenolepis*, *Heterakis* and *Trichostrongylus*.

Parasites on wild Galliformes have been proved by several studies to have a negative effect at the population level but at the same time their action can have a fine-tuned regulation.
Specifically, this regulation could be expected mainly by parasite species showing longer co-evolutionary history with a host while other parasites, that met the host species more recently, could be expected to show an indiscriminate pathogenic effect (Hudson et al., 1992, 1998; Holmstad et al., 2005). Moreover, species at the border of their distribution range are more sensitive to disturbing factors. As a consequence, the presence of parasites in a Rock ptarmigan population can be a real concern for the long-term conservation management.

Many abiotic environmental factors have an important role in the distribution, transmission and developmental success of parasites (Lafferty, 2009; Cable et al., 2017; Sanchis-Monsonís et al., 2019). Thus, understanding the factors that drive responses across parasite taxa in the Rock ptarmigan is essential to better tune conservation plans.

For these reasons, the purposes of this study are: (a) to increase the knowledge on parasites harboured by the southernmost populations of the Rock ptarmigan, both in terms of parasite community structure and distribution and (b) to assess the role of environmental factors on parasite infestation.

Methods

Study area and sample

Two Lagopus subspecies are reported in France: the Alpine Rock ptarmigan L. muta helvetica living in the Alps and the Pyrenean Rock ptarmigan L. muta pyrenaica whose range is limited to the Pyrenees. In our study, we collected samples from both subspecies. Most of the sampled animals were derived from birds killed during hunting activity (September–November), and few others found dead for other reasons (impact with cables, or predation). Usually, the whole carcases of the birds were collected and analysed. The sample was collected during the period 1987–2018.

The Alpine Rock ptarmigan is a small species of grouse Tetraonidae (Brenot et al., 2005) living in the higher subalpine and alpine zone between 1900 and 2600 m above sea level (Desmet, 1988). The Pyrenean Rock ptarmigan L. m. pyrenaica inhabits one of the most southernmost limits of the species range, around 400 km far from the Alpine population. Both subspecies are characterized by isolate and small populations, with low genetic variability.

Samples coming from L. m. pyrenaica represented only 8.2% (17 out of 207 samples) of the animals analysed. All these animals originated from the Eastern Pyrenees Department, located in Southern France in the Occitanie region. The other 91.8% of the samples (190 out of 207 samples) were collected in the Alpine range from the L. m. helvetica subspecies. Twelve out of the 39 massifs comprising the French Alps and Prealps were investigated: four massifs belonging to the Prealps, low to medium altitude mountains contouring the western side of the Alps, and eight belonging to the Alps which are located in the Auvergne-Rhône-Alpes and Provence-Alpes-Côte d’Azur regions. Figure 1 shows the distribution of the sampled animals.

Parasitological analysis

The gastrointestinal tract of the sampled animals was opened with a longitudinal incision, and the content of the individual sections (proventriculum, gizzard, small and large intestine) was analysed following the common parasitological standard
techniques. Adult worms were then counted under a stereo-
scope (Maff, 1986).
To evaluate Eimeria sp. infestation, we examined fecal samples,
collected from the rectum, using saturated sodium chloride flota-
tion and formol ether sedimentation techniques. Eggs or oocysts
were identified using a light microscope at x40.
For Amphimerus sp., only visual inspection of liver presence of
adult stage was carried out, thus only the presence of the parasite
was noted, but not the quantity of parasites for each positive host.
Parasites were identified using a light microscope and the
identification key suggested by Euzeby (1981, 1982). Eimeria
sp. identification was done only at the genus level, as all the
samples were frozen before the analysis, not allowing to evaluate the
sporulate form of the parasite (needed for identification at the
species level). Cestode identification was possible only for some
positive animals, due to the reduced preservation status of some
samples.
The same sampling and analytical methods were homoge-
neously applied through the whole period of study.

Statistical analysis
All statistical analyses were carried out with R version 3.5.2 soft-
ware (R Core Team, 2018). Epidemiological characteristics includ-
ing prevalence (percentage of infected host individuals in each
sample), intensity of infection (mean number of parasites per
infected host) and abundance (mean number of parasites per
host) were calculated for each parasite species. For Eimeria sp.,
the epidemiological indexes of intensity and abundance refer to
the number of oocysts per gram of feces. Next, we used the pack-
age lme4 (Bates et al., 2015) to build a generalized linear mixed
models (GLMMs) of the binomial family, with a logit link func-
tion and formol ether sedimentation techniques. Eggs or oocysts
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neously applied through the whole period of study.

Table 1. Environmental variables included in the model-building process

| Variable | Source |
|----------|--------|
| Digital elevation model (DEM) | http://srtm.csi.cgiar.org/srtmdata/ |
| Aspect (Northern [326–360; 0–45 degree], Eastern [46–135 degree], Southern [136–225 degree] and Western [226–325] exposure) | Derived from Digital Elevation Model (DEM) http://srtm.csi.cgiar.org/srtmdata/ |
| Slope | Derived from Digital Elevation Model (DEM) http://srtm.csi.cgiar.org/srtmdata/ |
| Longitude | Longitude of the sampled animals in UTM – WGS84 (32’N) coordinate |
| Latitude | Latitude of the sampled animals in UTM – WGS84 (32’N) coordinate |
| Distance from urban areas | Derived from CORINE Land Cover (CLC) https://land.copernicus.eu/ |
| CORINE Land Cover (CLC) (sparsely vegetated areas, natural grasslands and bare rocks) | https://land.copernicus.eu/ |

Table 1. Environmental variables included in the model-building process

model (GLM) was used. Finally, the area under the curve (AUC) value was computed to assess model performance.

Results

Gastrointestinal parasites
Eight parasites were found in the Alpine Rock ptarmigan, and one
in the Pyrenean subspecies. Prevalence, mean abundance and
intensity values, with confidence interval (CI) and standard devi-
ation (s.d.) are presented in Table 2. All the values have been cal-
culated at the host species level.
The results of the model are presented in Tables 3 and 4, for C.
caudinflata and Eimeria sp., respectively.
For C. caudinflata, the likelihood ratio test for the random
parameter is statistically significant (P value = 0.003). This
implies that the differences between the sampling areas contrib-
ute meaningfully to the model. The only significant factors
retained in the model is the altitude (P value = 0.02) whereas
the latitude P value present a marginal significance (exactly
equal to 0.05). Our results indicate that there is a higher risk
of C. caudinflata infestation at lower altitude [odds ratio (OR): 0.4]
and an increased risk for animals living at higher latitude
(OR: 2.3). Moreover, the predictive accuracy of C. caudinflata
model is very high (AUC = 0.85).

Regarding the risk factors analysis for Eimeria sp. infestation,
we built a GLM since the likelihood ratio test for the random
effect was not statistically significant (P value = 1).
In the case of Eimeria sp., there is a clear and statistically sig-
nificant increase of infestation risk as the distance from urban
areas increases (OR: 1.45). Compared to the bare rock (used as
reference baseline for land cover categories), the risk of infestation
is 2.3 times higher for birds living in natural grasslands whereas
those living in sparsely vegetated areas are at lower risk of infest-
ation (OR: 0.3).
With regards to the other parasites, descriptive analysis points
out that A. compar, Amphimerus sp. and Trichostrongylus tenuis
were located only in the northern part of the study area.
Moreover, the ptarmigans positive to A. compar and Amphimerus
sp. were also located at lower altitude compared to the uninfested
birds (A. compar 2254 vs 2633 m a.s.l. respectively; Amphimerus
sp.: 2248 vs 2633 m a.s.l.). All the positive ptarmigans (10) infested
by T. tenuis were reported from Vanoise massif only, with bare
rocks (8 samples out of 10) and southern exposition (8 samples
out of 10) as potential factors influencing the risk of infestation.
With regards to Cestodes, no specific pattern was revealed by
the descriptive analysis, suggesting that no particular risk factors
are driving the parasite distribution and prevalence at the popu-
lation level.
Table 3. Results from GLMM for Prevalence, 95% CI, mean abundance and mean intensity, standard deviation. For Table 2, gastrointestinal parasite species from Rock ptarmigan

| Parasite                      | Host species        | Prevalence (95% CI) | Mean abundance (S.D.) | Mean intensity (S.D.) |
|-------------------------------|---------------------|---------------------|-----------------------|-----------------------|
| A. compar                     | L. m. helvetica     | 1.6 (−0.2 to 3.4)   | 0.5 (5.4)             | 34.6 (31.3)           |
| C. caudinflata                | L. m. helvetica     | 38.9 (32.0−45.9)    | 8.8 (20.2)            | 22.5 (27.2)           |
| Cestodes (including *Hymenolepis microps*, *Raillietina sp.*, *Dovainea tetroensis*) | L. m. helvetica | 14.2 (9.2−19.2)    | 4.1 (20.8)            | 28.5 (49.1)           |
| Eimeria sp.                   | L. m. helvetica     | 34.7 (28.0−41.5)    | 229.8 (1267.3)        | 661.6 (2092.8)        |
| Amphimerus sp.                | L. m. helvetica     | 1.1 (−0.4 to 2.5)   | NA                    | NA                    |
| T. tenuis                     | L. m. helvetica     | 5.3 (2.1−8.4)       | 0.9 (4.7)             | 16.5 (13.3)           |
| D. nasuta                     | L. m. pyrenaica     | 52.9 (29.2−76.7)    | NA                    | NA                    |

Prevalence, 95% CI, mean abundance and mean intensity, standard deviation. For *Eimeria* sp., abundance and intensities values are referred to oocystis per gram of feces.

**Discussion**

Our study represents a comprehensive survey on the gastroenteric parasites community of the Rock ptarmigan subspecies living in the French Alps (*L. m. helvetica*) and French Pyrenees (*L. m. pyrenaica*). To date, information regarding the prevalence and diversity of parasites in the southernmost range of the species has been very limited. This is also the first work investigating the parasites of Rock ptarmigan based on a relatively large sample, covering a wide part of the species range in France and characterized by a long-term sampling (1987–2018). In comparison with the one found in the work of Zbinden and Hoerning (1985), or usually reported for other Alpine Galliformes hosts, a relative rich parasite richness was reported in our study. Moreover, the occurrence and distribution of the parasite at the population level seems to be influenced, at least in some species, by environmental variables. Regarding this last point, it is important to highlight that the environmental factors identified, have to be considered cautiously as they relate to the location where birds were collected, without considering their capacity to move inside the individual home range.

The different host parasite richness detected can be explained by different reasons. Even if the difference could be due to an unbalanced sample size, with a lower number of birds sampled in the Pyrenees, the difference found in the two subspecies might also be due to the geographical locations of the samples. Indeed, all the Pyrenean Rock ptarmigans sampled in our study came from the Eastern Pyrenees which are characterized by very dry climatic conditions, comparable with the ones recorded in the Southern Alps that probably do not allow the proper development of parasite cycles. In the Pyrenees, the amount of precipitation is greater in the western range. Most of the humidity coming from the Atlantic Ocean is dropped on the Western and Central Pyrenees, and the air arrives in the eastern part of the region mostly dry. This is also the reason why no glaciers are present in the Eastern Pyrenees (Hugh, 1911; Maris et al., 2009). A parasite richness is equal to 1 in the Pyrenean subspecies, due to a parasite species known for its pathogenic potential (*Dispharynx nasuta*). This is extremely important for several reasons: (i) the parasite has been reported in other avian species (Carreno, 2008), this is the first report of a parasite in this host species and in *Lagopus* genus in general, (ii) the parasite has been reported with quite high prevalence in our study and it seems to have an important pathogenic effect on the host (Rickard, 1985). For these reasons, the presence of *D. nasuta* could have very important effects on the population dynamics, and should be carefully monitored in the future. However, we cannot infer anything more because of the small sample size. Further studies with a larger sample size should be carried out in the future to better investigate the parasite community in *L. m. pyrenaica*. Indeed, our data are the first attempt to investigate the parasite community in this sub-species.
In the Alpine Rock ptarmigan, prevalence of the parasites varied, being *C. caudinflata* (37.5%) and *Eimeria* sp. (33.5%) the most common species detected. *A. compar*, *Amphimerus* sp., *T. tenuis* and *Cestoides* were present only in few samples. Indeed, these species are rare in *L. muta* whereas more common in other hosts belonging to the Lagopus genus (Dobson and Hudson, 1992; Daehlen, 2003).

Compared with Fanelli *et al.* (2020), who have found the Rock ptarmigan living in the Italian Alps free of parasites, this study presents a parasite richness higher than the one detected by Zbînden and Hoerning (1985) and similar, in terms of different parasite genus, to the one detected by Holmstad *et al.* (2005) in Norway and Skinnison *et al.* (2012) in Iceland. However, a comparison with these studies is difficult, due to the different epidemiological situations of the ptarmigan populations, and due to the distinct population and environmental conditions. Making reference to the work of Fanelli *et al.* (2020), that investigated the wild Galliformes parasite community (in three host species: *L. m. helvetcia*, *Tetrao tetrix tetrix* and *Alectoris graeca saxatilis*) in an area very close to the French Alps, it is interesting to notice that the parasite richness at the community level in this work is significantly lower, as well as the prevalence of *C. caudinflata* (detected in only 1.2–10% of the host species). At the contrary, *A. compar* in the work of Fanelli *et al.* (2020) was the most prevalent species. Also, parasite abundance and intensity described in our study were much higher than the one reported in Fanelli *et al.* (2020). These differences in parasite community richness and structure strongly support the need to carry out more specific study to better investigate the complex relationship among host, parasite and environment at the Alpine level. In the Alps, most of the Galliformes population exist in a situation of metapopulation, with possible significant differences among subpopulations, in terms of sanitary status and its possible impact on the long-term dynamics.

From a spatial point of view, we found an aggregated distribution of parasites in the northern part of the study area, probably due to the concomitant presence of favourable climatic conditions and high host density (census data from the Observatoire des Galliformes de Montagne – http://www.observatoire-galliformes-montagne.com/Lagopede-alpin.html).

In particular, altitude and latitude were significantly associated with *C. caudinflata* infestation. The majority of the infested ptarmigan came from the French Prealps which are characterized by lower elevation than the Alps, and are located in the northern part of the study area. The combination of these factors allows probably the parasite eggs to develop under more favourable climatic conditions. Indeed, significant climatic differences exist in the Alpine range, with the northern part receiving higher precipitations (Durand *et al.*, 2009).

Several studies have evaluated the impact of environmental factors on the development, survival and distribution of parasites characterized by a cycle with free-living stages (Stromberg, 1997; O’Connor *et al.*, 2006); however, very few studies have been carried out on wildlife for such long period of time (Iacopelli *et al.*, 2020). Our finding is in line with the study of Fanelli *et al.* (2020) who found a higher prevalence of gastrointestinal parasites in wild Galliformes living at higher latitude. As in this study, these authors interpreted latitude as a proxy of the climatic and environmental conditions required for the development of free-living stages of the parasite.

Interesting insights are available also from the model for *Eimeria* sp., showing a higher risk of infestation with the increase of the distance from urban areas. The distance from urban areas in our case should be considered as ‘close to urban-disturbed places like ski-pistes’. Indeed, it has been demonstrated that in the disturbed areas there is a strong correlation with coccidiosis (Giraudet *et al.*, 2014). In the Alps, the construction of ski-pistes has widely impacted the ecosystem, with a negative ‘edge effect’ on wild bird populations (Caprio *et al.*, 2014). In addition to the direct impacts on fauna, flora and microbiota, the edge effect favours transmission of parasites to wild birds and susceptibility to parasites among wild birds (Oliveira *et al.*, 2017). The negative effect of the presence of ski areas have been also demonstrated by Belleau (2013), in another study reporting a higher prevalence of *C. caudinflata* in Galliformes coming from human disturbed habitats.

In this way, a similar pattern can be seen also for *A. compar* and *Amphimerus* sp. distribution. In fact, despite the parasites infection affects few individuals, the positive samples are located in areas close to the ski-pistes. The anthropization can be from one side stressful to wild birds, as it leads to a chronic elevation of circulating glucocorticoids, impairing immunity in birds, and from the other side, increases the risk of higher presence of parasitic infectious stages (Bourgeon and Raclot, 2006; Giraudet *et al.*, 2014; Cable *et al.*, 2017). In addition, the positive animals derived also from an *L. m. helvetcia* population at low altitude. The combination of these factors has probably increased even more the risk of parasite occurrence.

In the *Eimeria* sp. model, a further result is related to the different risk of infestation according to the land cover, with higher risk in natural grasslands and lower in sparsely vegetated areas compared to bare rocks (that is used as baseline value for land cover risk evaluation). This result might be explained by the different amounts of soil moisture content. Indeed, land humidity might influence the oocyst survival and development, with moisture inducing higher sporulation ability (Nesheim *et al.*, 1979; Venkateswara Rao *et al.*, 2015).

Birds affected by *T. tenuis* came from a very specific area, showing a cluster in the Vanoise massif. This result is of particular interest, since the presence of this parasite has never been reported in France (Belleau, personal communication). Specifically, *T. tenuis* has been previously described in northern ptarmigan populations (Stenkewitz *et al.*, 2016) and widely studied in other host-species (Shaw and Moss, 1989; Freehling and Moore, 1993; Hudson and Dobson, 1997). However, due to the limited number of positive samples, no further statistical analysis was performed to evaluate environmental risk factors associated with the infestation. The presence of this parasite only in the Vanoise area could be due to particularly favourable environmental conditions. However, it is important to notice that there was no further report of this parasite since 1992, following several years with very dry summers that probably caused the local extinction of the nematode.

Although only prevalence was estimated for Cestodes infestations, this study made an important contribution to the understanding of the parasite community of the Alpine *L. muta* subspecies, describing three new parasite species. Moreover, the prevalence is among the most fundamental measures in epidemiology and it may be used to compare disease burden across locations or time periods. Additionally, there have been only few field studies published on this subject, and none of them on the Rock ptarmigan (Avery, 1969; Dick and Burt, 1971, 1971; Wissler and Halvorsen, 1977; Delahay, 1999; Daehlen, 2003).

To conclude, the broad implication of our study is to increase the information available on the structure and variability of the parasite community in the Rock ptarmigan. As parasites may impact on population dynamics and increase the risk of local extinction for threatened species (Herrera and Nunn, 2019),
future studies should explore the sanitary status of this species to correctly plan conservation measures. In particular, this work highlighted as the parasite in Rock ptarmigan have a clustered distribution, so specific monitoring plan should be carried out to assess the local health status and propose specific measures for a better conservation management.

Acknowledgments. We would like to acknowledge The ONCFS (Office national de la chasse et de la faune sauvage), the GRIEF (Groupe Rech Info Faune Ecosyst Montagne), the Fédérations des chasseurs des départements alpins’, and the Parcs Nationaux alpins’ for their contribution to sample collection; and also Dr Matthew Branan (USDA – APHIS – VS – CEAH – M&M) for useful discussions.

Author contributions. Data collection: Eric Belleau; data analysis: Angela Fanelli; writing – original draft preparation: Angela Fanelli; writing – review and editing: Paolo Tizzani and Eric Belleau; supervision: Paolo Tizzani and Eric Belleau.

Financial support. This research received no specific grant from any funding agency, commercial or not-for-profit sectors.

Conflict of interest. The authors declare that they have no conflict of interest.

Ethical standards. Not applicable: most sampled animals were derived from birds killed during hunting activity (September–November), others were found dead from other reasons (impact with cables, or predation).

References

Akaile H (1973) Information Theory and an Extension of the Maximum Likelihood Principle. In Petrov BN, Csaki F (eds), Proceedings of the 2nd International Symposium on Information Theory. Akadémiai Kiadó, Budapest, pp. 267–281.

Avery R (1969) The ecology of tapeworm parasites in wildfowl. Wildfowl 20, 59–68.

Bates D, Macchler M, Bolker B and Walker S (2015) Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67, 1–48.

Belleau E (2013) Suivi sanitaire des galliformes sur l’Arc alpin occidental: principaux résultats du programme ALCOTRA. Faune Sauvage 300, 45–49.

Bourgeois S and Raclet T (2006) Corticosterone selectively decreases humoral immunity in female eiders during incubation. Journal of Experimental Biology 209, 4953–4965.

Brenot J, Ellison L, Rotelli I, Novoa C, Calenge C, Léonard P and Ménóni E (2005) Geographic variation in body mass of rock ptarmigan Lagopus mutus in the Alps and the Pyrenees. Wildlife Biology 11, 281–285.

Cable J, Barber I, Bog B, et al. (2017) Global change, parasite transmission and disease control: lessons from ecology. Philosophical Transactions of the Royal Society B: Biological Sciences 372, 20160088.

Caizergues A, Bernard-Laurent A, Brenot J-F, et al. (2003) Population genet-ric structure of rock ptarmigan Lagopus mutus in Northern and Western Europe. Molecular Ecology 12, 2267–2274.

Caprio E, Chamberlain D and Rolando A (2008) Dispharynx, echinuria and streptocara. In Atkinson CT, Carreno RA, Caprio E, Chamberlain D and Rolando A (eds), Alpine habitats. In Skiing, birds and biodiversity in the Alps. Brussels: De Boeck, pp. 210–211.

Dafael S (2003) Health Assessment and Parasites of Willow Grouse (Lagopus lagopus) in Sweden. Swedish University of Agricultural Sciences, ISSN 1650-7045.

Dick T and Burt M (1971) The life cycle and seasonal variation of Davainea tetraenosis Fuhrmann 1919, a cestode parasite of ruffed grouse, Bonasa umbellus (L.). Canadian Journal of Zoology 49, 109–119.

Dobson A and Hudson P (1992) Regulation and stability of a free-living host-parasite system: Trichostrongylus tenius in red grouse. I. Population models. Journal of Animal Ecology 61, 487–498.

Duran, Y., Latersimer M., Giraud, G., et al. (2009) Reanalysis of 44 yr of climate in the French Alps (1958–2002): methodology, model validation, climatology, and trends for air temperature and precipitation. Journal of Applied Meteorology and Climatology 48, 429–449.

European Parliament and European Council (2009) Directive 2009/147/EC of the European Parliament and of the Council of 30 November 2009 on the conservation of wild birds. Official Journal Language 20, 7–25.

Ezeby J (1981) Diagnostic expérimental des helmintoses animales (animaux domestiques, animaux de laboratoire, Primates).Travaux pratiques d’hélmintologie vétérinaire. Livre 1 généralités. Diagnostic ante mortem. Informations techniques des services vétérinaires, Paris (France).

Ezeby J (1982) Diagnostic expérimental des helmintoses animales. Diagnostic direct post mortem, diagnostic indirect (diagnostic biologique), livre 2. Informations techniques des services vétérinaires, Paris (France).

Fanelli A, Menardi G, Chiomo M, Giordano O, Ficetto G, Bessone M, Lasagna A, Carpignano MG, Molinar Min A, Gugliatti A, Meneguz PG and Tizzani P (2020) Gastroenteric parasite of wild Galliformes in the Italian Alps: implications for conservation management. Parasitology 1–7. doi:10.1017/S003118201900177X.

Freehling M and Moore J (1993) Host specificity of Trichostrongylus tenius from red grouse and northern bobwhites in experimental infections of nor-thern bobwhites. Journal of Parasitology 79, 538–41.

Furrer R, Schauba M, Bossart A, et al. (2016) Variable decline of Alpine rock ptarmigan (Lagopus muta helvetica) in Switzerland between regions and sites. Journal of Ornithology 157, 778–796.

Giraudet M, Mousel M, Earl S and McGraw K (2014) Parasites in the city: degree of urbanization predicts poxvirus and coccidian infections in house finches (Haemorhous mexicanus). PLoS One 9, e86747.

Heuberger RM (2018) HH: Statistical Analysis and Data Display: Heiberger and Holland. R package version 3, pp. 1–35.

Herrera J and Nunn C (2019) Behavioural ecology and infectious disease: implications for conservation of biodiversity. Philosophical Transactions of the Royal Society B: Biological Sciences 374, 20180054.

Holmstad P, Hudson P, Vandvik V and Skorping A (2005) Can parasites synchronise the population fluctuations of sympatric tetraodonts? – Examining some minimum conditions. Oikos 109, 429–434.

Hudson P and Dobson A (1997) Transmission dynamics and host–parasite interactions of Trichostrongylus tenius in red grouse (Lagopus lagopus scoticus). Journal of Parasitology 83, 194–202.

Hudson P, Newborn D and Dobson A (1992) Regulation and stability of a free-living host–parasite system: Trichostrongylus tenius in red grouse. I. Monitoring and parasite reduction experiments. Journal of Animal Ecology 61, 477–486.

Hudson P, Dobson A and Newborn D (1998) Prevention of population cycles by parasite removal. Science (New York, N.Y.) 282, 2256–2258.

Hugh, C (1911) Pyrenees. In Encyclopædia Britannica, 11th Edn. London, UK: Cambridge University Press.

Iacopelli F, Fanelli A, Tizzani P, Berriatua E, Prieto P, Martinez-Carrasco C, Leon L, Rossi I and Candela MG (2020) Spatio-temporal patterns of sarcoptic mange in red deer and Iberian ibex in a multi-host natural park. Research in Veterinary Science 128, 224–229.

Imperio S, Bionda R, Viterbi R and Provenzale A (2013) Climate change and human disturbance can lead to local extinction of Alpine rock ptarmigan: new insight from the Western Italian Alps. PLoS One 8, e81598.

IUCN (2019) The IUCN Red List of Threatened Species. Version 2019-3. Available at http://www.iucnredlist.org. Downloaded on 10 December 2019.

Lafferty K (2009) The ecology of climate change and infectious diseases. Ecology 90, 888–900.

MAFF (1986) Manual of Veterinary Parasitological Laboratory Techniques. London, UK: Her Majesty’s Stationary Office, pp. 20–27.

Maris M, Giraud G, Durand Y, et al. (2009) Results of 50 years of climate reanalysis in the French Pyrenees (1958-2008) using the SAFRAN and CROCUS models. In Proceedings of ISWS2009. International Snow Science Workshop 2009, Davos, Switzerland.

Matsubayashi M, Tsuchida S, Kobayashi A, et al. (2018) Molecular identification of two Eimeria species, E. seiki and E. raihoi as type B, in wild
Japanese rock ptarmigans, Lagopus muta japonica. International Journal for Parasitology: Parasites and Wildlife 7, 243–250.

Moss R, Storch I and Müller M (2010) Trends in grouse research. Wildlife Biology 16, 1–11.

Murata K, Tamada A, Ichikawa Y, et al. (2007) Geographical distribution and seasonality of the prevalence of Leucocytozoon lovati in Japanese rock ptarmigans (Lagopus mutus japonicus) found in the Alpine Regions of Japan. Journal of Veterinary Medical Science 69, 171–176.

Nesheim M, Austic R and Müller M (2010) Trends in grouse research. Wildlife Biology 16, 1–11.

Novoa C, Desmet JF, Muffat-Joly B, Arvin-Bérod M, Belleau E, Birck C and Losinger I (2014) Le lagopède alpin en Haute-Savoie, biologie des populations et impact des activités humaines. ONCFS/Asters/GRIFEM, Paris.

O’Connor L, Walkden-Brown S and Kahn L (2006) Ecology of the free-living stages of major trichostrongylid parasites of sheep. Veterinary Parasitology 142, 1–15.

Oliveira PSD, Ferreira MA, Silva LMD, et al. (2017) Diversity and distribution of coccidia of wild birds in an Atlantic forest fragment area in southeastern Brazil Diversidade e distribuição de coccídios de aves silvestres em uma área de fragmento de Mata Atlântica no sudeste do Brasil. Revista Brasileira de Parasitologia Veterinária 26, 457–464.

R Core Team (2018) A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing.

Revermann R, Schmid H, Zbinden N, et al. (2012) Habitat at the mountain tops: how long can rock ptarmigan (Lagopus muta helvetica) survive rapid climate change in the Swiss Alps? A multi-scale approach. Journal of Ornithology 153, 891–905.

Rickard LG (1985) Proventricular lesions associated with natural and experimental infections of Dispharynx nasuta (Nematoda: Acuariidae). Canadian Journal of Zoology 63, 2663–2668.

Sanchis-Monsonis G, Fanelli A, Tizzani P and Martínez-Carrasco C (2019) First epidemiological data on Spirocerca vulpis in the red fox: a parasite of clustered geographical distribution. Veterinary Parasitology: Regional Studies and Reports 18, 100338.

Shaw J and Moss R (1989) The role of parasite fecundity and longevity in the success of Trichostrongylus tenuis in low density red grouse populations. Parasitology 99, 253–258.

Skirnisson K, Thorarinsdottir S and Nielsen O (2012) The parasite fauna of rock ptarmigan (Lagopus mutus) in Iceland: prevalence, intensity, and distribution within the host population. Comparative Parasitology 79, 44–55.

Skirnisson K, Jouet D, Ferté H and Nielsen Ó (2016) Occurrence of Mesocestoides canislagopodis (Rudolphi, 1810) (Krabbe, 1865) in mammals and birds in Iceland and its molecular discrimination within the Mesocestoides species complex. Parasitology Research 115, 2597–2607.

Stenkewitz U, Nielsen Ø, Skirnisson K and Stefánsson G (2016) Host–parasite interactions and population dynamics of rock ptarmigan. PLoS One 11, 1–19.

Storch I (2000) Grouse science as a process: where do we stand? Wildlife Biology 6, 285–290.

Stromberg B (1997) Environmental factors influencing transmission. Veterinary Parasitology 72, 247–264.

Tizzani P, Fanelli A, Negri E, Silvano F, Menzano A, Molinar Min A and Meneguz PG (2020) Haemoparasites in red-legged partridge (Alectoris rufa): first record of Haemoproteus sp. in Italy. Journal of Parasitic Diseases. doi: 10.1007/s12639-020-01211-x.

Venkateswara Rao P, Raman M and Gomathinayagam S (2015) Sporulation dynamics of poultry Eimeria oocysts in Chennai. Journal of Parasitic Diseases 39, 689–692.

Wissler K and Halvorsen O (1977) Helminths from Willow grouse (Lagopus lagopus) in two localities in North Norway. Journal of Wildlife Diseases 13, 409–413.

Zbinden N and Hoerning B (1985) Zum Endoparasitenbefall von Birkhahn (Tetrao tetrix), Alpenschneehuhn (Lagopus mutus) und Steinhuhn (Alectoris graeca). Der Ornithologische Beobachter 82, 117–120.