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Parasites in *Myodes glareolus* and their association with diet assessed by stable isotope analysis

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Vertebrates are hosts to numerous parasites, belonging to many different taxa. These parasites differ in transmission, being through either direct contact, a faecal-oral route, ingestion of particular food items, or by vectors. Assessing the impact of diet on parasitism can be difficult because analysis of faecal and stomach content are uncertain and labourious; and as with molecular methods, do not provide diet information over a longer period of time. We here explored whether the analysis of stable isotopes in hair provides insight into the impact of diet and the presence of parasites in the rodent *Myodes glareolus*. Twenty-one animals were examined for parasites and their hair analysed for stable isotopes (C and N). A positive correlation between δ\(^{15}\)N and one species of intestinal parasite was observed in females. Furthermore, several ectoparasites were negatively correlated with δ\(^{15}\)N, indicating that infections are further associated with foraging habits (size and layout of the home range, length and timing of foraging, interaction with other rodents, etc.) that set the rodents in direct contact with infected hosts. Although a limited number of animals were included, it seemed that the isotope values allowed for identification of the association between diet and parasite occurrence in this rodent. We therefore propose that this method is useful in providing further insight into host biology, feeding preferences and potential exposure to parasites species, contributing to the understanding of the complex relationship between hosts and parasites.

1. Introduction

Complex living environments define the selective pressures for animals and in turn shape their life history development by regulating population size and distribution (Vaughan et al., 2011). Although our insight into the relationship between parasites and hosts is steadily growing, the complexity of multiple infections (polyparasitism) is still not fully understood (Bordes and Morand, 2011) and nor is it quite understood why some host species might harbour more parasites species compared to others (Bordes and Morand, 2015). The nutritional status plays an important role in the outcome of infections because malnutrition will reduce the immune response due to a competition for nutrients and energy between the parasite, host and host defences (Bush et al., 2001). Hosts with better nutrition can better invest in immune responses and thus nutrition profiles can determine parasite prevalence (Neve et al., 2007).

Diet composition can be monitored through a number of methods; they range from visual analyses of stomach content (Andreasen et al., 2017), molecular analysis of faecal samples (Deagle et al., 2009), to assessment of stable isotopes (Panarello and Fernández, 2002; Hobbie et al., 2017; Reid and Koch, 2017). The latter can be used to trace the transfer of energy and matter through the food web because heavy isotopes accumulate at increasing trophic levels (Vaughan et al., 2011; Galetti et al., 2016). Isotope analysis is often preferred because it enables diet assessment over a substantial time period, for example covering the entire period of hair growth (Panarello and Fernández, 2002; Hobbie et al., 2017). Hair stable isotope composition reflects the isotope composition of the food eaten by the animal (Russo et al., 2017). For example, analysis of C stable isotopes enables distinction between consumed plants with different photosynthetic pathways (e.g. CAM, C3 pathways).
or C4 plants) (O’Leary, 1988) and thus carried over to the next trophic level (Jensen et al., 2012). More importantly, it has been shown that δ13C and δ15N values increase through the food chain i.e. is positively correlated with ingestion of animal protein (Petzke et al., 2005; Roth and Hobson, 2000), such that herbivorous animals in a C3-system often have δ13N values of ca. 2‰ while (top) predators have values of ca. 6‰ (Ben-David and Flaherty, 2012). Several studies have investigated trophic interactions by the analysis of stable isotope values and the presence of parasites. Although this has been studied in birds (Robinson et al., 2009) and mammals (rabbits: Boag et al., 1998; seals: Sinisalo et al., 2006; Vega et al., 2018), the majority of research has focused on aquatic environments and especially on fish (Johnson et al., 2004; Bertrand et al., 2011; Locke et al., 2013; Nachev et al., 2017).

Rodentia and Chiroptera are known to be the mammalian orders with the highest parasite diversity (Krasnov et al., 2006). The bank vole, Myodes glareolus (formerly Clethrionomyx glareolus, Schreber 1780), is a small member of the Cricetidae family that inhabits Palearctic forests (Wilson and Reeder, 2005). *M. glareolus* has a particularly wide and presumably plastic diet preferences (Sadowska et al., 2008), although it is generally considered to be herbivorous with a high preference for woody plants (Watts, 1968).

The aim of this study is to assess the association between parasite abundance and C and N stable isotopes in hair of *M. glareolus*. This approach could potentially provide a simple method to study the importance of a systematic diet preference in acquiring different parasites in free-ranging rodents.

2. Material and methods

2.1. Sample collection

Female (*n* = 13) and male (*n* = 8) *Myodes glareolus* specimens were captured in Kongelunden, Denmark (55°34'14.2"N, 12°35'12.7"E). Trapping was conducted in two sampling rounds (September (S1) and October (S2), 2014) with a total of 44 and 80 traps, respectively. Pairs of Ugglan special and Ugglan lemming (Grabhahn AB, Hillerstop, Sweden) were placed approximately 10 m distance apart in ca. 200 m long transects. The traps were baited with oatflakes and apples for 48 h and were left overnight during trapping.

2.2. Parasitological examination

The bank voles were transported to the University of Copenhagen, anesthetized by isoflurane inhalation and sacrificed by cervical dislocation. Immediately following euthanasia each animal was sexed, measured and weighed intact; then the liver and spleen were weighed separately. Shortly after, the liver, spleen, stomach and intestines were measured and weighed intact; then the liver and spleen were weighed. The thoracic area and subdermis were also examined. The coat, ears, nostrils and perianal region were inspected for ectoparasites. The conjunctival sacs were rinsed with physiological saline solution and examined for nematodes. The recovered parasites were preserved in 70% ethanol. The samples were reduced by stepwise exclusion of insignificant variables (PROC CORR). Arguably, a comparison of parasite intensity (δ13C and δ15N, ‰) and body attributes (sex [male, female], liver weight (g), spleen weight (g), body weight (g) and body length (cm)) and sampling rounds (S1 and S2) (PROC GENMOD; dist = normal, SAS 9.4, SAS Institute, Cary, NC, USA). The associations were further examined for simple one-to-one correlations between isotope ratios and each individual body attribute, to assess the risk of confounding (PROC CORR).

The prevalence rate (number of individuals infected/total number) was calculated (PROC FREQ; with exact CI-estimation under the binomial distribution) and the range of intensity was given as minimum and maximum parasite count. Mean abundance and intensity 95% bias-corrected and accelerated (BCa) bootstrap confidence intervals were calculated for each parasite species as suggested by Rózsa et al. (2000). The confidence intervals were calculated using the web tool Quantitative Parasitology, QPweb version 1.0.1.3 (Reiczigel et al., 2013) with the number of bootstrap replications set to 10000. The correlation between parasite abundance was characterised by rank-correlation (PROC CORR Spearman), in order to assess parasite interactions. This was done only for parasite species with prevalence rates ≥10% to avoid potentially weakly supported correlation (Bush et al., 1990).

Generalised linear models (PROC GENMOD, Dist = Poisson, log-linkfunction; and controlling for data heterogeneity by the pscaler-function; SAS 9.4, SAS institute) were used for assessment of the association between the abundance for each parasite that occurred on more than 5 hosts (*n* = 13), the independent effect of body attributes (sex, liver weight, spleen weight, body weight and body length), sampling round and stable isotopes (C and N), in order to assess whether the isotope values provided information beyond traditional simple morphological proxies of body condition and immune response. The models were reduced by stepwise exclusion of insignificant variables (p > 0.05). Arguably, a comparison of parasite intensity – rather than abundance would have been more appropriate for assessing the relationship between parasite infection and other variables, since parasite free individuals might never had been exposed. Similarly, a negative-binomial distribution would have been more appropriate for some parasites, but they were here assessed in identical models using parasite abundance in order to include all individuals and thereby allow direct comparisons.

Given the considerable biological differences between parasites, it was expected that there would be no consistent association between their parasite abundance and hosts diets as assessed from δ13C and δ15N. To assess and illustrate such potential heterogeneity, Pearsons Correlation Coefficient (PROC CORR; SAS 9.4) was used to obtain...
information about the magnitude of association between 13C values and parasite abundance in each sex. The average Correlation Coefficient was calculated from parasites that occurred on at least five individuals (n = 13). The host's body measurements and isotope values are expressed as the range, followed by mean and the S.E.M. in parenthesis.

3. Results

Rodent body length ranged from 8 to 11.2 (9.57 ± 0.19 cm) and the body weight from 17.7 to 34.5 (23.23 ± 1.09 g). The liver and spleen weighed 0.8 to 4.4 (1.65 ± 0.17 g) and 0.04 to 1.9 (0.38 ± 0.11 g), respectively. The values of 13C and 15N ranged from −28.94 to −27.05 (−27.97 ± 0.11‰) and 4.34 to 6.88 (5.19 ± 0.13‰), respectively (Fig. 1). There were significant differences in 13C and 15N values between females and males; 15N values were also related to season (Table 1). There were no apparent correlation between isotope ratio variation and body attributes (liver weight, spleen weight, body weight and body length) in the generalised linear models and nor in simpler one-to-one correlation analyses (8 analyses, p > 0.22).

All voles had ectoparasites and 90% were infected with endoparasites. A total of 699 endoparasites and 2753 ectoparasites were collected (Table 2). Ectoparasites such as Laelaps hilaris and Hyperlalaps microti were the most prevalent (95% CI: 76–99 and 90% CI: 69–98, respectively) and Listrophorus brevipes had the highest mean abundance (97.9 CI: 42.8–216) per host. Among the endoparasites, Heligmosoides glareoli had the highest prevalence (52% CI: 29–74) and Rhabditis orbitalis the highest mean intensity and abundance (97.5 CI: 16.3–213 and 27.8 CI: 4.8–79, respectively) per host.

Spearman’s rank correlation coefficient (rs) showed that the common parasite species had significant correlations with up to 3 other species of parasites (Table 3), which did not indicate widespread interactions between parasites.

The Generalised Linear Model of parasite abundance (Table 4) showed that the load of only one parasite was correlated with host sex. Seasonal variation was indicated for several ectoparasites (Ctenophthalmus agyrtis, Myocoptes japonensis, L. brevipes and H. microti) and one endoparasite (H. glareoli). Rodent’s body weight was correlated with Trichuris sp., Dermarcarus hypudaei, Radfordia lemmina and L. hilaris; body size was correlated with ectoparasites D. hypudaei and L. brevipes (negative and positive, respectively). The nematode R. orbitalis, as well as the mites M. japonensis and L. brevipes were significantly correlated with liver weight. Spleen weight was found positively correlated with R. orbitalis and negatively with D. hypudaei and R. lemmina. Three species of ectoparasites (Trichoeclis tenax, R. lemmina and L. brevipes) and one endoparasite (H. glareoli) were correlated to either 13C or 15N. Notably, the parasite with the largest range in intensity showed clear effect of 15N and sampling round (Fig. 2).

The association between isotopes and parasite abundance included both positive and negative associations, indicating that the correlations across parasites are quite variable. For simple one-to-one correlation between endoparasites and 13C and 15N the average Pearsons Correlation Coefficients ranged from −0.20 to 0.34 (0.08 ± 0.16) and 0.01 to 0.39 (0.06 ± 0.17) respectively. For ectoparasites it ranged from −0.04 to 0.36 (−0.07 ± 0.10) for 13C and −0.001 to 0.43 (−0.10 ± 0.11) for 15N. The average Pearsons Correlation Coefficient for correlations between 13C and endoparasites were positive for both males and females, but not significantly (Fig. 3). There was no consistent correlation for 15N (Fig. 3). Here females with lower 13C levels had negative correlations, while males with higher 13C levels had positive correlations.

4. Discussion

The average of the 13C values (−27.97 ± 0.11‰) indicates that the rodents fed mainly on C3 plants (OLeary, 1988), while the range indicates that they all ingested food items at a higher trophic level. Large ranges in isotope levels have been found in other rodent species (Baitensperger et al., 2015) and have also been previously found in M. glareolus (Balciuskas et al., 2016). The variation in the isotope values between sexes might indicate differences in foraging habits in this species. Moreover, values of 15N related to sampling round indicate a seasonal change in diet (Fig. 1), but there was no apparent correlation to other host attributes such as body weight and length. This suggests that the isotope ratios carry added information on the individual hosts.

It should be noted that there were positive correlations between some ectoparasites (M. japonensis with C. agyrtis and T. tenax), but most of the correlations between members of this group were negative (Table 3). Negative correlations between ectoparasite species could indicate competition or interference due to their shared distribution on the host’s body. A negative correlation was also present between the intestinal helminths H. glareoli and Parasitoclypeus amphiades.

From the 13 species of parasites analysed under the generalised linear model (Table 4), four were significantly correlated with 13C or 15N. The results indicate that the abundance of the endoparasite H. glareoli is higher in rodents foraging in a higher trophic level and the

Table 1

| Parameter          | Estimate | SE  | Wald 95% Conf. Limits | Wald Chi-Sq | Pr > ChiSq | AIC  |
|--------------------|----------|-----|-----------------------|-------------|------------|------|
| 15N                | Intercept| 5.79| 0.15                  | 5.50        | 6.09       | 1462.89| <.0001 | 24.8 |
| S1 vs S2           | −0.56    | 0.19| −0.93                 | −0.20       | 9.07       | 0.0026|          |      |
| Females vs. Males  | −0.58    | 0.19| −0.96                 | −0.21       | 9.30       | 0.0023|          |      |
| Intercep           | −27.62   | 0.14| −27.90                | −27.34      | 38040.70   | <.0001| 23.1   |      |
| Females vs. Males  | −0.57    | 0.18| −0.92                 | −0.22       | 9.99       | 0.0016|          |      |
| Scale              | 0.40     | 0.00| 0.40                  | 0.40        |            |      |        |      |
abundance of the ectoparasites *T. tenax*, *R. lemminala* and *L. brevipes* is higher in rodents feeding on a lower trophic level. The positive correlation found between *H. glareoli* with sex, sample round and δ¹⁵N indicates that this nematode is present in a higher number in females with a Nitrogen enriched diet in September (S1). Female-biased parasitism has been previously reported in bank voles (Grzybek et al., 2015), and as in our study, foraging habits of females were related to the exposure to an endoparasite.

Another parasite significantly correlated with sample round and isotope levels is *L. brevipes*. The results for this particular mite translates into large sized rodents feeding mainly in a low Nitrogen enriched diet present a high number of this mite, which further increases later in the season (Fig. 2). A possible explanation for this correlation is that older rodents, which have larger bodies, offer more host area for *L. brevipes* and have different foraging habits than younger rodents.

It should be noted that while we found significant correlation for three out of the six mite species present on more than 5 of the rodents, the association across parasite groups were quite variable (Fig. 3). The variable association can be due to the diversity of parasite biology and the varying impact of other important factors, which clouds the impact of diets and foraging habits.

Seasonal variation in the parasitic numbers can be related to abiotic factors that allow better development of the parasite as well as to changes in the bank vole’s population. Such seasonal effects have already been documented for mites (Zhang et al., 2010) and for helminths (Abu-Madi et al., 2000) and is usually explained by differences in environmental factors and increasing host densities that affect parasite transmission. This could explain why *H. glareoli*, *C. agyrtes* and *M.

### Table 2

Parasite infracomunity structure of 21 Myodes glareolus collected in September and October.

| Parasites | Prevalence % (CI 95%) | Range of intensity | Mean intensity (CI 95%) | Mean abundance (CI 95%) | Infection site | Transmission route |
|-----------|------------------------|-------------------|------------------------|-------------------------|----------------|------------------|
| **ENDOPARASITES** | | | | | | |
| **Nematodes** | | | | | | |
| Heligmosomoides glareoli | 52 (9-74) | 1-24 | 4.18 (1.91-11.2) | 2.19 (0.86-6.09) | Intestine | Faecal-Oral |
| Rhadinostomum orbitalis | 28 (11-52) | 2-275 | 97.5 (16.3-213) | 27.9 (4.48-79) | Eye | Contact |
| Trichurus sp. | 23 (14-56) | 1-4 | 1.29-2.86 | 0.67 (0.29-1.24) | Cecum | Faecal-Oral |
| **Trematodes** | | | | | | |
| Corrigia vitta | 19 (5-41) | 3-14 | 8 (4.25-12.2) | 1.52 (0.38-3.95) | Pancreatic ducts | I. H. |
| **Cestodes** | | | | | | |
| Paragonimopsulcma ophiomaleholades | 19 (2-35) | 1-3 | 1.75 (1-2.5) | 0.33 (0.05-0.76) | Intestine | I. H. |
| Hydatigina uncertain | 23 (8-47) | 1-7 | 3 (1-5) | 0.71 (1.43-1.9) | Liver (cysts) | Oral |
| **ECTOPARASITES** | | | | | | |
| *Fleas* | | | | | | |
| Ctenophthalmus agyrtes | 57 (35-78) | 1-10 | 2.58 (1.58-4.83) | 1.48 (0.76-2.95) | Body surface | Contact |
| Megabothris walkerii | 33 (13-53) | 1-3 | 1.86 (1.14-2.43) | 0.62 (0.34-1.1) | Body surface | Contact |
| Catallagia dacenkoi dacenkoi | 4 (0-23) | 1 | 1 (0/a) | 0.05 (0-0.14) | Body surface | Contact |
| *Lice* | | | | | | |
| Hystricopsylla orientalis | 4 (0-23) | 1 | 1 (0/a) | 0.05 (0-0.14) | Body surface | Contact |

**Note**: I.H. refers to the ingestion of an intermediate host; contact refers to direct contact between rodents.

Table 3

| Output from Spearman's rank correlation test between parasite species with prevalence ≥ 10% in 21 Myodes glareolus. |
|---------------------------------------------------------------|
|                   | H. g. | R. o. | T. sp. | C. v. | P. o. | C. a. | C. d. | D. h. | M. j. | T. t. | R. l. | L. h. |
| **Nematodes**     |       |       |       |       |       |       |       |       |       |       |       |       |
| H. glareoli (H. g.) | 1.00  |       |       |       |       |       |       |       |       |       |       |       |
| R. orbitalis (R. o.) | −0.14 |       |       |       |       |       |       |       |       |       |       |       |
| Trichurus sp. (T. sp.) | −0.15 | −0.03 |       |       |       |       |       |       |       |       |       |       |
| **Trematodes**    |       |       |       |       |       |       |       |       |       |       |       |       |
| C. vitta (C. v.)  | −0.1  | 0.3   |       |       |       |       |       |       |       |       |       |       |
| **Cestodes**      |       |       |       |       |       |       |       |       |       |       |       |       |
| P. ophiomaleholades (P. o.) | −0.47* | −0.03 | 0.17 | 0       |       |       |       |       |       |       |       |       |
| **Fleas**         |       |       |       |       |       |       |       |       |       |       |       |       |
| C. agyrtes (C. a.) | 0.42  | −0.37 | −0.15 | −0.12 | −0.34 |       |       |       |       |       |       |       |
| C. dacenkoi (C. d.) | −0.21 | −0.14 | 0.33  | 0.54*  | −0.11 | −0.23 |       |       |       |       |       |       |
| **Mites**         |       |       |       |       |       |       |       |       |       |       |       |       |
| D. hypudaii (D. h.) | −0.2  | −0.05 | −0.13 | −0.16 | 0.15  | −0.07 | −0.15 |       |       |       |       |       |
| M. japonensis (M. j.) | 0.55* | 0.15  | −0.04 | 0.04  | −0.33 | 0.56**| −0.25 | −0.13 |       |       |       |       |
| T. tenax (T. t.)  | 0.19  | 0.54* | 0.09  | 0.04  | −0.19 | −0.02 | −0.17 | −0.26 | 0.44* |       |       |       |
| R. lemminala (R. l.) | 0.02  | −0.08 | 0.58**| 0.44* | 0.04  | 0.15  | 0.29  | −0.12 | 0.19* | 0.16  |       |       |
| L. helialis (L. h.) | −0.55 | 0.10  | 0.21  | 0.21  | 0.49* | 0.49* | 0.11  | 0.21  | −0.45*| −0.09 | −0.04 |       |
| H. microti (H. m.) | −0.31 | 0.25  | −0.33 | −0.15 | 0.23  | −0.31 | −0.13 | −0.01 | −0.41 | −0.06 | −0.55**| 0.09 |

**Note**: An asterisk indicates the significance level (p < 0.05) and two asterisks (p < 0.01).

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japonensis were more abundant in September (S1) and L. brevipes and H. microti in October (S2).

As stated previously, parasites and hosts have a complex association and therefore differences in the host's characteristics and behaviour have an impact on the exposure to parasites and similarly, parasite characteristics will have an influence on the host (Krasnov et al., 2006). Accordingly, in this study parasite abundance was found to be correlated to host's traits such as body weight, size and also liver and spleen weight. Although these traits have been previously found correlated to parasitism (Gowan et al., 2009; Hayward et al., 2017), some studies have not found enough evidence for these correlations (Schulte-Hostedde and Elsasser, 2011; Sackett, 2018). In accordance with Sackett (2018) we consider these associations challenging to explain in detail, because of the complexity of the factors contributing to these correlations, especially in free-ranging rodents.

The interpretation of the correlations between stable isotopes and parasite infection must be considered with caution because a number of relevant factors, such as the occurrence of other parasites were excluded from the analysis. Still, the method allowed the identification of associations between parasitic occurrences and foraging habits of this rodent. The advantages of this method are: the use of a model animal with a broad diet, easy sample collection, assessment of diet and foraging habits over a long period of time and the tracing of energy transfers throughout the foodweb, - which has been previously studied with a broad diet, easy sample collection, assessment of diet and foraging habits over a long period of time and the tracing of energy transfers throughout the foodweb, - which has been previously studied with stable isotopes (Panarello and Fernández, 2002; Vaughan et al., 2017). Additionally, this method can provide an insight into host biology by capturing the difference in foraging habits of rodents and its association with potential parasitism (Cowan et al., 2009; Hayward et al., 2017), some studies have not found enough evidence for these correlations (Schulte-Hostedde and Elsasser, 2011; Sackett, 2018). In accordance with Sackett (2018) we consider these associations challenging to explain in detail, because of the complexity of the factors contributing to these correlations, especially in free-ranging rodents.

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To conclude, this method allows for correlation of infection with certain parasites to the bank vole's foraging habits, exposing the

Table 4

Output from analysis of parasite abundance in 21 Myodes glareolus that included the independent effects of body attributes (sex, liver weight, spleen weight, body weight and body length), sampling round (S1 or S2) and hair 13C and 15N values. In all analyses, more than five individuals were infected with the given parasite. Insignificant variables (p < 0.05) were step-wise removed.

| Taxa (no of non-zero values) | Parameter | Estimate | SE | Wald 95% Conf. Limits | Wald Chi-Sq | Pr > ChiSq | AIC |
|-----------------------------|-----------|----------|----|-----------------------|-------------|------------|-----|
| Heligmosoides glareoli      | Intercept | −24.81   | 4.42| −33.47                | 16.15       | 31.50 <.0001| 57.8 |
| (11) S1 vs. S2              |            |          |    |                       |             |            |     |
| Female vs. males            |           |          |    | −20.67                | 18.34       | 2.90       | 80.9 |
| Rhabditis orbitalis         | Intercept  | −1.76    | 2.29| −6.25                 | 2.72        | 0.59       | 0.4410| 864.6|
| (6) Liver weight            |           |          |    |                       |             |            |     |
| Spleen weight               |            |          |    |                       |             |            |     |
| Trichurus sp.               | Intercept  | −5.25    | 1.74| −8.66                 | 1.85        | 0.97       | 0.0023| 41.8 |
| (7) Body weight             |            | 0.19     | 0.06| 0.07                  | 0.31        | 9.84       | 0.0017|     |
| Capnophthalmus asperatus    | Intercept  | −0.54    | 0.58| −1.67                 | 0.60        | 0.87       | 0.3516| 75.3 |
| (12) S1 vs. S2              |            | 1.52     | 0.66| 0.23                  | 2.81        | 5.34       | 0.0208|     |
| Dermacarus hypudasi         | Intercept  | 9.15     | 4.34| 6.55                  | 17.66       | 4.45       | 0.0349| 58.6 |
| (7) Spleen weight           |            | −158.72  | 48.28| −233.35               | −44.08      | 8.25       | 0.0041|     |
| Body weight                 |            | 0.53     | 0.14| 0.27                  | 0.80        | 15.49      | 0.0001|     |
| Body length                 |            | −2.19    | 0.72| −3.60                 | −0.78       | 9.30       | 0.0023|     |
| Myocoptes japonensis        | Intercept  | −2.77    | 1.85| −6.39                 | 0.85        | 2.25       | 0.1335| 129  |
| (13) S1 vs. S2              |            | 2.02     | 0.90| 0.25                  | 3.79        | 4.98       | 0.0256|     |
| Liver weight                |            | 38.16    | 18.33| 73.50                 | 4.48        | 0.0343     |     |
| Trichoecus tenax            | Intercept  | −103.05  | 32.89| −167.52               | −38.58      | 9.82       | 0.0017| 237.4|
| (8) d13C                    |            | −3.70    | 1.15| −5.95                 | −1.45       | 10.39      | 0.0013|     |
| Radfordia lemnina           | Intercept  | 7.19     | 3.03| 1.25                  | 13.13       | 5.63       | 0.0177| 56.8 |
| (9) d15N                    |            | −2.32    | 0.60| −3.49                 | −1.15       | 15.11      | 0.0001|     |
| Spleen weight               |            | −39.43   | 16.63| −72.02                | −6.84       | 5.62       | 0.0177|     |
| Body weight                 |            | 0.21     | 0.04| 0.13                  | 0.29        | 27.93      | 0.0001| 1475.1|
| Lisophorus brevis           | Intercept  | 14.76    | 3.75| 7.42                  | 22.11       | 15.52      | 0.0001|     |
| (17) S1 vs. S2              |            | −5.34    | 1.26| −7.81                 | −2.88       | 18.03      | 0.0001|     |
| d15N                        |            | −2.32    | 0.52| −3.35                 | −1.30       | 19.66      | 0.0001|     |
| Liver weight                |            | 42.65    | 19.72| −81.24                | −3.95       | 4.67       | 0.0308|     |
| Body weight                 |            | 0.59     | 0.28| 0.05                  | 1.13        | 4.64       | 0.0312|     |
| Laelaps hilaris             | Intercept  | −0.24    | 0.88| −1.96                 | 1.49        | 0.07       | 0.7890| 164.8|
| (20) Body weight            |            | 0.09     | 0.03| 0.02                  | 0.16        | 7.15       | 0.0075|     |
| Hyperlaelaps microti        | Intercept  | 2.58     | 0.19| 2.22                  | 2.95        | 194.56     | 0.0001| 194  |
| (19) S1 vs. S2              |            | −0.81    | 0.37| −1.54                 | −0.08       | 4.79       | 0.0286|     |

Note: No significant correlation was observed for Megabothris walker (7) or Ixodes ricinus (10).

Fig. 2. The relationship between parasite intensity and 15N values for the mite Lisophorus brevis in September (S1) and October (S2) samples of Myodes glareolus. Note the log-scale for parasite abundance.
expected links to differences in foraging habits. Here it is suggested that, rodents with low nitrogen in their diet presented more ectoparasites and in contrast, feeding at higher trophic levels was associated with endoparasitic infection. Additional contributions to these associations could arise from other mechanisms i.e., for ectoparasites it can includes 13 parasites occurring on 5 or more individuals and indicate consistent correlations for endoparasites and δ15N, while this is not the case for δ13C.

**Fig. 3.** The average Pearsons Correlation Coefficient (error bars: SE) between abundance and δ13C and δ15N for the two parasite groups: ecto and endoparasite for females (left) and males (right). The data includes 13 parasites occurring on 5 or more individuals and indicate consistent correlations for endoparasites and δ15N, while this is not the case for δ13C.

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**Declarations of interest**

None.

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