Journal of Helminthology (2015) **89,** 175–181 doi:10.1017/S0022149X13000710
© *Cambridge University Press 2013*

Why are the prevalence and diversity of helminths in the endemic Pyrenean brook newt *Calotriton asper* (Amphibia, Salamandridae) so low?

M. Comas[1]* and A. Ribas[1,2]

[1]Laboratory of Parasitology, Faculty of Pharmacy, University of Barcelona,
Avda Diagonal s/n, 08028 Barcelona, Spain: [2]Museu de Granollers-
Ciències Naturals, Francesc Macià 51, 08402 Granollers, Spain

(Received 15 May 2013; Accepted 23 September 2013; First Published Online 25 October 2013)

Abstract

A cornerstone in parasitology is why some species or populations are more parasitized than others. Here we examine the influence of host characteristics and habitat on parasite prevalence. We studied the helminths parasitizing the Pyrenean brook newt *Calotriton asper* ($n = 167$), paying special attention to the relationship between parasites and ecological factors such as habitat, sex, ontogeny, body size and age of the host. We detected two species of parasites, *Megalobatrachonema terdentatum* (Nematoda: Kathlaniidae) and *Brachycoelium salamandrae* (Trematoda: Brachycoeliidae), with a prevalence of 5.99% and 1.2%, respectively. Marginally significant differences were found in the prevalence between sexes, with females being more parasitized than males. The present results show significant differences in the body length of paedomorphic and metamorphic individuals, the former being smaller. Nevertheless, no significant correlations between parasite prevalence and either newt body length, ontogenetic stage or age were found. In comparison with other Salamandridae living in ponds, prevalence and diversity values were low. This may be due to a long hibernation period, the species' lotic habitat and its reophilous lifestyle, which probably do not allow for a high parasite load.

Introduction

Host–parasite interactions may vary in accordance with ecological factors, habitat characteristics and phylogeny (Dobson, 2009; Lafferty, 2009; Akoll *et al.*, 2011). An interesting question in parasitology is why some species or populations are more parasitized than others. Information on this issue is scarce, and studies on a number of species and environments are necessary in order to understand the diversity of parasitism. Here we examine the influence of host characteristics and habitat on parasite prevalence in a reophilous newt member of the Salamandridae, the Pyrenean brook newt *Calotriton asper* (Dugès, 1852).

To our knowledge, there are no previously published studies of the helminths of the genus *Calotriton*. Nevertheless, other Salamandridae have been studied (Barus & Groschaft, 1962; Barus *et al.*, 1963; Vojtková *et al.*, 1963; Vojtek & Vojtkova, 1972; Sattmann, 1986, 1990; Shimalov *et al.*, 2001; Yildirimhan, 2008; Yildirimhan & Öz, 2008), including the Corsican brook newt *Euproctus montanus*, which shares a similar reophilous lifestyle with *Calotriton*. The Corsican brook newt has been found to harbour *Brachycoelium salamandrae* (with a prevalence of 25% and from 1 to 36 individuals per host) and *Acanthocephalus falcatus* (with a prevalence of 13% and from 1 to 5 individuals per host) (Combes & Knoepfler, 1968).

---

*E-mail: mar.comasmanresa@gmail.com

https://doi.org/10.1017/S0022149X13000710 Published online by Cambridge University Press

Therefore, the study of the parasitic helminths of this reophilous newt has an inherent interest if compared with the parasitological fauna of other newts that inhabit lentic waters. These lentic habitats have more trophic resources and so it is likely that there will be greater diversity and density of invertebrates that can act as intermediate hosts for parasites with complex life cycles. Thus, it is to be expected that newts inhabiting lentic waters, such as *Lissotriton* and *Triturus*, will have greater helminth diversity and levels of infestation than reophilous newts such as *C. asper.*

We also compared prevalence between metamorphic and paedomorphic individuals, which use habitats in different ways. Paedomorphic individuals show a fully aquatic life cycle but metamorphics have a terrestrial life stage. The habitat or use of habitat could determine the richness of helminth communities in amphibians. In fact, amphibians with semi-aquatic life cycles show a peak in helminth species richness (Aho, 1990; Hamann *et al.*, 2013). Furthermore, as far as we know, no previous studies have ever been undertaken on the prevalence of infection in ontogenetic stages. Moreover, one might expect certain species to show a sex-biased prevalence due to sexual dimorphism in body size or different life span depending on sex. Also, age-biased prevalence might occur due to differences in immune defences depending on age (Dare & Forbes, 2008).

The Pyrenean brook newt is endemic to the Pyrenees and nearby mountain ranges. The only other member of its genus is the Montseny brook newt *Calotriton arnoldi* Carranza & Amat, 2005. Although sub-adults have a terrestrial life stage (García-París *et al.*, 2004), adults essentially occur in cool, oligotrophic, well-oxygenated mountain streams. The species is found at altitudes between 700 and 2500 m (Carranza & Amat, 2005) and is widely distributed throughout most of the Pyrenees (Andorra, France and Spain) and pre-Pyrenees (see fig. 1). Its large geographic range and wide vertical distribution greatly influence this species' annual activity period, which varies from 3 to 12 months (García-París *et al.*, 2004). The Pyrenean brook newt generally shares its habitat with only one other caudate, *Salamandra salamandra*, which as an adult is terrestrial but whose larvae co-occur in syntopy with those of *C. asper*.

In this first-ever study of the helmintofauna of the Pyrenean brook newt, we examined the influence of habitat and factors such as the sex, ontogeny (paedomorphosis or metamorphosis), body size and age of the host on prevalence and parasite richness. We also tested for possible differences in prevalence in Pyrenean populations.

Materials and methods

Collection and examination of newts

A total of 167 preserved Pyrenean brook newts from the following institutions were studied: Muséum National d'Histoire Naturelle de Paris (MNHN), Museo Nacional de Ciencias Naturales de Madrid (MNCN), Museu de Granollers de Ciències Naturals (MDGCN) and Museu de Zoologia de Barcelona (MZB), along with individuals from private collections. The studied newts came from several localities homogeneously distributed throughout the Pyrenees (fig. 1) and the sample used was a representative sample of the whole population of

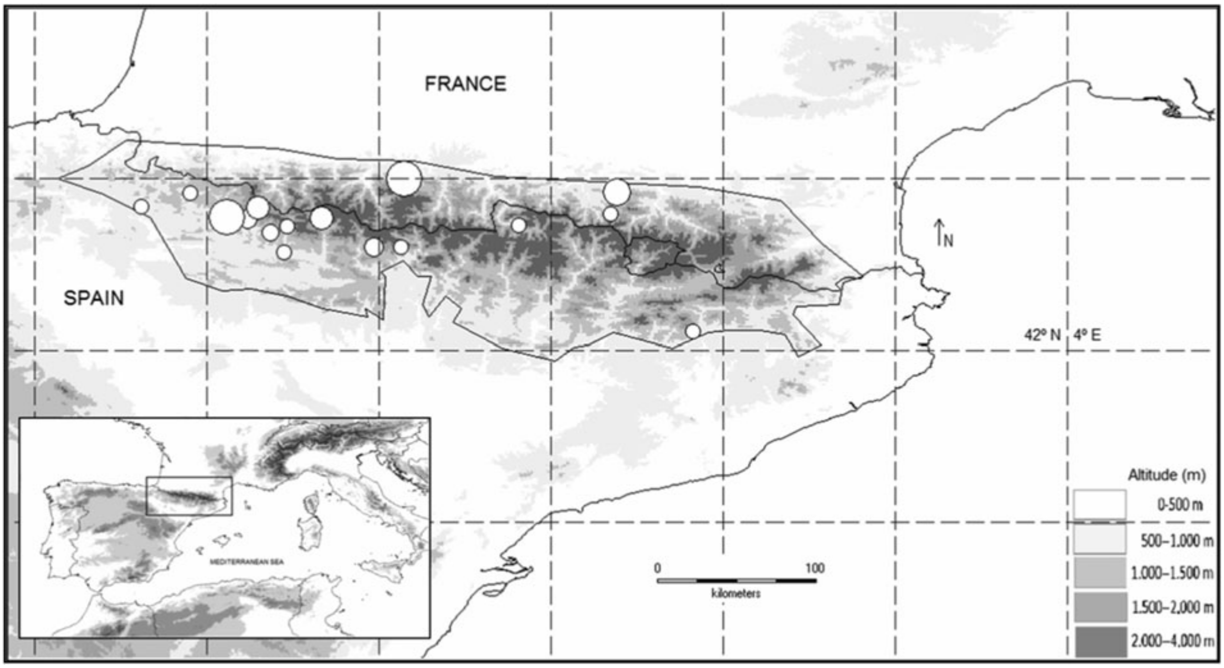

Fig. 1. The distribution and collecting sites of *C. asper* in the Pyrenees; circle size (○) is approximately proportional to the size of the sample collected from each point; smaller circles have been magnified (×4) for clarity.

https://doi.org/10.1017/S0022149X13000710 Published online by Cambridge University Press

C. asper (Milá *et al.*, 2010). Localities from Spain were: Ibón Acherito and Barranco de Acherito (42.8°N, 0.9°W), Escuaín Cuello Viceto (42.6°N, 0.1°E), San Juan de la Peña (42.6°N, 0.6°W), Canfranc, Ibón de Ip (42.7°N, 0.5°W), Sallent de Gallego (42.8°N, 0.3°W), Aísa (42.7°N, 0.6°W), Fanlo, Valle de Añisclo (42.6°N, 0°W), Selva de Oza (42.8°N, 0.7°W), Alto Aragón (42.8°N, 0.8°W), Huesca, Aragon; Ochagavía (42.9°N, 1.1°W) and Ustárroz (42.8°N, 1.5°W), Navarre; Vall d'Aran (42.7°N, 0.8°E) and Berga (42.1°N, 1.8°E), Catalonia. Localities from France were: Bagnères de Bigorre, Torrent de Castelmouly, Hautes Pyrénées (43.0°N, 0.1°E), Aulus-les-Bains (42.8°N, 1.3°E) and Ariège (42.9°N, 1.4°E).

Before dissection, the following biometric measurements were taken: length from snout to posterior side of the cloacal protuberance (snout–vent length; SVL), length from posterior angle of the cloacal protuberance to tip of tail (tail length; Tail.L) and total length (TL), where TL = SVL + Tail.L (table 1).

Measurements were taken to the nearest 0.01 mm using a digital calliper. Other than the newts whose state of preservation was deficient, all the brook newts dissected were included in the biometrical analyses. Sex was determined by vent morphology and tail length (shorter in males) and confirmed after dissection by examination of the gonads. The sex ratio was almost 1:1 (75 males and 76 females). The presence of paedomorphosis was determined by examining gill development (Denoël, 2002; Denoël *et al.*, 2005, 2009). A total of 22 paedomorphic individuals (with gills and/or gill slits) were analysed. Individuals were classified as either adult or juveniles according to the presence of mature gonads (151 adults and 15 juveniles).

The gastrointestinal tract (oesophagus, stomach, and small and large intestines), as well as the lungs, urinary bladder, liver, heart and kidneys, were dissected and placed separately in Petri dishes containing 0.9% saline solution. Then they were examined separately for helminths under a stereomicroscope. Recovered helminths were placed in vials in 70% ethanol for subsequent examination. Nematodes were examined on a temporary mounting in Amann lactophenol. Trematodes were post-fixed in Bouin's solution, stained in Semichon's acetocarmine and mounted in Canada balsam. Helminth identification was carried out according to the literature (López-Neyra, 1947; Hartwich, 1960; Căpuşe, 1967; Ribas *et al.*, 2010). A subset of helminths recovered was deposited in the Museu de Zoologia de Barcelona (MZB), Catalonia, Spain, with accession numbers MZB 2013–2609 (*Megalobatrachonema terdentatum*) and MZB 2013–2610 (*Brachycoelium salamandrae*).

Data analysis

In order to determine differences in parasite populations and the proportion of infected hosts, prevalence, mean abundance and mean intensity were calculated for each helminth species according to Bush *et al.* (1997). Mean diversity or mean species richness is the sum of helminth species per individual divided by the total sample size. Numerical dominance was determined using the Berger–Parker dominance index (Berger & Parker, 1970). One-tailed Fisher exact tests were performed to analyse the effects of sex, ontogenetic stage (paedomorphosis or metamorphosis) and age on both parasite prevalence and parasite richness. The effect of host sex on parasite abundance and intensity was tested using a Mann–Whitney (*U*) test, given that data did not follow a normal distribution (according to a Kolmogorov–Smirnov test). When data followed a normal distribution and showed homoscedasticity, Student's *t*-test was used, specifically to test sexual dimorphism in body size and differences in body length (SVL) according to ontogenetic stage and age. Logistic regression analysis was used to determine the differences in both parasite prevalence and parasite richness (as dichotomous dependent variables) related to host body length (as a continuous independent variable). A logistic regression analysis was performed in order to test possible differences in prevalence (as a dichotomous dependent variable) depending on the newts' distribution (latitude and longitude as continuous independent variables). Means of descriptive statistics are given with the standard deviation. All statistical analyses were performed using STATISTICA 10.0 (StatSoft Inc., Tulsa, Oklahoma, USA).

Results

The helminth community of the Pyrenean brook newts consisted of two species with a total prevalence of 7.2%. Both recovered species were present at low levels of prevalence. The nematode *Megalobatrachonema terdentatum* (Linstow, 1890) showed a prevalence of 5.99%, mean intensity of 3 and mean abundance of 0.192 ± 0.1. The trematode *Brachycoelium salamandrae* (Frolich, 1789) showed a prevalence of 1.2%, mean intensity of 1 and mean abundance of 0.012 ± 0.1. *Megalobatrachonema terdentatum* had the highest prevalence, abundance and intensity and had a Berger–Parker index value of 0.34. Thus, *M. terdentatum* can be considered a core species, unlike the scarce *B. salamandrae*, of which only two individuals were recovered. The mean diversity was 0.072. Only 12 parasitized newts were found, all with

Table 1. Descriptive statistics (snout–vent length (SVL), total length (TL), mean ± SD, in mm) of *Calotriton asper* relative to sex and ontogenetic stages; *n* = sample size.

	Juveniles	Males	Females	Paedomorphics	Metamorphics
n	13	73	70	21	127
SVL	42.23 ± 4.99	57.68 ± 7.08	55.59 ± 7.34	49.99 ± 10.21	56.37 ± 7.38
TL	76.72 ± 9.33	100.31 ± 9.78	104.77 ± 11.14	88.99 ± 16.57	102.01 ± 10.53

https://doi.org/10.1017/S0022149X13000710 Published online by Cambridge University Press

just one helminth species and 1–11 individuals; the remaining individuals (155) were found to be uninfected.

No sexual dimorphism was found with respect to snout–vent length ($T_{140} = 1.6$, $P = 0.1$). Nevertheless, marginally significant differences were found in prevalence between sexes (Fisher exact test, $P = 0.067$), with females being more parasitized than males (prevalence in males was 4% and in females was 11.84%). However, there were no significant differences in either parasite abundance by sex (mean abundance in males = 0.08 ± 0.43 and in females = 0.34 ± 1.47; $U = 11.5$, $P = 0.72$) or by intensity (mean intensity in males = 2 ± 1 and in females = 2.89 ± 3.48; $U = 11.5$, $P = 0.71$).

Paedomorphic individuals showed smaller snout–vent length than metamorphic ones ($T_{146} = 3.46$, $P < 0.001$), and as expected, immatures were smaller than adults ($T_{153} = 7.05$, $P < 0.001$). Nevertheless, no significant differences were found in the prevalence of infection as a result of snout–vent length (chi-square = 0.047, df = 1, $P = 0.828$, fig. 2). Although no parasitized paedomorphic or immature individuals were found, there were no significant differences in prevalence between paedomorphic and metamorphic individuals (Fisher exact test, $P = 0.158$), either in adults or immature individuals ($P = 0.285$). Lastly, our results showed that in the Pyrenees there are no significant differences in prevalence depending on the newts' distributions (longitude or latitude; chi-square = 2.438, df = 2, $P = 0.295$).

Given that only one parasite species was found in parasitized individuals, parasite richness had exactly the same pattern as prevalence for all the host ecological factors studied.

Discussion

The helminth community in the Pyrenean brook newts was composed of only two species, each present with low prevalence, intensity and diversity. To our knowledge, these low values of prevalence, intensity and diversity are the lowest recorded to date in amphibians, at least, that is, with a sample size as large as ours (Sattmann, 1986, 1990; Aho, 1990; Paredes-Calderón *et al.*, 2004; Hamann *et al.*, 2006; Hamann *et al.*, 2013). The mean species richness per individual host recorded in other amphibian species in temperate regions is 0.8 (Aho, 1990), much less than in amphibian species from tropical regions, where values range from 2.4 to 3.49 (Paredes-Calderón *et al.*, 2004; Hamann *et al.*, 2006). The mean diversity values per host found in the present study were much lower (0.072), even in comparison with those reported for other temperate regions (0.7 on average for Caudata; Aho, 1990). Only two species of helminths were found within a large sample size, a surprisingly low number in comparison with other newts in which the number of helminths reported ranges from 3 to 11, even with much smaller sample sizes (Aho, 1990). In comparison with studies with similarly large sample sizes, the diversity found for the Pyrenean brook newt was much smaller than in other species, such as *Nothophtalmus viridescens* which harbours six helminth species (n = 127) (Aho, 1990).

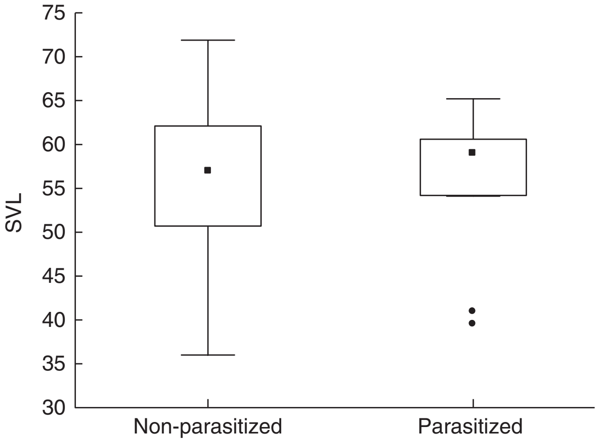

Fig. 2. The relationship between snout–vent length (SVL, mm) of Pyrenean brook newts and parasitic status, with median values (black squares), ranges between the quartiles 25 and 75 (boxes) and ranges between non-outliers (bars) and outliers (black circles).

In fact, parasite richness exhibited exactly the same pattern as parasite prevalence for all the ecological factors studied, since all parasitized individuals harboured just one helminth species. Given the low levels of parasite richness found in this study, the likelihood of a newt being parasitized by one helminth species is 0.07, while the likelihood of it being parasitized by two helminth species is 0.005. Thus, even with a large sample size, it is highly unlikely that a newt will be parasitized by two helminth species. Consequently, the helminth communities in the present study may be considered as pauperized, particularly in comparison with helminth communities found in other amphibians (Combes & Knoepfler, 1968; Sattmann, 1986, 1990; Aho, 1990; Shimalov *et al.*, 2001; Paredes-Calderón *et al.*, 2004; Hamann *et al.*, 2006; Yildirimhan, 2008; Yildirimhan & Öz, 2008; Hamann *et al.*, 2013).

Calotriton asper was found to be infected with one nematode species, *M. terdentatum*, and a trematode species, *B. salamandrae*, thereby adding to the list of species known to host these parasites. Although both of these helminth species are widely distributed throughout Europe (Combes & Knoepfler, 1968; Galeano *et al.*, 1990; Yildirimhan *et al.*, 2005), to our knowledge, neither has previously been recorded in the study area.

Both detected helminths have an indirect life cycle. In the nematode *M. terdentatum* the intermediate hosts are molluscs (Planorbidae), tadpoles and annelids (Petter & Chabaud, 1971), while in the genus *Brachycoelium*, terrestrial molluscs act as first intermediate hosts (Cheng, 1960; Jordan & Byrd, 1967). *Megalobatrachonema terdentatum* has been found in the sister group *Triturus*, with prevalence ranging from 71.4 to 80% (Shimalov *et al.*, 2001), as well as in the alpine newt *Ichthyosaura alpestris*, with prevalence ranging from 25 to 28.6% (Sattmann, 1986, 1990). Such values are much higher than those found in *C. asper* during this study. *Brachycoelium salamandrae* was only found in two individuals (from a total of 167) with a very low prevalence (1.2%), particularly in comparison with other caudates such as *Euproctus montanus*, *Mertensiella caucassica* and *Salamandra*

https://doi.org/10.1017/S0022149X13000710 Published online by Cambridge University Press

salamandra, in which prevalences range between 14 and 43% (Combes & Knoepfler, 1968; Yildirimhan *et al.*, 2005; Ribas *et al.*, 2010).

The results of the present study show that females are more parasitized than males. In many populations, females live longer than males (Montori, 1990; Miaud & Guillaume, 2005) and so one would expect females to have greater parasite loads. Moreover, no parasitized immature individuals were found. This may reflect infrequent infection in young newts, as occurs in other species (Aho, 1990; Sanchis *et al.*, 2000), possibly because larger individuals harbour more helminths owing to their greater exposure to parasite transmission. However, the present results do not show any significant differences in parasite prevalence according to snout–vent length. Likewise, studies of other amphibian species have revealed no relationship between snout–vent length and parasite prevalence (Santos & Amato, 2010; González & Hamann, 2012).

Paedomorphic newts were significantly smaller than metamorphic individuals, probably because paedomorphic individuals inhabit oligotrophic habitats such as caves or alpine lakes with few trophic resources (Denoël, 2004). Amphibians that exploit semi-aquatic habitats have higher values of parasite species richness than those that have a fully aquatic or terrestrial life (Hamann *et al.*, 2013), which may indicate that metamorphics that present a terrestrial phase are exposed to a greater diversity of parasites (e.g. metamorphic newts are exposed to terrestrial snails that can act as intermediate hosts, as in the case of *B. salamandrae*; Avery, 1971). Consequently, paedomorphic individuals are less likely to harbour parasites because they are only exposed to helminth infective stages in aquatic environments. In fact, no parasitized paedomorphic newts were found.

No significant differences were found in prevalence among the different Pyrenean populations. Despite the large sample size, the low levels of prevalence found in newts complicated the task of discerning any distribution pattern in the parasites and of determining the influence of ecological factors.

The pauperized parasite fauna of this newt and its low prevalence may be a consequence of its long hibernation period (Baur & Baur, 2005) and its ecological isolation (Sanchis *et al.*, 2000). It has little interaction with other amphibian species and low metabolism, which would reduce the consumption of potential intermediate hosts due to the low energetic demands of poikilothermy (Aho, 1990; Schabetsberger, 1994).

However, the influence of habitat should also be taken into account. Parasite species richness is influenced by the local availability of parasite species, the possibilities of colonization (Poulin, 1997), and host and parasite dispersal (Aho, 1990). Consequently, one of the factors that would restrict the exposure of the host to many helminth species is a lack of colonization possibilities by parasites and their poor vagility.

Water speed may interrupt parasite transmission pathways (Akoll *et al.*, 2011), which would imply lower levels of both prevalence and diversity in lotic habitats than in lentic habitats. Our results show that there is a lower prevalence in *C. asper* than in other newts such as *Lissotriton*, *Triturus* and *Ichthyosaura* that occur in lentic habitats (Sattmann, 1986, 1990; Aho, 1990; Shimalov *et al.*, 2001). Even in newts such as the alpine newt *I. alpestris* that live at high altitudes, the prevalence and diversity of helminth communities (Sattmann, 1990) are higher than the prevalence found in the Pyrenean brook newt. Consequently, this low prevalence and diversity might also be due to an effect of its lotic habitat. If lotic habitats interrupt the control of parasite transmission pathways, then parasitism could be controlled by increasing water speed, an issue of certain importance for aquicultural enterprises and one that should be considered in future studies.

Acknowledgements

Special thanks are due to Fèlix Amat, for his contributions for increasing the sample size of this study and for his helpful improvements to the early drafts of this manuscript. We also thank Gregorio Moreno-Rueda, Francesc Oliva and Francesc Carmona for their statistical advice. We are also grateful to the two anonymous referees, the editor Sharon Ryan, the English referee, Laia Mestre, Daniel Escoriza, Laura Mihaela Stefan and Gregorio Moreno-Rueda, who provided helpful improvements to the manuscript. We are also grateful to Pilar Navarro and Javier Lluch Tarazona. Salvador Carranza and Ferran Bargalló allowed us to examine individuals from their private collections. We are also indebted to the staff of the Centre de Recuperació de Fauna Salvatge de Torreferrussa and to all the museums that allowed us to examine their collections: the Muséum National d'Histoire Naturelle of Paris (MNHN), above all to Laure Pierre and Victoire Koyamba, the Museu de Granollers de Ciències Naturals (MDGCN), Museu de Zoologia de Barcelona (MZB) and the Museo Nacional de Ciencias Naturales de Madrid (MNCN), especially to Enrique Fernández.

Financial support

The Museu de Granollers-Ciències Naturals has partially supported this study.

Conflict of interest

None.

References

Aho, J.M. (1990) Helminth communities of amphibians and reptiles: comparative approaches to understanding patterns and processes. pp. 157–196 *in* Esch, G.W., Bush, A.O. & Aho, J.M. (*Eds*) *Parasite communities: patterns and processes*. London, Chapman & Hall.

Akoll, P., Konecny, R., Mwanja, W.W. & Schiemer, F. (2011) Infection patterns of Nile tilapia (*Oreochromis niloticus* L.) by two helminth species with contrasting life styles. *Parasitology Research* **110**, 1461–1472.

Avery, R.A. (1971) Helminth parasite populations in newts and their tadpoles. *Freshwater Biology* **1**, 113–119.

Barus, V. & Groschaft, J. (1962) Helmintofauna colku *Triturus alpestris* (Laurenti, 1768) a *Triturus vulgaris* L. ze Sumavske Oblasti. *Zoologicke Listy* **11**, 253–264.

https://doi.org/10.1017/S0022149X13000710 Published online by Cambridge University Press

Barus, V., Groschaft, J. & Otcenasek, M. (1963) The helminth fauna of caudate amphibians from the territory of Czechoslovakia. *Ceskoslovenská Parasitologie* **10**, 43–59.

Baur, A. & Baur, B. (2005) Interpopulation variation in the prevalence and intensity of parasitic mite infection in the land snail *Arianta arbustorum*. *Invertebrate Biology* **124**, 194–201.

Berger, W.H. & Parker, F.L. (1970) Diversity of planktonic foraminifera in deep-sea sediments. *Science* **168**, 1345–1347.

Bush, A.O., Lafferty, K.D., Lotz, J.M. & Shostak, A.W. (1997) Parasitology meets ecology on its own terms: Margolis et al. revisited. *Journal of Parasitology* **83**, 575–583.

Căpuşe, I. (1967) Contributions à l'étude de l'helminthofaune parasite de la *Salamandra salamandra* L. de la Roumanie. *Travaux de Muséum d'histoire Naturelle 'Grigore Antipa'* **7**, 65–69.

Carranza, S. & Amat, F. (2005) Taxonomy, biogeography and evolution of *Euproctus* (Amphibia: Salamandridae), with the resurrection of the genus *Calotriton* and the description of a new endemic species from the Iberian Peninsula. *Zoological Journal of the Linnean Society* **145**, 555–582.

Cheng, T.C. (1960) The life history of *Brachycoelium obesum* Nicoll, 1914, with a discussion of the systematic status of the trematode family Brachycoelliidae Johnston 1912. *Journal of Parasitology* **46**, 464–474.

Combes, C. & Knoepfler, L.-P. (1968) *Euproctus montanus* (Savi, 1838), amphibien uròdele endémique de Corse, hôte nouveau pour un acanthocéphale et un trématode digène. *Vie et Milieu* **19**, 485–489.

Dare, O.K. & Forbes, M.R. (2008) Rates of development in male and female wood frogs and patterns of parasitism by lung nematodes. *Parasitology* **135**, 385.

Denoël, M. (2002) Paedomorphosis in the Alpine newt (*Triturus alpestris*): decoupling behavioural and morphological change. *Behavioral Ecology and Sociobiology* **52**, 394–399.

Denoël, M. (2004) Terrestrial versus aquatic foraging in juvenile Alpine newts (*Triturus alpestris*). *Ecoscience* **11**, 404–409.

Denoël, M., Joly, P. & Whiteman, H.H. (2005) Evolutionary ecology of facultative paedomorphosis in newts and salamanders. *Biological Reviews of the Cambridge Philosophical Society* **80**, 663–671.

Denoël, M., Ficetola, G.F., Ćirović, R., Radović, D., Džukić, G., Kalezić, M.L. & Vukov, T.D. (2009) A multi-scale approach to facultative paedomorphosis of European newts (Salamandridae) in the Montenegrin karst: Distribution pattern, environmental variables, and conservation. *Biological Conservation* **142**, 509–517.

Dobson, A. (2009) Climate variability, global change, immunity, and the dynamics of infectious diseases. *Ecology* **90**, 920–927.

Galeano, M., Navarro, P. & Lluch, J. (1990) Helmintofauna de *Hyla* spp. (Amphibia, Hylidae) en algunas localidades españolas. *Miscellània Zoològica* **14**, 1–6.

García-París, M., Montori, A. & Herrero, P. (2004) *Amphibia. Lissamphibia. Fauna Iberica* Vol. 24. 639 pp. Madrid, Museo Nacional de Ciencias Naturales, Centro Superior de Investigaciones Científicas.

González, C.E. & Hamann, M.I. (2012) Seasonal occurrence of *Cosmocerca podicipinus* (Nematoda: Cosmocercidae) in *Pseudopaludicola boliviana* (Anura: Leiuperidae) from natural environments in Corrientes Province, Argentina and aspects of its population structure. *Parasitology Research* **111**, 1923–1928.

Hamann, M.I., González, C.E. & Kehr, A.I. (2006) Helminth community structure of the oven frog *Leptodactylus latinasus* (Anura, Leptodactylidae) from Corrientes, Argentina. *Acta Parasitologica* **51**, 294–299.

Hamann, M.I., Kehr, A.I. & González, C.E. (2013) Biodiversity of trematodes associated with amphibians from a variety of habitats in Corrientes Province, Argentina. *Journal of Helminthology* **87**, 286–300.

Hartwich, G. (1960) Über *Megalobatrachonema terdentatum* (Linstow, 1890) nov. Comb. Und die Stellung von *Megalobatrachonema* Yamaguti 1941 im system der Ascaridina (Nematoda). *Zeitschrift für Parasitenkunde* **19**, 606–616.

Jordan, H.E. & Byrd, E.E. (1967) The life cycle of *Brachycoelium mesorchium* Byrd, 1937 (Trematoda: Digenea: Brachycoeliinae). *Zeitschrift für Parasitenkunde* **29**, 61–84.

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

López-Neyra, C.R. (1947) *Helmintos de los vertebrados ibéricos*. Vol. 1. 408 pp. Granada, Patronato Santiago Ramón y Cajal, CSIC.

Miaud, C. & Guillaume, O. (2005) Variation in age, body size, and growth among surface and cave-dwelling populations of the Pyrenean newt, *Euproctus asper* (Amphibia; Urodela). *Herpetologica* **61**, 241–249.

Milá, B., Carranza, S., Guillaume, O. & Clobert, J. (2010) Marked genetic structuring and extreme dispersal limitation in the Pyrenean brook newt *Calotriton asper* (Amphibia: Salamandridae) revealed by genome-wide AFLP but not mtDNA. *Molecular Ecology* **19**, 108–120.

Montori, A. (1990) Skeletochronological results in the Pyrenean newt *Euproctus asper* (Dugès, 1852) from one prepyrenean population. *Annales des Sciences Naturelles* **11**, 209–211.

Paredes-Calderón, L., León-Regagnon, V. & García-Prieto, L. (2004) Helminth infracommunities of *Rana vaillanti brocchi* (Anura: Ranidae) in Los Tuxtlas, Veracruz, Mexico. *Journal of Parasitology* **90**, 692–696.

Petter, A.J. & Chabaud, A.G. (1971) Life-cycle of *Megalobatrachonema terdentatum* (Linstow) in France. *Annales de Parasitologie Humaine et Comparee* **46**, 463–477.

Poulin, R. (1997) Species richness of parasite assemblages: Evolution and patterns. *Annual Review of Ecology and Systematics* **28**, 341–358.

Ribas, A., Amat, F. & Veciana, M. (2010) Helmints paràsits de *Salamandra salamandra* al Parc Natural del Montseny. *Trobada d'Estudiosos del Parc del Montseny* **7**, 367–371.

Sanchis, V., Roig, J.M., Carretero, M.A., Roca, V. & Llorente, G.A. (2000) Host–parasite relationships of *Zootoca vivipara* (Sauria: Lacertidae) in the Pyrenees (North Spain). *Folia Parasitologica* **47**, 118–122.

Santos, V.G.T. & Amato, S.B. (2010) Helminth fauna of *Rhinella fernandezae* (Anura: Bufonidae) from the

https://doi.org/10.1017/S0022149X13000710 Published online by Cambridge University Press

Rio Grande do Sul coastland, Brazil: analysis of the parasite community. *Journal of Parasitology* **96**, 823–826.

Sattmann, V.H. (1986) Über die Helminthenfauna von *Triturus alpestris* (Laurenti 1768) und *Rana temporaria* L. aus Almtümpeln in Oberösterreich (Amphibia, Plathelminthes und Nemathelminthes). *Annalen des naturhistorischen Museums in Wien Serie B* **87**, 193–196.

Sattmann, V.H. (1990) Endohelminths of some amphibians from Northern Greece (Trematoda, Acanthocephala, Nematoda; Amphibia: *Triturus*, *Rana*, *Bombina*). *Herpetozoa* **3**, 67–71.

Schabetsberger, R. (1994) Gastric evacuation rates of adult and larval alpine newts (*Triturus alpestris*) under laboratory and field conditions. *Freshwater Biology* **31**, 143–151.

Shimalov, V.V., Shimalov, V.T. & Shimalov, A.V. (2001) Helminth fauna of newts in Belorussian Polesie. *Parasitology Research* **87**, 356.

Vojtek, J. & Vojtková, L. (1972) Larvální stadia motoric v plazech CSSR. *Casopis Národního Musea. Oddíl Pírodovédny* **140**, 201–208.

Vojtková, L., Moravec, F. & Nabelkova, L. (1963) On the recent stage of investigation of the amphibian helminth fauna of CSSR. *Casopis Národního Musea. Oddíl Pȓírodovédny* **9**, 121–131.

Yildirimhan, H.S. (2008) Şeritli Semender (*Triturus vittatus* (Jenyns, 1835)) ve Pürtüklü Semender (*Triturus karelinii* (Strauch, 1870))'lerin Helmint Faunası Üzerine Bir Ön Çalışma. *Türkiye Parazitoloji Dergisi* **32**, 158–160.

Yildirimhan, H.S. & Öz, M. (2008) Antalya'dan Toplanan Lycisalamandra billae (Franzen & Klewen) (Kara Semenderi)'nin Helmint Faunası. *Türkiye Parazitoloji Dergisi* **32**, 390–392.

Yildirimhan, H.S., Bursey, C.R. & Goldberg, S.R. (2005) Helminth parasites of the Caucasian salamander (*Mertensiella caucasica*) from Turkey. *Comparative Parasitology* **71**, 75–87.

https://doi.org/10.1017/S0022149X13000710 Published online by Cambridge University Press