S. Morand, B.R. Krasnov, R. Poulin (Eds.)
Micromammals and Macroparasites
From Evolutionary Ecology to Management
Preface

The idea for a book reviewing current knowledge on mammals and their parasites emerged during a visit by one of us (SM) to the laboratory of another of us (BK) at the Jacob Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev (Israel) in December 2004, with RP becoming associated with the project from its very beginning.

Frankly, we decided to restrict our focus to macroparasites, i.e., metazoan parasites such as helminths and arthropods. A second volume at least would be necessary to cover microparasites, i.e., viruses, bacteria, and protozoans. We also decided to restrict our scope to small (=micro) mammals, because they are the most abundant and diversified species in the order Mammalia. Moreover, most of our knowledge on the interactions between mammals and their macroparasites concerns small mammalian species, mainly rodents, but also insectivores, lagomorphs, and bats.

Our idea was to associate disciplinary fields (taxonomy, phylogenetics, physiology, genetics, ecology, evolution, conservation biology, mathematical epidemiology) that may not have enough opportunities to exchange and debate ideas. What better opportunity can there be than a book on the evolution and ecology of host–parasite interactions, and moreover, a book that focuses on and emphasizes a particular group of hosts and their parasites? A symposium on “Parasites and mammals: A macroecological perspective” (organized by BK and SM) at the 9th International Mammalogical Congress in Sapporo (Japan), held in August 2005, allowed us to finalize the project with Springer Japan.

The book is conceived for a broad audience. Students will find up-to-date reviews and state-of-the-art syntheses in several domains. We hope that they will find ideas and opportunities for new research and new applications. Senior researchers, who try to maintain themselves at the forefront of their discipline, will also be interested readers. They are forced to specialize, leaving them little time for exploring other fields, even those closely related to their interest. This volume is organized in order that they will easily find reviews, summaries, data and references. Environmental managers, veterinarians, and conservationists have to use the results of fundamental science for their daily tasks: evaluating different options to manage natural populations and habitats. They have to deal with and/or
know that parasitism and diseases are important emerging problems. They need to have a clear picture of current knowledge, and the contributions in this book will prove invaluable.

The volume is divided into six parts, including a brief opening introduction explaining what micromammals and macroparasites are. The second part presents the major taxa that parasitize small mammals: helminths (trematodes, cestodes, nematodes, acanthocephalans) and arthropods (ticks, mites, lice, fleas and bat flies). We did not include dipterans that are not normally considered as parasites but as blood feeders. Besides, the main victims of dipterans are large rather than small mammals. In addition, we did not consider the chewing lice (Ischnocera, Amblycera) because they are generally understood to be commensals rather than parasites. A review of the diversity of species, life traits and life cycles, and also of the known effects of these parasites on their hosts, is provided for each of these taxa. The third part deals with some ecological and evolutionary patterns of parasite associations: parasite species diversity, host specificity, co-speciation and co-phylogeography. The fourth part explores the processes that operate in parasite associations at both higher (populations and communities) and lower (individuals) levels of biological organization. Mathematical epidemiology, community ecology, physiology (with endocrinology, metabolism and immunology) and genetics are explored. The fifth part provides practical examples or applications of ecological concepts to management purposes: conservation biology, and the ecology of human and animal health. The volume ends with a conclusion that explores the future of host–parasite interactions in the face of global change.

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Part I. Introduction and definitions
1 Micromammals and macroparasites: Who is who and how do they interact?

Serge Morand, Boris R. Krasnov, Robert Poulin and A. Allan Degen

1 Introductory remarks

Parasites are associated with their hosts, by definition, over both a long evolutionary term and in an ecologically transient time. Mammals and their parasites have co-interacted in a historical framework, which is revealed by cophylogenetic studies (Page 2003; Hugot et al. 2003). The interactions between micromammals and their macroparasites can be investigated in the light of history, i.e. within a phylogenetic framework. Although macroparasites are easy to define as metazoan parasites corresponding to well-defined clades, micromammals are more problematical and they necessitate a more thorough full definition (see below).

Fig. 1. Tangled trees of Metazoa (with groups including parasites in black) and the Mammalia (with groups including small-bodied forms in black)
Four major phyla of metazoans include members that parasitize micro-mammals (Fig. 1): the Rhabditophorea (cestodes and trematodes), the Syndermata (acanthocephalans), the Nematoda and the Arthropoda (fleas, lice, ticks, mites and flies). They are found as parasites of practically all micromammals. They have direct or indirect life-cycle, and mammals can be either intermediate host (such as for larval cestodes) or definitive host. Arthropod parasites are mostly ectoparasites, whereas helminths (cestodes, nematodes, trematodes and acanthocephalans) are internal. Some of these internal parasites show complex migrations within the host.

Parasites have evolved specialized adaptations to find and exploit their hosts, and these have in turn evolved mechanisms to avoid or to eliminate infections (Hart 1990; Moore 2002). The first line of defense involves behavioral activities such as grooming or avoiding potentially infected habitats or congeners. The second line of defense involves non- and specific immune responses, which can be costly in terms of energetic requirements. Costly defenses are at the basis of several physiological trade-offs.

All these reciprocal interactions between mammals and their parasites occur in within a complex network of other ecological interactions, giving them opportunities for new adaptation and even for new evolutionary outcomes.

2 Micromammals

Terrestrial mammals range in body mass from less than 2 g for the Etruscan (*Suncus etruscus*) and pygmy (*Sorex tscherskii*) shrews to more than 5 tons for the African elephant (*Loxodonta africana*). However, the frequency distribution of mammalian body masses is highly skewed, with the great majority of mammals weighing between a few grams and several kilograms (Fig. 2). In addition, there are a large number of mammals above 20 kg, but a paucity of species between 5 and 20 kg. The definition of a micromammal (=small mammal) is rather arbitrary. In their article on the energetics of small mammals, Grodzinski and Wunder (1975) restricted body mass to the range between 3 and 300 g and Happold (1984), in his article on small mammals of the Sahara, used an upper body mass of 3 kg. Heusner (1991) designated 20 kg in dividing mammals into small and large sizes. The International Biological Programme (IBP) Small Mammals Working Group decided that mammals weighing up to 5 kg are to be classified as small (Boulière 1975).

This definition will be partly adopted in the present text. This is because, using this guideline, Artiodactyla such as the 1.6 kg lesser mouse
deer (Tragulus javanicus), 4 kg dik-diks (Madoqua phillipsi and Madoqua guentheri), duiker (Cephalus dorsalis) and suni (Neotragus pygmaeus) would be considered as small mammals, but Rodentia such as the 9 kg agouti (Agouti paca) and 15 kg Indian crested porcupine (Hystrix indica) would not.

Fig. 2. Body size distribution of terrestrial mammals including Chiroptera (data from Walker’s Mammals of the World, Nowak 2003). Note that half of the described mammals weight less than 100 g.

Consequently, we decided to adopt not only a purely size-related but also a taxonomic approach. Therefore, we included in our consideration mammals of the orders Rodentia, Insectivora and Chiroptera as well as most Lagomorpha and some marsupials. Together, these taxa contain more genera and species than all other orders combined. It should be noted, however, that bats (Chiroptera) differ from other micromammals in that they are “metabolically” more similar to large mammals. This, for example, is reflected in their relatively long lifespan and gestation period. Indeed, in general, bat lifespan is about 3.5 times longer than that of other mammals of comparable body sizes (Jurgens and Protero 1987; Wilkinson and South 2002). Nevertheless, bats share with other small mammals many other ecological characteristics. They are conspicuous and important components of any biota. Their populations are large and many of them inhabit large territories. As such, they represent an important element of biodiversity all over the world.

Micromammals are a major component of predator diets and perform vital ecosystem services, particularly in seed and spore dispersal and germination. Many of them are also keystone species (e. g., ecological engineers). Consequently, the existence of countless other animals and plants depends on small mammals. As a result, micromammals have to be one of
the primary targets of conservation effort. On the other hand, many micromammals are aggressive agricultural pests that are responsible for huge harvest losses in many countries. They are also hosts for numerous parasite species and reservoirs for many diseases dangerous for both humans and livestock. For example, huge plague epidemics that struck Europe, Asia and Africa in the 6th, 14th, 17th and early 20th centuries with a total death toll of about 137 million victims were related to small mammals and their flea parasites.

This duality (being an important positive component of biodiversity on one hand and an important negative factor of human well-being on the other hand) is the driving force behind the intense study effort devoted to small mammals worldwide. Small mammals offer the most spectacular and explosive examples of evolutionary radiations in modern mammals and are also of interest in that light. In addition, the ubiquity of small mammals and the large sizes of their populations made them one of the favourite models for studies aimed at elucidating fundamental rules and patterns of various physiological, behavioural, ecological and evolutionary processes.

Conservation of biodiversity as well as control of animal populations is impossible without understanding the factors that govern the dynamics of populations and communities of target organisms. Parasites are one of these factors. They strongly affect the abundance and composition of populations and communities of their hosts. Understanding the relationships between micromammals and their parasites is, therefore, crucially important for our attempts to manage small mammal populations from both conservation and control points of view.

3 Macroparasites

Parasites are traditionally divided into two main groups: microparasites and macroparasites. Microparasites are primarily single-celled organisms, including viruses, bacteria and protozoans, as well as some multicellular organisms of small size such as myxozoans, that typically reproduce directly within the cells of the host. They are generally associated with disease in which transmission is direct, but can also be indirectly transmitted via alternate hosts or vectors. Macroparasites are “large” metazoan parasites, including several major taxa of endoparasitic helminths (worms) and ectoparasitic arthropods. In contrast to microparasites, macroparasites are characterized by longer generation times, and (except for some trematodes and cestodes in their intermediate hosts) by the absence of direct multiplication within the host. Thus, eggs are produced while the parasites are in
or on the host, or off the host in the case of many arthropod ectoparasites, with each offspring then infecting a host different from that on which its parents lived. Immune responses elicited by macroparasites generally depend on the number of parasites present in a given host, and tend to be of relatively short duration, i.e. there is usually no long-lasting acquired immunity following an initial infection. Macroparasite infections therefore tend to be of a persistent nature, with hosts being continually reinfected (Anderson and May 1979).

All the above issues have led to a sharp increase in empirical, comparative and theoretical studies of small mammal-parasite relationships during the last two decades. Patterns and processes in small mammalian host-macroparasite systems have been documented and studied at a variety of scales, across various habitats, in different biogeographic regions and for various parasite taxa. All these efforts call for regular syntheses of original data and generalizations. The present book is an attempt to compile and generalize such data on the relationships between small mammals and their metazoan parasites.

We intentionally restrict ourselves to consideration of macroparasites only, and put aside the role of small mammals in the transmission of viral, fungal, bacterial and rickettsial infections as well as the regulating role of microparasites in populations and communities of small mammals. The reason for this is that including microparasites into our synthesis would require a great deal more space. In addition, patterns of macro- and microparasite relationships with their hosts are often strikingly different; furthermore, these two groups of parasites seem to develop along quite different evolutionary pathways.

4 A complex of dynamic interactions...

Hosts are unequal with respect to parasite infections, at the individual level, among populations, or among species. Why is that so? Even if a clear picture emerges from our existing knowledge, the pattern of parasite diversity must be confronted with ecological hypotheses. Numerous hypotheses have been proposed and we review the relative importance of host attributes that explain the large disparity in parasite species richness among and within host species. Similarly, some macroparasite species are very host specific, whereas others are not. We try to analyse the reasons and we explore the consequences of this.

Macroparasites have the potential to regulate their host populations due to their sub-lethal effects that cause reductions in host survival, host fecundity or progeny size. Population modelling is a tool that allows the investigators to better understand the potential roles of parasites in host regu-
lation, but also to predict emergences of the microparasitic diseases they transmit (arthropod vectors such as fleas and ticks).

![Diagram of parasite diversity and its determinants](attachment:attachment.png)

**Fig. 3.** Parasite diversity (parasite species richness), its determinants, and its interactions with host genetics, physiology and behaviour

Hosts can avoid parasite infection with their first line of defence, i.e. behaviour, or with the second line of defence, i.e. immune systems. Both lines of defences involve genetic background and physiological adaptation, which may be paid at the expense of other physiological functions (Fig. 3).

However, the world is full of worms, fleas and lice, and whatever its choice a host has few chances of escaping infection. The host has then to manage with the parasite, and vice versa. The detrimental effect of the infection and/or the manipulation of the host immune system may impose strong selective pressures, which may compromise many aspects of host life including behaviour or survival.

### 5 ... with a human component

The human footprint on the earth is dramatically modifying the epidemiological environment (Daily and Erhlich 1996). Climate change, biotic invasion and landscape modification are affecting the biology of hosts and their parasites, which are displaced within and outside their geographical
ranges. Parasites are becoming greater threats for biological conservation, but we show how parasites have their own roles and values and should be conserved. The alteration of the epidemiological environment increases the potential contacts between humans and parasites and pathogens of wildlife, favouring the risks of emerging zoonoses. Humans, by their outgrowing activities, affect the very nature of the host-parasite coevolutionary dynamics (Thompson 2005). The changes that affect our planet will encourage collaborations between evolutionary ecologists, epidemiologists, conservationists, physicians and veterinarians.

References

Part II. Major taxa parasitic on micromammals
2 Digenean trematodes

Carlos Feliu, Jordi Torres, Jordi Miquel, Juan Matías Segovia and Roger Fons

1 Introductory remarks

Trematodes of the class Digenea belong to the phylum Platyhelminthes (see Gibson et al. 2002 for a recent update on taxonomy). They are parasites with complex life cycles and often use micromammals as definitive hosts. Trematodes are distributed all around the world. In Europe, for example, monographs or articles that deal with the helminthofauna of small mammals have always reported the ubiquitous presence of digenean trematodes (López-Neyra 1947; Prokopic and Genov 1974; Merkusheva and Bobkova 1981; Genov 1984; Goüy de Bellocq et al. 2002). In this chapter, we offer general information on the trematode faunas of micromammals, with a focus on parasites of small mammals of the Iberian Peninsula. Recent extensive studies of helminths in this Peninsula provide an opportunity to investigate various aspects of the ecology of these helminths.

2 Distribution of trematodes among small mammals

Available data on digeneans parasitic in small mammals are summarized in Tables 1-4. These tables have been compiled from an extensive bibliographical search (CAB Abstracts 1973-2005) with additional data from Yamaguti (1971), Gibson et al. (2002) and Jones et al. (2005), and show the records of trematode families in mammalian families belonging to four orders (Insectivora, Rodentia, Lagomorpha and Chiroptera). In general, small mammals harbour a great variety of trematodes representing a total of 37 families. Rodentia harbours the most diverse trematode fauna consisting of 30 families, while Lagomorpha have the least diverse spectrum of trematodes with seven families only.
Parasitic digeneans belonging to 19 families have been recorded from four families of Insectivora (Table 1). All of these digenean families have been reported for Soricidae. They were found mainly in the most extensively studied genera such as Crocidura, Neomys and Sorex. In contrast, among tenrecids (represented by 10 genera), only Limnogale mergulus was found to be parasitized by trematodes (omphalometrid Neoglyphe polylecithos and plagiorchiid Plagiorchis limnogale; Yamaguti 1971).

Table 1. Trematodes parasitic in Insectivora

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Among Rodentia, data on trematodes are available for 13 of 29 recent families (Table 2). Of these, Muridae show the most diverse trematode fauna with 29 of the 30 digenean families recorded for Rodentia. The least diverse trematode faunas occur in four rodent families that each harbour a single digenean family. These rodent families are Chinchillidae with Lagidium viscacia boxi parasitized by Fasciola hepatica (Fasciolidae) (Led et al. 1979); Dasyproctidae with Dasyprocta agouti parasitized by two species of Cladorchiidae (Cladorchis pyriformis and Stichorchis giganteus) (Yamaguti 1971); Erethizontidae with Erethizon dorsatum parasitized by Schistosoma douthitti (Schistosomatidae) (Choquette et al. 1973); and Heteromyidae with Liomys pictus parasitized by Brachylaima bravoae (Brachylaimidae) (Yamaguti 1971).
Table 2. Digenean trematodes parasitic in Rodentia

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Cas Castoridae, Cav Caviidae, Chi Chinchillidae, Das Dasyproctidae, Dip Dippidae, Ech Echimyidae, Ere Erethizontidae, Het Heteromyidae, Hyd Hydrochaeridae, Mur Muridae, Myc Myocastoridae, Myx Myoxidae, Sci Sciuridae.

All seven trematode families characteristic of Lagomorpha were found in Leporidae (Table 3). In contrast, only two trematode species from two families have been reported for Ochotonidae: *Dicrocoelium dendriticum* (Dicrocoeliidae) in *Ochotona alpina* (Gvozdev and Orlov 1985) and *Ochotona hyperborea* (Sakamoto et al. 1982) and *Hasstilesia ochotonae* (Hasstilesiidae) in *Ochotona rutila* (Zdarska and Soboleva 1990).
Table 3. Digenean trematodes parasitic in Lagomorpha

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Table 4. Digenean trematodes parasitic in Chiroptera

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Finally, 15 digenean families were found in 13 families of Chiroptera (Table 4). Vespertilionidae and Phyllostomidae harbour the richest digenean faunas (10 and eight parasite families, respectively). Lecithodendriidae parasitize all of the 13 chiropteran families. Plagiorchiidae and Dicrocoeliidae are also well represented (recorded in 11 and 10 chiropteran families, respectively). Representation of the remaining trematode families among chiropteran families is more restricted, including Cyathocotylidae with Prohemistomum azimi parasitizing Nycteris thebaica (Nycteridae) (Saoud and Ramadan 1977); Diplostomidae with Neodiplostomum vaucherii parasitizing Chrotopterus auritus (Phyllostomidae) (Dubois
Digeneans 17

Echinostomatidae with *Echinochasmus megadermi* and *E. perfoliatus* found in *Megaderma lyra* (Megadermatidae) (Salem 1975); Nudacotylidae with *Nudacotyle* species reported from the phyllostomid genera *Carollia*, *Artibeus* and *Phyllonycteris* (Zdizitowiecki 1980; Zdizitowiecki and Rutkowska 1980; Vélez and Thatcher 1990); Pleurogenidae with *Maxbraunium baeri* parasitic on *Myotis siligorensis* (Vespertilionidae) (Yamaguti 1971); and Rhopaliidae with *Rhopalias coronatus* found in *Carollia perspicillata* (Phyllostomidae) (Marshall and Miller 1979).

3 Small mammals as experimental models for studies of Digenea

Several small mammals have been used in experiments to investigate the life cycles of parasites and to serve as models of human infections. Although the ideal scenario would be to monitor in the laboratory the entire trematode life cycle, it has not always been possible. Often, only the adult stage has been studied. In both situations, the availability of adult trematodes required experimental infection of the definitive hosts, usually rodents. However, some experimental models involved also lagomorphs and, on rarer occasions, bats and insectivores (see Yamaguti 1971 for details).

Among rodents, most experimental infections with digeneans have been carried out on Muridae, though guinea pigs (*Cawiidae: Cavia porcellus*) has also been frequently used in experiments. Among murids, Murinae (*Mus* and *Rattus*) have been used for experimental infections mainly by Brachylaimidae, Echinostomatidae, Heterophyidae, Paragonimidae, Plagiorchiidae and Schistosomatidae. Other Murinae, such as *Apodemus*, *Mastomys*, *Praomys*, *Thallomys*, *Arvicantis* and *Bandicota* have been less frequently used, although they also have been experimentally infected with Fasciolidae, Brachylaimidae, Schistosomatidae and Paragonimidae. Gerbillinae of the genus *Meriones*, especially *M. unguiculatus*, have been extensively used in experiments with digeneans. Another gerbilline, *Tatera indica*, has also been experimentally infected with Fasciolidae (Sahba et al. 1972) and Schistosomatidae (Massoud 1973). Among Cricetinae, *Mesocricetus auratus* has served as experimental model mainly for investigations with Schistosomatidae, Echinostomatidae and Heterophyidae. Other cricetines (*Phodopus*, *Tscherckia* and *Cricetulus*) have also been used in experiments with digeneans of particular public health importance such as *Fasciola hepatica*, *Dicrocoelium dendriticum*, *Opistorchis felineus*, *Clonorchis sinensis* and *Schistosoma mansoni* (Gitsu and Kova-
lenko 1983; Zelya and Sergeeva 1987; Terasaki et al. 2003; etc.). Additional models include schistosomatids in Cricetomys sp. and Saccostomus campestres (Crycetominae); Schistosomatium, Notocotylus and Nudacotyle in Microtus pennsylvanicus and M. montanus; and Euryhelmis in Ondatra zibethica (Arvicolinae); as well as some schistosomatids, brachylaimids, heterophyids and opisthorchiids in Sigmodontinae (Sigmodon, Holochilus, Holochistus, Nectomys, Zygodontomys and Peromyscus) (Pitchford 1975; Zajac and Williams 1981; Gitsu and Kovalenko 1983; Kawazoe and Pinto 1983; McKown et al. 2000; Terasaki et al. 2003).

Representatives of other rodent families (Echimyidae, Dasyproctidae, Hystricidae, Myoxidae, Sciuridae and Myocastoridae) have rarely been used for experimental infections with digeneans. Nevertheless, Myocastor coypus (Myocastoridae) has been described as a useful experimental model for Fasciola, Schistosoma, Paragonimus and Clonorchis (Kuntz et al. 1975; Hatsushika et al. 1979). Paragonimus skrjabini and Brachylaima ruminae have been maintained in Hystrix hodgsoni (Hystricidae) and Eliomys quercinus (Myoxidae) (Yamaguti 1971; Mas-Coma and Montoliu 1986). Finally, Proechimys (Echimyidae), Dasyprocta (Dasyproctidae), Marmota and Callosciurus (Sciuridae) have been infected with some Schistosoma species (Chiu and Kao 1973; Anderson et al. 1991).

4 Digeneans and Iberian small mammals

The mammal fauna of the Iberian Peninsula comprises 65 species of small mammals (14 Insectivora, 21 Rodentia, four Lagomorpha and 26 Chiroptera; Palomo and Gisbert 2002). Continuous extensive studies of the helminth fauna of Iberian small mammals started in the mid 70s (beginning with insectivores and rodents, then involving bats and, finally, hares and rabbits). At present, detailed information on the helminth faunas and, in particular, on trematodes, of a substantial number of the Iberian micromammalian species is available. The information provided here has been extracted from our own studies that included detailed examination of around 7000 individual hosts (500 Insectivora, 5500 Rodentia and 1000 Lagomorpha). Data on trematodes parasitic in Chiroptera were taken from the literature.

4.1 Faunistic aspects

Forty-six species of digeneans have been found in Iberian micromammals. In fact, this number may be greater, because of some unclear and unre-
solved taxonomical issues (Mas-Coma and Montoliu 1986; Botella et al. 1993; Esteban et al. 1999; Gracenea and González-Moreno 2002). These 46 trematodes were recorded in 36 host species (10 Insectivora, 13 Rodentia, two Lagomorpha and 11 Chiroptera).

Table 5 shows the number of families, genera and species of trematodes that infect small mammals belonging to different orders and families, whereas numbers of digenean families and species recorded in each host species are shown in Fig. 1.

**Table 5.** Number of families, genera and species of trematodes recorded in Iberian small mammals

<table>
<thead>
<tr>
<th>Hosts</th>
<th>Families</th>
<th>Genera</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>INSECTIVORA</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Talpidae</td>
<td>4</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td>Erinaceidae</td>
<td>2</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td>Soricidae</td>
<td>8</td>
<td>9</td>
<td>11</td>
</tr>
<tr>
<td>RODENTIA</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Myoxidae</td>
<td>6</td>
<td>7</td>
<td>8</td>
</tr>
<tr>
<td>Muridae</td>
<td>10</td>
<td>12</td>
<td>15</td>
</tr>
<tr>
<td>LAGOMORPHA</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Leporidae</td>
<td>2</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>CHIROPTERA</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rhinolophidae</td>
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<td>5</td>
<td>8</td>
</tr>
<tr>
<td>Vespertilionidae</td>
<td>3</td>
<td>6</td>
<td>12</td>
</tr>
<tr>
<td>Molossidae</td>
<td>2</td>
<td>3</td>
<td>3</td>
</tr>
</tbody>
</table>

A high diversity of trematode species is the characteristic for Muridae and Soricidae, whereas the lowest number of trematode species has been found in Leporidae and Erinaceidae. One of the reasons for this is the high number of host species within both Muridae (17) and Soricidae (nine), and their broad distribution across the Peninsula. Among dormice (Myoxidae), trematodes have been found only in *Eliomys quercinus*, whereas no trematode has been recorded in *Glis glis*. Leporidae is the only family that does not have specific trematodes, but its members are hosts of euryxenous trematodes (*Fasciola hepatica* and *Dicrocoelium dendriticum*) that are frequently found in other mammals. Rhinolophidae and Vespertilionidae are parasitized by a relatively high number of genera and species of trematodes, although these belong to only few families. Bats are the most frequently infected by Plagiorchiidae and Lecithodendriidae (Botella et al. 1993; Esteban et al. 1990, 1992, 1999).