# 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).

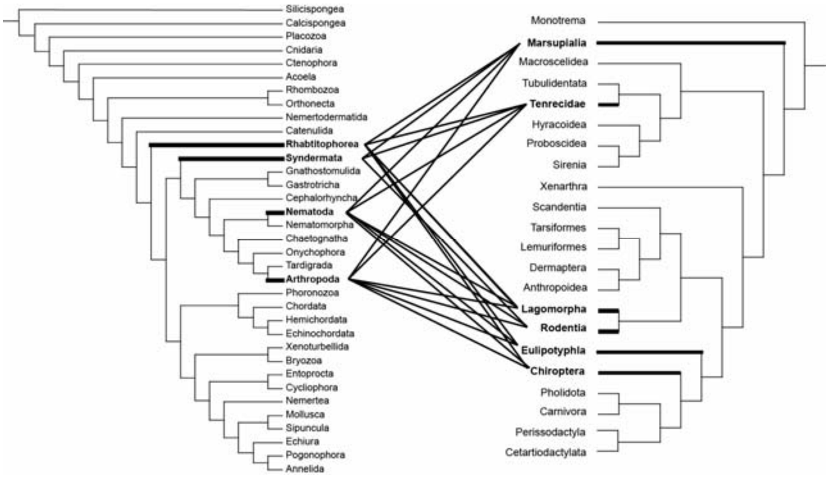

**Fig. 1.** Tangled trees of Metazoa (with groups including parasites in black) and the Mammalia (with groups including small-bodied forms in black)

Four major phyla of metazoans include members that parasitize micromammals (Fig. 1): the Rhabdtitophorea (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.

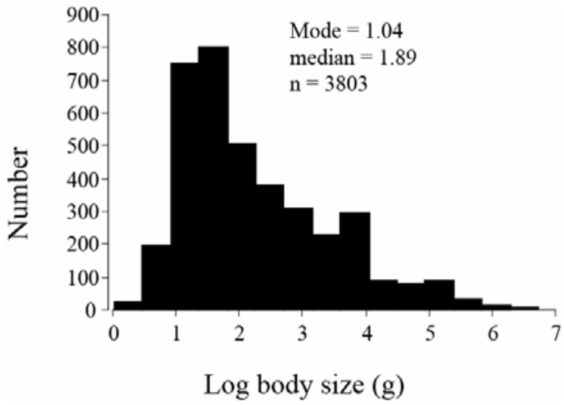

**Fig. 2.** Body size distribution of terrestrial mammals including Chiroptera (data from Walker's Mammals of the World, Nowak 2003). Note that half of the described mammals weight less than 100 g.

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 regulation, but also to predict emergences of the microparasitic diseases they transmit (arthropod vectors such as fleas and ticks).

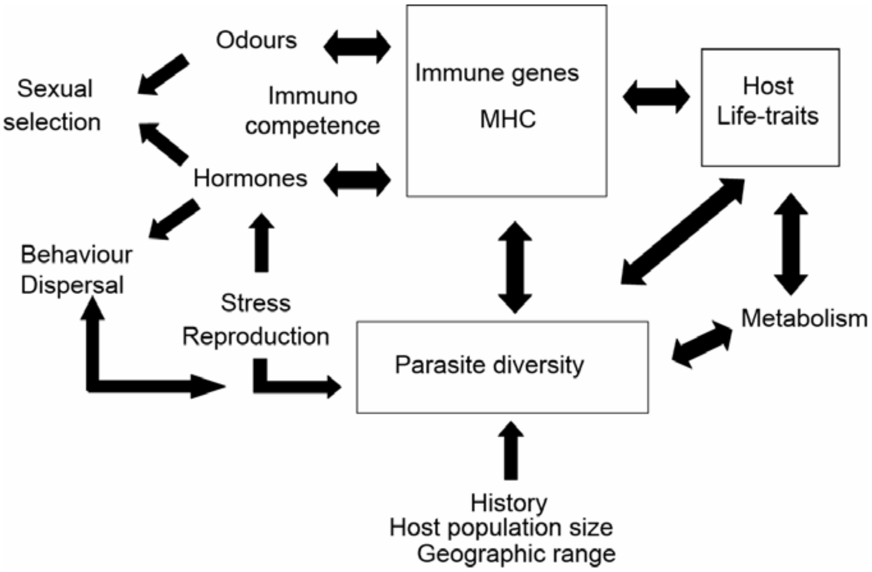

**Fig. 3.** Parasite diversity (parasite species richness), its determinants, and its interactions with host genetics, physiology and behaviour

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.

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