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Searching for generality in the patterns of parasite abundance and distribution: Ectoparasites of a South African rodent, *Rhabdomys pumilio*

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ABSTRACT

We studied abundance and distribution of seven ectoparasite species (fleas *Chiastopsylla rossi* and *Dynopsyllus ellobius*, a louse *Polyplax arvicanthis*, mites *Androlaelaps fahrenholzi* and *Laelaps giganteus* and two ticks *Haemaphysalis elliptica* and *Hyalomma truncatum*) exploiting the same populations of the rodent host *Rhabdomys pumilio* in South Africa. We considered three general patterns of abundance and distribution, namely (i) aggregated distribution of parasites amongst individual hosts; (ii) positive relationships between mean parasite abundance and their prevalence; and (iii) applicability of a simple epidemiological model based on mean parasite abundance and its variance to predict the observed patterns of prevalence. Our aims were to evaluate the relative role of host- versus parasite-associated factors by looking at similarity amongst different parasites in these patterns. In general, all parasites demonstrated strong similarity in each of the three patterns of abundance and distribution. However, the strength of these patterns differed amongst parasite species. We conclude that these patterns are driven mainly by hosts, but differences are caused by differences between various life-history traits of parasite species. Our results support the idea that general laws apply to parasite population ecology.

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1. Introduction

Although the ecology of parasites is a relatively young discipline, it is rapidly developing and large quantities of data have been collected during recent decades (Combes, 2001; Poulin, 2007a). In particular, patterns of abundance and distribution have been investigated in a variety of parasite taxa exploiting various hosts in varying environments and in different geographic regions. Parasitism has evolved independently in many animal taxa. As a result, parasites are different in their life histories and strategies of host exploitation. Consequently, the question about the generality of patterns observed in different parasites still remains one of the crucial problems in parasite ecology. For example, almost four decades ago, Crofton (1971) had already proposed that an aggregated distribution of parasites amongst their hosts should be considered as a characteristic feature of parasitism because this pattern was widely observed amongst different parasites exploiting different hosts. This idea was further substantiated by a number of seminal papers (Anderson and May, 1978; Shaw and Dobson, 1995). In a recent review, Poulin (2007b) demonstrated that not only the aggregation of parasites amongst host individuals, but other patterns of abundance and distribution (e.g., positive relationship between prevalence and mean abundance of parasites) are strikingly similar in different parasite taxa.

Most studies in the long history of investigating patterns of parasite abundance and distribution have been either restricted to one parasite taxon (e.g., Godfrey et al., 2006) or based on meta-analyses of patterns found in different parasites exploiting different hosts in different locations and/or times (e.g., Shaw and Dobson, 1995). Comparisons of patterns of abundance and distribution amongst different parasites exploiting the same host from the same population(s) (i.e., in the same locations at the same time) have been undertaken more rarely (Haukisalmi, 1986; Boag et al., 2001; Newey et al., 2005; Poulin and Dick, 2007; Seifertová et al., 2008). Such comparisons may not only further validate the universality of abundance and distribution patterns and give insights into the scale-dependence of this universality, but may also allow evaluation of the relative role of host- versus parasite-associated factors that generate these patterns.

A number of factors driving each universal pattern have been suggested (Anderson and May, 1978; Shaw and Dobson, 1995; Poulin, 2007a,b). Essentially, these factors can be divided into two groups, namely host-related and parasite-related factors. For example, aggregated distribution of parasites may be caused by, on the one hand, heterogeneity of hosts in the face of parasitism, or, on

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the other hand, by stochastic demographic processes in parasite populations and/or the effect of mating probability of a parasite (Anderson and Gordon, 1982; Poulin, 2007a). Host-related factors have been suggested to be more important in generating the universal aggregative pattern of parasite distribution than the parasite-related mechanism (see reviews in Wilson et al., 2001 and Poulin, 2007a), although, to the best of our knowledge, this has never been tested specifically. If patterns of abundance and distribution are similar amongst different parasites exploiting the same hosts then, most likely, these patterns are governed by some features of host biology. If, however, these patterns are produced by parasite-related processes, then they would be likely to differ amongst parasites that showed differences in their behaviour. Furthermore, if the main trend of a pattern is similar in different parasites, but these parasites differ in the strength of the pattern, then these differences are likely to be produced by amongst-parasite differences in life-history. For example, whilst all parasites appear to be aggregated, considerable differences are observed in the degree of aggregation between parasite species or populations, and the causes of these differences are not well understood (Morand and Krasnov, 2008).

We studied the abundance and distribution of different ectoparasites exploiting the same rodent host, *Rhabdomys pumilio*, in the Western Cape Province of South Africa. These parasites belong to different arthropod taxa, namely fleas (Insecta: Siphonaptera), lice (Insecta: Phthiraptera), mites (Acari: Parasitiformes) and ticks (Acari: Parasitiformes). The four taxa vary with respect to life-history and the length of time spent on the host. Lice are permanent parasites, they reproduce directly on the host and transmission takes place through direct contact, whereas fleas, mites and ticks usually do not reproduce on the host. Fleas and mites are generally associated with the nest of the host and periodically attach to the host to obtain food and/or for dispersal (Marshall, 1981; Radovsky, 1985). Engorged ticks drop off the host and re-emerge after development to the next stage, on the vegetation in close proximity to the point of drop-off (Sonenshine, 1993).

We considered three general patterns of abundance and distribution that have been reported earlier for some, but not all of these taxa as follows. Firstly, we considered aggregated distribution of parasites amongst individual hosts and tested whether the degree of aggregation is similar between parasites. Earlier, aggregated distribution has been demonstrated for fleas (Krasnov et al., 2002), lice (Shaw et al., 1998; Qian et al., 2004), mites (Guo, 1997) and ticks (Randolph, 1995; Randolph et al., 1999; Nava et al., 2006) as well as for numerous other parasite taxa. Second, we searched for a positive relationship between local parasite abundance (mean number of parasites per individual host) and their prevalence. This relationship was suggested to be a reflection of one of the most pervasive macroecological patterns, namely, the positive relationship between local abundance and occupancy (Gaston, 2003). In the application of this relationship to host–parasite systems, a positive correlation between mean abundance and prevalence has been confirmed for nematodes (Morand and Guégan, 2000), monogeneans (Simkova et al., 2002) and fleas (Krasnov et al., 2005a). The explanation for this pattern may be straightforward. The probability that a parasite infests a new host individual is higher when the mean abundance of the parasite is higher. Third, we tested whether a simple epidemiological model based on mean parasite abundance and its variance can predict the observed patterns of prevalence. It has been shown that up to 96% of variance in flea (Krasnov et al., 2005a,b) and tick (Stanko et al., 2007) prevalence can be explained solely by their mean abundance, so there was no need to invoke more complex factors for the explanation of the variation in parasite prevalence.

2. Materials and methods

2.1. Study area and sampling

The striped mouse, *R. pumilio*, is one of the most abundant rodents in southern Africa. It occupies a variety of habitats and is a host for numerous ecto- and endoparasite species (De Graaf, 1981; Matthee et al., 2007). We captured *R. pumilio* in 2003–2004 at nine localities in the Western Cape Province of South Africa. The localities included five pristine lowland Fynbos/Renosterveld regions and four bordering agricultural areas (Matthee et al., 2007). Seven localities were sampled once, mainly during the breeding season, whereas two remaining localities were sampled four times with 3–4 month intervals between trapping sessions. Nevertheless, we considered each trapping session as independent because animals captured during each session were sacrificed (see below). Rodents were captured using Sherman-type live traps (90–180 traps per locality) baited with peanut butter and oats. A trapping session in each locality lasted 3–12 days. Parasites were collected from adult rodents, i.e. individuals with a body mass of more than 40 g. These animals were euthanised with Fluothane, placed in an individual pre-marked plastic bag and transferred to a laboratory where each animal was systematically examined under a stereoscopic microscope. All ectoparasites found were removed using forceps, counted and identified to species level. A total of 510 individuals of *R. pumilio* were trapped (24–57 animals per locality) from which eight flea species, one louse species, 11 mite species and 13 ixodid tick species were identified. In the analysis we included seven ectoparasite species that were either most abundant or recorded in at least five trapping sessions. These were two fleas (*Chiastopsylla rossi* and *Dynopsyllus ellobius*), a louse (*Polyplax arvicanthis*), two mites (*Androlaelaps fahrenholzi* and *Laelaps giganteus*) and two ticks (*Haemaphysalis elliptica* and *Hyalomma truncatum*).

2.2. Data analysis

We calculated mean abundance (mean number of parasites per host individual; M), variance of abundance (V) and prevalence (proportion of infested host individuals; P) for each trapping survey for each of seven parasite species. We evaluated the degree of aggregation of each parasite species amongst host individuals using the empirical relationship known as Taylor's power law (Taylor, 1961). According to this law, mean abundance of a species is related to variance of abundance as $V = aM^b$. The exponent (parameter b or slope of Taylor's relationship) of this function usually varies amongst species as $1 < b < 2$ (Kilpatrick and Ives, 2003). For parasites, it has been shown to be an inverse indicator of parasite-induced host mortality (Anderson and Gordon, 1982). An increase in b suggests that at least some of the hosts are infected with heavy burdens of parasites and it is commonly used as a measure of parasite aggregation (Perry, 1988; Shaw and Dobson, 1995; Morand and Guégan, 2000; Simkova et al., 2002; Krasnov et al., 2005a; Morand and Krasnov, 2008). We regressed log-transformed variance of parasite abundance against log-transformed mean of parasite abundance (both calculated within a trapping survey) and used t-tests to test whether the slope differs significantly from 1. To avoid an inflated Type I error, we applied a Bonferroni adjustment of α-level which resulted in $\alpha = 0.007$. We then compared amongst slopes of the resulting relationships using ANCOVA. We ran an ANCOVA across all parasites with a parasite species or parasite higher taxon (fleas, louse, mites and ticks) as a categorical predictor, then we ran ANCOVAs separately within fleas, mites and ticks.

To estimate the proportion of variance in parasite prevalence explained by their mean abundances, we fitted the observed rela-

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