

Distribution of fleas (Siphonaptera) among small mammals: Mean abundance predicts prevalence via simple epidemiological model

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Abstract

We used data on the abundance and distribution of fleas parasitic on small mammals in Slovakia and aimed: (i) to confirm a positive relationship between abundance and distribution fleas within and across host species; and (ii) to test if prevalence of fleas can be reliably predicted from a simple epidemiological model that takes into account flea mean abundance and its variance. Prevalence of a flea species increased with an increase in its mean abundance both within and across host species. We calculated prevalences both for each flea–host association and for each flea species across all hosts. Observed prevalences did not differ significantly from those predicted by the epidemiological model using parameters of Taylor's power relationship between mean abundance of fleas and its variance. Regressions of predicted prevalences against observed prevalences produced slope values that did not differ significantly from unity and were independent of scale (within or across host species). Our results demonstrated that up to 96% of variance in flea prevalence can be explained solely by their mean abundance. We concluded that, in general, there is no need to invoke other, more complex factors for the explanation of the variation in flea prevalence.

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1. Introduction

A positive relationship between abundance (mean number of individuals) and occupancy (proportion of occupied patches) is one of the most general ecological patterns (e.g. Gaston, 2003). This pattern has been reported on a variety of scales, across various habitats, in different biogeographic regions and for various taxa (Gaston, 2003). In particular, in the application of this relationship to host–parasite systems, a positive correlation between the mean number of parasite individuals per host (mean abundance) and the percentage of infected hosts (host occupancy by parasites, i.e. prevalence) was supported in a number of

studies (Shaw and Dobson, 1995; Morand and Guégan, 2000; Krasnov et al., 2002; Simkova et al., 2002).

The positive abundance/occupancy relationship has been explained by a variety of mechanisms (Gaston, 2003). In fact, Gaston et al. (1997) and Gaston (2003) listed nine different hypotheses aimed at explaining this relationship. Morand and Guégan (2000) tested several of these hypotheses using nematodes parasitic on mammals. In particular, they found that prevalence of nematodes could be successfully predicted using an epidemiological model with a minimal number of parameters such as mean abundance of a parasite, its variance and an indicator of aggregation. The latter parameter, in turn, can be calculated from an empiric relationship between mean abundance and its variance, also known as Taylor's power law (Taylor, 1961). Consequently, Morand and Guégan (2000) concluded that the abundance/distribution relationship in parasites could be explained by demographic and stochastic mechanisms revealed by simple

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epidemiological models without invoking more complex explanations such as, for example, niche breadth hypothesis (Brown, 1984). However, the generality of the hypothesis that positive abundance/prevalence relationship in parasites could be explained by demographic parameters described by epidemiological models needs to be tested more extensively.

Here, we used data on the abundance and distribution of fleas (Siphonaptera) parasitic on small mammalian hosts in central Europe (Slovakia). We aimed: (i) to confirm a positive relationship between abundance and distribution fleas within and across host species; and (ii) to test if the pattern of occupancy of host individuals by fleas (prevalence) can be reliably predicted from a simple epidemiological model that takes into account the most parsimonious set of abundance parameters, namely mean abundance and variance of mean abundance.

2. Materials and methods

Small mammals were sampled from 1983 to 2001 in 18 locations across Slovakia (see details in Stanko, 1987, 1988, 1994). Overall, we carried out 120 trapping sessions with 100–2000 traps per session and 1–32 sessions per location. A total of 5876 individuals of 24 species of small mammals (rodents and insectivores) were trapped from which 9508 individual fleas of 30 species were collected (see species lists in Stanko et al., 2002).

Parameters of abundance and distribution were calculated for each flea species parasitising each host species as well as for each flea species across all host species. We included in the analyses: (a) flea–host associations that occurred in at least six trapping sessions (39 flea–host associations, see Supplementary material, Table S1); and (b) flea species that occurred in at least four trapping sessions (19 species, see Supplementary material, Table S2). We calculated mean abundance, variance of abundance and prevalence for each flea–host association and for each flea across all hosts within each trapping session. The relationship between mean abundance and prevalence (arcsin-transformed) was tested using linear regression.

Mean abundance (M) and variance of abundance [$V(M)$] of an organism's distribution are related as (Taylor, 1961)

$$V(M) = aM^b \quad (1)$$

This empirical relationship, known as Taylor's power law (Taylor, 1961), has been supported by numerous data on various taxa of both free-living and parasitic organisms (Taylor and Taylor, 1977; Shaw and Dobson, 1995; Morand and Guégan, 2000; Simkova et al., 2002). We obtained values of a and b parameters by regression of the log-transformed variance of flea abundance against log-transformed mean of flea abundance for each flea–host association and for each flea across all hosts.

Epidemiological models (Anderson and May, 1985) predict that the probability distribution of parasite numbers per host individual, being negative binomial, determines the relationship between the prevalence of infection $P(t)$ (proportion of infested hosts) at any given time t as

$$P(t) = 1 - \left(1 + \frac{M(t)}{k}\right)^{-k}, \quad (2)$$

where $M(t)$ is the mean number of parasites per host individual at time t and k is the parameter of the negative binomial distribution. Parameter k of the negative binomial distribution is related to parameters a and b of Taylor's power law as (Perry and Taylor, 1986)

$$\frac{1}{k} = aM^{b-2} - \frac{1}{M} \quad (3)$$

Based on the above equations, we calculated the expected prevalence (P_{exp}) for each flea–host association and each flea across all hosts using (2), where k is replaced by the sample estimate from (3). We compared the predicted prevalence (2) with the observed prevalence using (i) t -tests on arcsin-transformed values and (ii) linear regressions on untransformed values of prevalences.

3. Results

The estimated slope of the relationship between mean abundance and its variance in log–log space was significantly greater than one in 34 of 39 flea–host associations ranging from 1.03 ± 0.01 to 1.59 ± 0.04 (see Supplementary material, Table S1). When calculated across host species, this slope was significantly greater than one in all flea species ranging from 1.05 ± 0.01 to 1.62 ± 0.06 (see Supplementary material, Table S2). This indicates that fleas were aggregated in their hosts (Taylor, 1961). Prevalence of a flea species increased with an increase in its mean abundance both within and across host species ($r^2 = 0.75$, $F_{1,37} = 112.4$ and $r^2 = 0.96$, $F_{1,17} = 479.9$; $P < 0.001$ for both). The relationship between mean abundance of a flea species and its prevalence across host species is shown in Fig. 1.

Observed prevalences for each flea–host association or for each flea species across all hosts did not differ significantly from prevalences predicted by the epidemiological model using parameters a and b of Taylor's power relationship ($t = -0.6$ and -0.3 , respectively, $P > 0.5$ for both). Regressions of predicted prevalences on observed prevalences produced slope values that did not differ significantly from unity and were independent of scale (within or across host species) (Table 1, Fig. 2). When used at the within-host species scale, the epidemiological model strongly over- or underestimated prevalences in only two cases; *Doratomylla dasyncnema* on *Neomys fodiens* (overestimation) and *Megabothris turbidus* on *Clethrionomys*

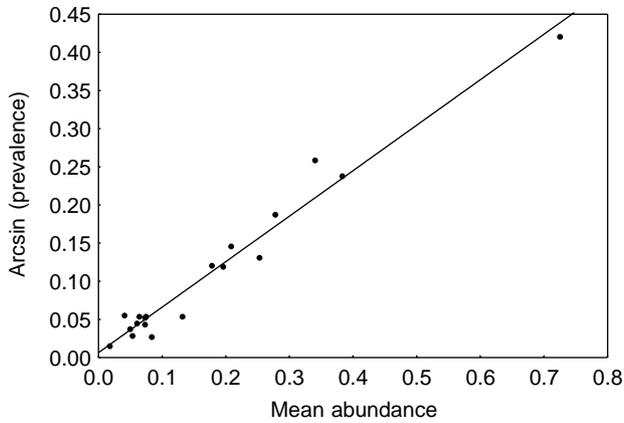


Fig. 1. Relationship between mean abundance and prevalence across all host species among 19 flea species.

glareolus (underestimation) (Fig. 2A). Removal of these two outliers increased the coefficient of determination to 96%.

4. Discussion

This study demonstrated that: (i) prevalence of fleas on their mammalian hosts (occupancy) was positively correlated with mean abundance of the fleas; and (ii) a simple epidemiological model successfully predicted observed prevalences. Fleas, thus, do not differ from the majority of plant and animal taxa for which a positive relationship between abundance and occupancy has been reported (Gaston, 2003). Furthermore, this positive relationship was supported by numerous studies of various parasite taxa including both endo- (Poulin, 1999; Morand and Guégan, 2000) and ectoparasitic (Simkova et al., 2002) helminths and ectoparasitic arthropods (Krasnov et al., 2002). Model for across-host species data provided better fit to observed prevalence values compared with model for within-host species data. The reason for this difference can be a variation between-host species in their relationships with a given parasite species. For example, acquired resistance against the same parasite species can be manifested differently in different hosts. This will likely be reflected in between-host difference in the abundance/prevalence relationships. Mean abundance of a parasite in

Table 1
Summary of regression analyses of prevalences predicted from an epidemiological model against observed prevalences for each flea species within or across host species

Scale	r^2	df	F	Slope \pm SE	Intercept \pm SE
Within host species	0.87	1.37	242.0	1.08 \pm 0.07*	-0.06 \pm 0.02
Across host species	0.98	1.17	1105.2	1.04 \pm 0.03*	0.007 \pm 0.004

Both regressions are significant, $P < 0.001$.

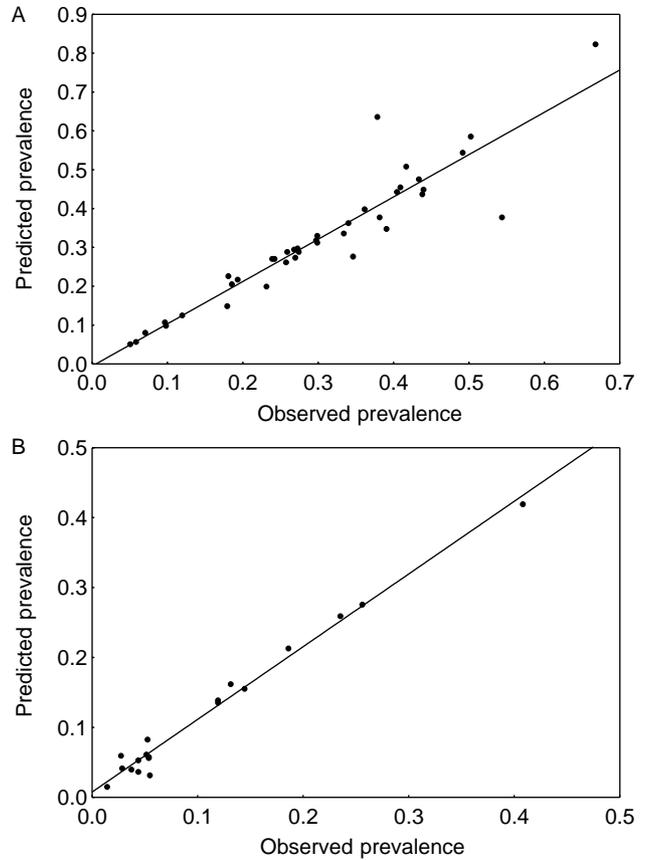


Fig. 2. Relationship between observed and predicted (from the epidemiological models and Taylor’s power law) prevalences of fleas within (A) and across (B) host species.

a host species with stronger acquired resistance will be lower than that in a host with weaker acquired resistance, all else (e.g. prevalence) being equal. Indeed, a study of acquired resistance of the same host (guinea pig) to larvae of the ticks *Amblyomma hebraeum* and *Amblyomma marmoratum* showed that repeated infestation of the host resulted in a 30% (weaker resistance) and 50% (stronger resistance) reduction, respectively, in body mass of engorged larvae (Fielden et al., 1992).

Although positive abundance/occupancy relationships were explained using various mechanisms, the most parsimonious explanation appears to be stochastic relationships between demographic heterogeneity of a species (such as variation in birth, death, migration rates) and heterogeneity of a species’ environment (Anderson and Gordon, 1982). Consequently, this study supports the demographic hypothesis of parasite abundance and distribution (Anderson et al., 1982) which suggests that the observed distributions of parasites across host individuals are generated by two opposing forces, namely those leading to over-dispersion (aggregation) and those leading to under-dispersion (regularity). Stochastic variability in demographic parameters may generate both over- (pure birth process) and under-dispersion (pure death process), whereas

stochasticity in environmental processes creates overdispersion. Environmental processes include those acting in host individuals, being both (a) purely dependent on hosts and hosts' environment (e.g. variability in the susceptibility to parasitism or the level of resistance in dependence on genetic background, age, nutritional state) and (b) dependent on host–parasite relationships (e.g. the level of parasite-induced host mortality, past experience with a parasite, innate and acquired resistance against parasite). In addition, Hanski et al. (1993) argued that the positive correlation between abundance and occupancy can arise from a simple random process. However, significant departure of flea distribution among host individuals from randomness (as indicated by $b > 1$) suggests that this explanation of positive abundance/occupancy relationship is not satisfactory (see also Brown, 1995; Morand and Guégan, 2000).

Our results demonstrated that up to 96% of variance in flea prevalence can be explained solely by their mean abundance. We concluded that, for most flea–host associations, there is no need to invoke other, more complex factors (such as the degree of parasite host specificity or level of host resistance against flea parasitism) for the explanation of the variation in prevalence. Nevertheless, in two cases, observed flea prevalence was either higher or lower than that predicted from the epidemiological model. There were more individuals of *C. glareolus* infested with *M. turbidus* and fewer individuals of *N. fodiens* infested with *D. dasyncnema* than predicted from the model. Flea prevalence overestimated by predictions can be explained by either a relatively low negative effect of flea parasitism on a host and/or strong resistance of a host to flea parasitism, whereas underestimated by predictions can be explained either by high flea-induced host mortality or low preference of a particular host by a particular flea. However, the relationship between a particular host and a particular flea remains to be studied. At present, no detailed information is available for the majority of flea–mammal associations. Furthermore, the statistical description cannot replace specific research aimed to reveal the underlying mechanisms of the relationship between abundance and prevalence of parasites.

Periodic ectoparasites such as fleas are affected not only by hosts but also by the off-host environment (Krasnov et al., 1997). Environmental factors such as ambient temperature and relative humidity can strongly affect their survival (especially, that of pre-imago; Krasnov et al., 2001) and, thus, affect their birth and death rates. Therefore, a confounding effect of the off-host environment on the relationship between flea abundance and distribution can be expected. However, our results demonstrated that this is not the case. This means that purely environmental factors play a minor role in flea distribution among hosts. It should be noted, however, that in temperate regions, stochastic (as opposed to seasonal) environmental fluctuations are less sharp and the environment is more predictable than in

regions such as deserts. Consequently, abundance/distribution relationship in ectoparasites of terrestrial hosts in other regions could be expected to be more complicated than in this study.

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Supplementary material

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.ijpara.2005.05.006](https://doi.org/10.1016/j.ijpara.2005.05.006).

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