

Environment-related and host-related factors affecting the occurrence of lice on rodents in Central Europe

MICHAL STANKO¹, JANA FRIČOVÁ¹, DANA MIKLISOVÁ¹, IRINA S. KHOKHLOVA²
and BORIS R. KRASNOV^{3*}

¹ *Institute of Parasitology, Slovak Academy of Sciences, Lofflerova 10, SK-04001 Kosice, Slovakia*

² *Wylar Department of Dryland Agriculture, French Associates Institute for Agriculture, French Associates Institute for Agriculture and Biotechnology of Drylands, Jacob Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Sede-Boqer Campus, 84990 Midreshet Ben-Gurion, Israel*

³ *Mitrani Department of Desert Ecology, Swiss Institute of Dryland Environmental and Energy Research, Jacob Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Sede-Boqer Campus, 84990 Midreshet Ben-Gurion, Israel*

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SUMMARY

We studied the effects of environment- (habitat, season) and host-related (sex, body mass) factors on the occurrence of four species of lice (Insecta:Phthiraptera:Anoplura) on six rodent species (Rodentia:Muridae). We asked how these factors influence the occurrence of lice on an individual host and whether different rodent–louse associations demonstrate consistent trends in these effects. We found significant effects of at least one environment-related and at least one host-related factor on the louse occurrence in five of six host–louse associations. The effect of habitat was significant in two associations with the occurrence of lice being more frequent in lowland than in mountain habitats. The effect of season was significant in five associations with a higher occurrence of infestation during the warm season in four associations and the cold season in one association. Host sex affected significantly the infestation by lice in three associations with a higher frequency of infestation in males. Host body mass affected the occurrence of lice in all five associations, being negative in wood mice and positive in voles. In conclusion, lice were influenced not only by the host- but also by environment-related factors. The effects of the latter could be mediated via life history parameters of a host.

Key words: body mass, habitat, lice, rodents, season, sex.

INTRODUCTION

Parasitic organisms are characterized by a ‘dual’ environment. On the one hand, this environment is represented by their hosts that provide parasites with both food resources and a place for living, mating and reproducing. On the other hand, it is represented by abiotic factors surrounding the hosts. This is especially true for ectoparasitic arthropods that are strongly affected by the off-host environment (see Marshall, 1981 for review). However, duration of a contact with a host varies among taxa of ectoparasitic arthropods. Based on this duration, Lehane (2005) proposed to distinguish temporary, periodic and permanent ectoparasites. Temporary ectoparasites are largely free-living and visit a host for enough time to take a blood meal (e.g. mosquitos). Periodic ectoparasites spend considerably longer time on a host than is required merely to obtain a blood meal but nevertheless spend a significant amount of time off-host (e.g.

most fleas and gamasid mites). Permanent ectoparasites spend their entire life on a host which thus represents their ultimate habitat (lice).

Obviously, the relative effects of factors associated with the abiotic environment and factors associated with the hosts *per se* on distribution of ectoparasites are expected to differ among the three categories. Temporary ectoparasites are affected mainly by the abiotic environment, permanent ectoparasites mainly by the host-related factors and periodic parasites equally by both. These expectations were largely supported by many studies of temporary (e.g. Jore *et al.* 2014) and periodic (e.g. Linardi and Krasnov, 2013) ectoparasites. In contrast, studies of the environment- and host-related effects on distribution of permanent ectoparasites such as sucking lice (Insecta: Anoplura) are rare (but see Balashov *et al.* 2002). In fact, the majority of studies on sucking lice (apart from studies of lice parasitic on humans) are either taxonomical (e.g. Durden and Eckerlin, 2001; Durden and Timm, 2001; Musser *et al.* 2010) or present description(s) of the assemblages of lice recorded on one or more host species from a defined geographic region (e.g. Haitlinger, 1983; Durden *et al.* 1997; Smith *et al.* 2008; Oguge *et al.* 2009). Ecological studies of sucking lice are scarce and unevenly distributed

* Corresponding author. Mitrani Department of Desert Ecology, Swiss Institute for Dryland Environmental and Energy Research, Jacob Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Sede-Boqer Campus, 84990 Midreshet Ben-Gurion, Israel. E-mail: krasnov@bgu.ac.il

among host taxa. For example, and taking aside studies of lice of high medical and veterinary importance (those parasitic on humans and domestic animals), the ecology of lice parasitic on aquatic mammals (pinnipeds and sea otters; see review in Leonardi and Palma, 2013) is known better than the ecology of lice parasitic on small mammals.

Earlier studies that considered the ecology of sucking lice on small mammals were purely descriptive and presented a narrative rather than formal analyses of the factors affecting abundance and/or distribution of lice (e.g. Sosnina *et al.* 1981). A few recent studies that analysed these factors usually focused on a single host species and either single louse species (e.g. Mize *et al.* 2011; Archer *et al.* 2014) or the pooled data on several louse species (Fernandes *et al.* 2012) and did not reveal whether the effects they found represented a general trend. Here, we studied the relative effects of the environment- (habitat and season) and host-related (sex and body mass) factors on the occurrence of louse infestation in six rodent–louse associations from Eastern Slovakia. We asked how these factors influenced the occurrence of lice on an individual host and whether different rodent–louse associations demonstrated consistent trends in these effects.

We predicted that the probability of an individual rodent being infested by lice will be higher in lowland than in mountain habitats, during warm rather than cold seasons, in males rather than females and will either increase or decrease with increasing body mass. Higher probability of louse infestation in lowlands as compared with mountains and during warm as compared to cold seasons was expected because of the positive effect of higher temperature on fecundity and rate of development in lice (see Marshall, 1981 for review). Slovakian lowlands are, in general, warmer than mountains (Mazur and Jakal, 1982). In addition, earlier observations reported higher abundance and prevalence of lice on rodents during warm seasons (e.g. Sosnina *et al.* 1981). Male-bias in louse infestation was reported for a variety of louse–host associations (Krasnov and Matthee, 2010; Matthee *et al.* 2010; Fernandes *et al.* 2012) and has been considered as a manifestation of a commonly observed phenomenon of male-biased parasitism in small mammals (see Krasnov *et al.* 2012 for review). The effect of body mass was expected due to the correlation between body mass and age of a rodent. Earlier studies of age-dependence of non-lice ectoparasites on rodents demonstrated contrasting patterns of the effect of host age on parasite abundance and/or prevalence (either predominantly positive or predominantly negative), being dependent on natural history parameters of a host species, such as patterns of post-natal growth and dispersal, spatial distribution and the structure of shelters (Krasnov *et al.* 2006a; see also Pacala and Dobson, 1988).

In this study, we used data from a broad ectoparasitological survey that was aimed to investigate abundance and distribution of various taxa of blood-feeding arthropods parasitic on small mammals. Data on fleas, ticks and gamasid mites from this survey can be found elsewhere (e.g. Stanko, 1994; Stanko *et al.* 2002, 2007; Krasnov *et al.* 2006b, 2007, 2010).

MATERIALS AND METHODS

Data collection

Small mammals were sampled and lice were collected during 15 years across Eastern Slovakia. Mammals were captured using snap-traps following the same protocol at each of 102 trapping sessions (see details in Stanko, 1988, 1994). In brief, traps were distributed in lines of 50 traps with 10 m distance between the consecutive traps. Trapping sessions (on average, 700 traps per session, ranging from a total of 100–2000 traps/nights) lasted one to six nights. In each session, traps were opened in the late evening, checked early in the morning and operated, on average, for 7 h. The number of trapped mammals ranged from eight to 395 per trapping session. Each trapped animal was identified, sexed, weighed and examined for ectoparasites. The animal's fur was combed thoroughly, using a toothbrush, over a plastic pan and ectoparasites (lice, fleas, ticks and mites) were carefully collected. Trapping grids were distributed across two main habitat types, namely the lowlands (70 trapping sessions) and the mountains (32 trapping sessions). Lowland habitats were situated at elevations between 100 and 200 m above sea level. They included lowland river valleys with floodplain forests (dominated by *Fraxinus angustifolia*, *Quercus robur*, *Carpinus betulus*, *Salix alba*, *Salix fragilis* and *Populus alba*), woodland belts (represented by 3–8 rows of a poplar, *Populus canadensis*, and various shrubs such as *Prunus* sp., *Rosa* sp., *Sambucus nigra*, with herbal floor composed mainly of *Urtica dioica*), and agricultural fields (mainly wheat and maize as well as stubble and shrubbery dominated by *Prunus spinosus*, *Rosa canina* and *Crataegus* sp. with sporadic occurrence of poplar and willow trees). Mountain habitats were situated at elevations from 300 to 1100 m above sea level. They included submontane and montane brook valleys (dominated by *Alnus glutinosae*, *Alnus incanae*, *Fagus sylvaticus* and *C. betulus*), submontane (oak-hornbeam) and montane (beech and beech-maple) forests, shrubbery patches on pastures (*P. spinosus*, *Corylus avellana* and *R. canina*) as well as gardens and orchards in public green spaces within cities at elevation of 650–750 m above sea level. Mean July and January air temperatures in the lowlands are 20 and –4 °C,

respectively; while in the mountains they are 15.5 and -6°C , respectively (Mazur and Jakal, 1982). Mean annual amount of rainfall is 550–560 mm in the lowlands and 800–1000 mm in the mountains (Mazur and Jakal, 1982).

A total of 9490 individuals belonging to 23 species of small mammals (rodents and insectivores) were trapped, of which 2348 individuals were infested with lice belonging to five species (see Results section).

Data analysis

We analysed factors affecting the occurrence of lice separately for each host and each louse species. For these analyses, we selected only those host–louse associations in which (a) at least 50 host individuals were captured and (b) mean louse abundance and prevalence attained at least 0.10 lice per individual or 10%, respectively. This resulted in six associations used in the analyses (see Results section).

We chose to analyse the occurrence rather than the number of lice on an individual host because the majority of animals were not infested, thus resulting in a large number of zeroes in the dataset. Consequently, our response variable was dichotomous and took a value of either 1 or 0 if an individual was either infested with at least one louse or not, respectively. We analysed the response variable using generalized linear mixed-effects models (GLMM) with the binomial error and logit-link function. Categorical independent variables were habitat (lowland *vs* mountain), sex, and season (warm *vs* cold). We considered 16 April till 15 October as the warm season and 16 October to 15 April as the cold season. In addition, we included in the models body mass of an individual mammal (a proxy for age) as a continuous variable. This variable was log-transformed prior to analysis. Because more than one sample was taken per year, we included a year of sampling as a random variable in our models. To fit GLMMs, we used the function *glmer* from the package ‘lme4’ (Bates *et al.* 2014a, b) implemented in R 3.0 environment (R Core Team, 2013). First, we ran the models with all fixed effects, the interactions between season and either sex or habitat, and a random effect (a year of sampling). We included (a) the interaction between sex and season because host sex-related pattern of infestation by ectoparasites could depend on season (Krasnov *et al.* 2005a, 2012; Kiffner *et al.* 2013) and (b) the interaction between habitat and season because seasonal variation in climate can be pronounced differently in lowland and mountain habitats, resulting in differential seasonal effects on ectoparasites. Then, we selected the best model based on Akaike Information Criterion (AIC) using the function *dredge* from package ‘MuMIn’ (Barton, 2014) implemented in R, and ran the best

model again. This repeatedly fits models with different number of predictors extracted from the global model (Barton, 2014). We calculated both marginal (that is for the model containing fixed effects only) and conditional (for the model containing both fixed effects and a random effect) coefficients of determination (R^2) following Nakagawa and Schielzeth (2013). Finally, to evaluate the overall fit of the best model, we compared it and the model with an intercept and a random effect only using the likelihood ratio test.

Confidence intervals for values of prevalence for the six host–louse associations in dependence of habitat, sex and season were calculated as the adjusted Wald–Sterne’s intervals (Reiczigel, 2003) using Quantitative Parasitology 3.0 (Rózsa *et al.* 2000). Differences in rodent densities between habitat types were analysed using Student’s *t*-test.

RESULTS

Data on mean abundance and prevalence of five louse species recorded on 23 species of small mammals are presented in Table 1. Based on the cut-off values (see Methods section), in the following analyses we focused on six host–louse associations, namely *Apodemus agrarius*–*Hoplopleura affinis*, *Apodemus agrarius*–*Polyplax serrata*, *Apodemus flavicollis*–*P. serrata*, *Apodemus uralensis*–*P. serrata*, *Microtus arvalis*–*Hoplopleura acanthopus* and *Myodes glareolus*–*Hoplopleura edentula*.

GLMMs indicated significant effects of at least one environment-related factor and at least one host-related factor on the occurrence of lice on a host individual in five of six host–louse associations (except for *A. uralensis*–*P. serrata* association; Table 2). Effects of the categorical factors were manifested in the patterns of prevalence of louse infestation within host–louse associations between habitats, sexes and seasons (Table 3). The significant effect of habitat was found in two associations (*A. agrarius*–*P. serrata* and *M. glareolus*–*H. edentula*). The sign of the estimate suggests that the occurrence of lice was more frequent in individual rodents occupying lowland than mountain habitats (Tables 2 and 3). The effect of season on the occurrence of lice was significant in five associations with the estimate being positive (higher occurrence during warm seasons) in four associations and negative (higher occurrence during cold seasons) in one association (*M. arvalis* and *H. acanthopus*) (Tables 2 and 3). Sex of an individual affected significantly the occurrence of lice in three associations (*A. agrarius* and *A. flavicollis* with *P. serrata* and *M. arvalis* with *H. acanthopus*) being higher in males (Tables 2 and 3). Finally, the effect of host body mass on the occurrence of lice was found in all five associations, being negative in *A. agrarius* and *A. flavicollis* and positive in *M. glareolus* and *M. arvalis* (Table 2,

Table 1. Mean abundance (A) and prevalence (P, %) of five louse species recorded on 23 small mammalian species in Eastern Slovakia

| Louse Host | <i>Hoplopleura acanthopus</i> | | <i>Hoplopleura affinis</i> | | <i>Hoplopleura edentula</i> | | <i>Polyplax reclinata</i> | | <i>Polyplax serrata</i> | |
|--------------------------------------|-------------------------------|------|----------------------------|------|-----------------------------|------|---------------------------|------|-------------------------|------|
| | A | P | A | P | A | P | A | P | A | P |
| <i>Apodemus agrarius</i> (2816) | 0.01 | 0.9 | 1.56 | 29.4 | 0 | 0 | 0 | 0 | 1.00 | 19.2 |
| <i>Apodemus flavicollis</i> (3009) | 0.01 | 0.8 | 0.04 | 1.8 | 0.01 | 0.7 | 0 | 0 | 1.79 | 13.0 |
| <i>Apodemus sylvaticus</i> (39) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.44 | 10.3 |
| <i>Apodemus uralensis</i> (1112) | 0.02 | 1.0 | 0.03 | 2.2 | 0 | 0 | 0 | 0 | 0.17 | 6.6 |
| <i>Arvicola amphibius</i> (5) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Crocidura leucodon</i> (13) | 0 | 0 | 0.15 | 7.7 | 0 | 0 | 0.85 | 0.23 | 0.08 | 7.7 |
| <i>Crocidura suaveolens</i> (8) | 0 | 0 | 0 | 0 | 0 | 0 | 7.88 | 75.0 | 0.75 | 25.0 |
| <i>Micromys minutus</i> (3) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Microtus agrestis</i> (6) | 2.67 | 50.0 | 0.16 | 16.7 | 0 | 0 | 0 | 0 | 0.17 | 16.7 |
| <i>Microtus arvalis</i> (712) | 5.05 | 51.2 | 0.01 | 1.1 | 0 | 0 | 0 | 0 | 0.04 | 3.2 |
| <i>Microtus subterraneus</i> (81) | 0.77 | 14.8 | 0.01 | 1.2 | 0 | 0 | 0 | 0 | 0.04 | 2.5 |
| <i>Mus musculus</i> (7) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Muscardinus avellanarius</i> (11) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.27 | 9.1 |
| <i>Myodes glareolus</i> (1312) | 0.03 | 1.2 | 0.02 | 1.1 | 1.10 | 19.7 | 0 | 0 | 0.03 | 2.7 |
| <i>Myoxus glis</i> (5) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Neomys anomalus</i> (26) | 0 | 0 | 0.04 | 3.8 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Neomys fodiens</i> (61) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Sicista betulina</i> (2) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1.50 | 50.0 |
| <i>Sorex alpinus</i> (3) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Sorex araneus</i> (213) | 0 | 0 | 0.01 | 1.4 | 0 | 0 | 0 | 0 | 0.02 | 1.9 |
| <i>Sorex minutus</i> (36) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.03 | 2.8 |
| <i>Spermophilus citellus</i> (5) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Talpa europaea</i> (5) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

In parenthesis – number of captured and examined individuals.

see illustrative examples with *A. agrarius* and *M. arvalis* in Fig. 1).

DISCUSSION

Although the explanatory power of models of the occurrence of lice on an individual host as affected by the environment- and host-associated factors was not especially high, results of our study indicate that these factors affect the probability of an individual host to be infested. We found this indication in the majority (five of six) of studied host–louse associations. It is unclear why no significant effect of any factor was found for the occurrence of *P. serrata* on *A. uralensis*. Extremely low numbers and prevalence of this louse on this host is the most likely explanation of this lack of significant effects (Table 1). In addition, *A. uralensis* is the least promiscuous among *Apodemus* species, so that each animal usually contacts with a very limited number of individuals of the opposite sex (Bryja *et al.* 2008) which may impede the transmission of lice.

Furthermore, we found consistent trends in the effect of a factor on the louse occurrence for some factors (habitat and sex) and contrasting patterns for other factors (season and body mass). The mechanism behind these effects is interplay between louse and host ecology. This is because the occurrence of lice on a host is determined by a variety of factors

including the effects of physiology, immunology and ant-parasitic behaviour of an individual host on louse reproduction and survival as well as the effects of the host population density and its social/spatial behaviour on the processes of louse transmission.

Habitat-dependence

In both host–louse associations for which the effect of habitat was significant, higher frequency of infestation occurred in the lowlands. Earlier studies that reported habitat differences in louse infestation often explained this pattern by difference in the host density that, in turn, could affect the transmission of lice among host individuals (e.g. Fernandes *et al.* 2012 for lice on *Oligoryzomys nigripes* in Brazil). However, this explanation does not look feasible in our study because in both hosts for which the significant habitat effect on louse infestation was found, densities (calculated as the number of animals captured per 100 trap/nights) in lowland and mountain habitats were similar (Student's *t*-test; $t = -0.28$ for *A. agrarius* and $t = 0.12$ for *M. glareolus*; D.F. = 100, $P > 0.80$ for both), while they differed in those hosts which did not demonstrate habitat-dependence of infestation ($t = -7.28$ for *A. flavicollis* and $t = 2.55$ for *M. arvalis*; D.F. = 100, $P < 0.05$ for both). It is likely therefore that

Table 2. Summary of GLMM (binomial error and logit-link function) of the effects of habitat, host sex, season and host body mass on the occurrence of lice on an individual host for six host–louse associations

| Association | Fixed effect | Coefficient estimate ±s.e. | z value | AICw | margR ² | condR ² | χ ² |
|---|--------------------|-------------------------------|---------------------|------|--------------------|--------------------|----------------|
| <i>Apodemus agrarius</i> – <i>H. affinis</i> | Season (warm) | 0.57 ± 0.09 | 6.04*** | 0.45 | 0.02 | 0.05 | 39.57*** |
| | Body mass | −0.97 ± 0.35 | −2.74** | | | | |
| <i>Apodemus agrarius</i> – <i>Polyplax serrata</i> | Habitat (mountain) | −0.39 ± 0.18 | −2.17* | 0.22 | 0.02 | 0.12 | 17.98** |
| | Season (warm) | 0.22 ± 0.11 | 2.00* | | | | |
| | Sex (male) | 0.27 ± 0.10 | 2.78** | | | | |
| | Body mass | −0.73 ± 0.21 | −2.10* | | | | |
| <i>Apodemus flavicollis</i> – <i>Polyplax serrata</i> | Season (warm) | 0.59 ± 0.16 | 3.67*** | 0.32 | 0.03 | 0.19 | 29.35*** |
| | Sex (male) | 0.41 ± 0.11 | 3.48*** | | | | |
| | Body mass | −0.70 ± 0.29 | −2.05* | | | | |
| <i>Apodemus uralensis</i> – <i>Polyplax serrata</i> | Habitat (mountain) | −0.55 ± 0.36 | −1.52 ^{ns} | – | – | 0.11 | – |
| | Sex (male) | 0.39 ± 0.26 | 1.53 ^{ns} | | | | |
| | Body mass | 2.78 ± 1.89 | 1.68 ^{ns} | | | | |
| <i>Microtus arvalis</i> – <i>Hoplopleura acanthopus</i> | Season (warm) | −0.71 ± 0.22 | −3.25** | 0.10 | 0.12 | 0.36 | 54.90*** |
| | Sex (male) | 0.38 ± 0.16 | 2.32* | | | | |
| | Body mass | 3.62 ± 0.55 | 6.48*** | | | | |
| <i>Myodes glareolus</i> – <i>Hoplopleura edentula</i> | Habitat (mountain) | −0.62 ± 0.20 | −3.13** | 0.04 | 0.49 | 0.51 | 31.64*** |
| | Season (warm) | 0.50 ± 0.17 | 2.82** | | | | |
| | Body mass | 2.13 ± 0.78 | 2.72** | | | | |

Year of sampling was introduced as a random effect in each model. Reference levels for the fixed effects were lowland (for habitat), female (for sex) and cold (for season). AICw – Akaike Information Criterion weight of the best model from a set of models derived from a full model (all fixed effects, the interactions between sex and season and between habitat and season, and a year of sampling as a random effect; see main text for explanations). margR² – marginal coefficient of determination, condR² – conditional coefficient of determination. Significance levels: * – <0.05, ** – <0.01, *** – <0.001 ns – non-significant. χ² – likelihood ratio χ² when comparing the best model with the model of intercept and a random effect only.

habitat dependence of the occurrence of lice was due to abiotic variables that undoubtedly differ between the two habitat types.

Lowland habitats in Slovakia are warmer than the mountains (Mazur and Jakal, 1982). Consequently, the occurrence of lice could be higher in the lowlands because higher temperature (although not too high) favours survival of pre-imaginal lice (e.g. Colwell, 2014) as well as their rate of development (e.g. Leeson, 1941) and the rate of oviposition by adults (e.g. Schrader *et al.* 2008). However, Slovakian lowlands are also drier than the mountains (Mazur and Jakal, 1982). The results of studies of the effects of habitat-associated moisture on lice parasitic on mammals are contradictory and differ among louse species, host species and geographic regions. For example, infestation of small mammals by sucking lice was found to be higher in drier than wetter habitats in North America (Mize *et al.* 2011), but the opposite was true in Africa (Oguge *et al.* 2009; see also Moyer *et al.* 2002 and Calvete *et al.* 2003 for chewing lice parasitic on birds in North America and Southern Europe, respectively). This contradiction could arise due to, for example, among-louse species variation in the response to humidity.

The reason why the effect of habitat was found in only two host–louse associations is still unclear and

warrants further investigation. On the one hand, the fact that this pattern was found in *P. serrata* but not in *H. affinis*, both parasitic on the same host (*A. agrarius*) suggests that some between-louse differences in sensitivity to abiotic factors play a role. On the other hand, habitat-dependence of the louse occurrence was found in *P. serrata* parasitic on *A. agrarius* but not on *A. flavicollis*. This suggests also a role of some host-associated mechanisms. However, *P. serrata* exploiting *A. agrarius* and those exploiting *A. flavicollis* might belong to different lineages (see Štefka and Hypša, 2008) and thus the former explanation seems more likely.

Seasonal changes

Three of four hosts (four of five host–louse associations) demonstrated higher occurrences of louse infestation during the warm season. Seasonal differences in abundance and prevalence of sucking lice on small mammals have been reported for a variety of geographic regions (Sosnina *et al.* 1981; Wilson *et al.* 1991; Archer *et al.* 2014). Similarly to our results, the highest abundance and prevalence of lice in the temperate areas have been found in the warmer months (Sosnina *et al.* 1981; Haitlinger, 1983; Krištofik and Lysy, 1992). This was explained

Table 3. Prevalence (%) (in parentheses 95% confidence intervals) of infestation of five rodent species by four lice species in dependence of habitat, host sex and season

| Host | Louse | Habitat | | Sex | | Season | |
|-----------------------------|-------------------------------|------------------|------------------|------------------|------------------|------------------|------------------|
| | | Lowland | Mountain | Male | Female | Cold | Warm |
| | | | | | | | |
| <i>Apodemus agrarius</i> | <i>Hoplopleura affinis</i> | 30.3 (28.1–33.1) | 27.2 (24.2–30.0) | 29.4 (27.2–31.2) | 29.6 (27.1–32.1) | 23.7 (21.5–26.1) | 34.6 (32.2–37.0) |
| | <i>Polyplax serrata</i> | 21.7 (19.9–23.6) | 12.3 (10.0–12.0) | 21.1 (19.8–23.0) | 17.4 (15.3–19.6) | 16.6 (13.7–16.6) | 22.9 (20.7–25.2) |
| <i>Apodemus flavicollis</i> | <i>Polyplax serrata</i> | 15.2 (13.4–17.2) | 10.8 (9.4–12.5) | 14.9 (13.2–16.7) | 10.5 (9.0–12.2) | 6.8 (5.3–8.6) | 15.7 (14.2–17.4) |
| <i>Apodemus uralensis</i> | <i>Polyplax serrata</i> | 7.3 (5.7–9.3) | 4.1 (2.1–7.2) | 7.5 (5.7–9.8) | 5.2 (3.5–7.7) | 4.1 (2.2–7.4) | 7.3 (5.7–9.2) |
| <i>Microtus arvalis</i> | <i>Hoplopleura acanthopus</i> | 51.5 (47.2–55.8) | 50.0 (41.8–58.2) | 55.9 (51.2–61.4) | 46.5 (41.5–50.6) | 56.5 (53.8–63.9) | 49.3 (44.9–52.7) |
| <i>Myodes glareolus</i> | <i>Hoplopleura edentula</i> | 24.0 (21.2–25.4) | 17.6 (16.1–20.2) | 20.2 (17.2–23.4) | 19.2 (16.3–22.4) | 17.3 (16.1–18.5) | 21.9 (19.2–23.9) |

not only by the favourable air temperature but also by an increase in density and mobility of hosts (Sosnina *et al.* 1981). The latter presumably facilitates transmission of lice among host individuals, thus not only increasing louse prevalence but also mating chances of lice. This, in turn, may lead to higher reproductive rates and, eventually, to higher abundances. The only host species in our study in which more individuals were infested by lice during cold than warm seasons was the common vole, *M. arvalis*. In contrast to other studied rodents, this species is colonial. In winter, non-hibernating small mammals of the temperate zone, such as *M. arvalis*, spend much time in the subnivean space (i.e. between the snow cover and the ground) (e.g. Bashenina, 1962; Fuller, 1967; Pruitt, 1984; Korslund and Steen, 2006) and their activity level decreases at this time (e.g. Eccard and Herde, 2013). Thus, in *M. arvalis*, time spent in contact with other members of the colony might substantially increase in the cold season, which results in a greater rate of the louse transmission between individuals and, eventually, in a higher occurrence of infestation. In addition, the summer nests of *M. arvalis* are usually occupied by a single female with its offspring, whereas the winter nests are occupied by many unrelated individuals (Chelkowska, 1978). This is another, but not necessarily an alternative mechanism of the higher number of individual voles infested by lice during cold as compared to warm seasons.

Male bias

Male-biased parasitism has long been a popular concept based on numerous observations that mammalian and avian males are usually infested with more parasite individuals and/or species than females (see reviews in Zuk and McKean, 1996; Krasnov *et al.* 2012). However, recent studies challenged this concept and demonstrated that it is far from being universal rule (Kiffner *et al.* 2013, 2014). Nevertheless, whenever a significant effect of host sex on the occurrence of lice was found in our study (three of six host–louse associations), it indicated that the probability being infested was higher for a male than a female rodent. Male-biased infestation by sucking lice has been found in a variety of louse and host species in different geographic regions including *Polyplax arvicantis* on *Rhabdomys pumilio* in South Africa (Mathee *et al.* 2010) and several *Hoplopleura* lice on *O. nigripes* in South America (Fernandes *et al.* 2012). However, the lack of any gender bias in louse infestation has been reported as well (Scantlebury *et al.* 2010; Viljoen *et al.* 2011). Explanations of male-biased infestation usually involve either lower immunocompetence in males due to the immunosuppressive effect of testosterone or their higher mobility

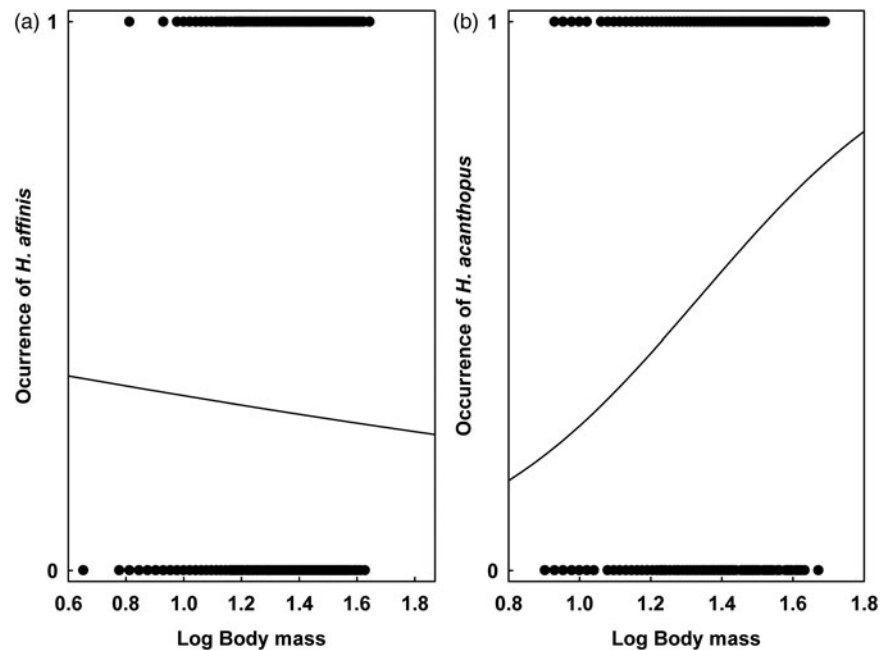


Fig. 1. The effect of body mass of an individual (a) *A. agrarius* and (b) *M. arvalis* on the occurrence of lice.

resulting in higher exposure to parasites or both. Both these mechanisms could be implied for the explanation of the patterns found in our study. In other words, gender-specific behaviour and physiology of the host are the most likely reasons behind gender-biased infestation. For example, male *M. arvalis* are more often involved in aggressive interactions than females and the testosterone levels in these males are elevated (Gromov and Voznesenskaya, 2010). In contrast, male *M. glareolus* usually avoid one another (Łopucki, 2007). These differences explain why the male bias in louse infestation was found in the former but not in the latter species. Although lice spend their entire life on the hosts, they are transmitted between hosts via their contacts. Males of *M. arvalis* continuously migrate from colony to colony while this is not the case for females (Gauffre *et al.* 2009). This dispersal pattern might be another mechanism underlying male-biased parasitism in this rodent. However, we also found male-biased infestation of the same host species (*A. agrarius*) by one (*P. serrata*) but not another (*H. affinis*) louse species. This suggests that the manifestation of gender-biased parasitism may depend not only on the life history and/or physiological traits of a host species, but also on some, still unknown, traits of a parasite species.

Effect of host body mass: age or body condition?

Body mass of an individual rodent could be indicative of either its age or body condition. It is commonly known that parasite abundance and the pattern of its distribution often vary between younger and older hosts (e.g. Goater and Ward,

1992). Moreover, studies from the number of host–parasite systems demonstrated that shape of the relationships between host age and parasite abundance and/or distribution varies among host–parasite associations because these relationships are generated by different mechanisms (see review in Hudson and Dobson, 1995). Indeed, substantial variation in the relationships between abundance and distribution of parasites and host age/body size has been shown for small mammals and fleas (Krasnov *et al.* 2006a). Similar results were found for lice in this study. The most likely reason for the variation in host age–louse occurrence patterns is differences in the natural history of host species. We found a decrease in louse occurrence with increasing body mass in both wood mice (*Apodemus*) and the opposite trend in both voles (*Myodes* and *Microtus*). The explanation for this difference is that the relationship between host age and louse infestation is affected by the pattern of the host's postnatal growth. Indeed, wood mice attain a definitive size at about 40 days and grow extremely slow afterwards (e.g. *Apodemus semotus*; Lin *et al.* 1993). In contrast, period of continuous growth in voles is at least twice (*Microtus cabreræ*; Fernández-Salvador *et al.* 2001) or thrice (*Microtus montebelli*; Nakatsu, 1975) longer. Consequently, the heaviest cohort of wood mice is a mix of individuals of median age and old individuals, whereas the heaviest cohort of voles is represented mainly by old individuals. The immune function in the individuals of median age is strong, whereas it deteriorates in old individuals (see review in Miller, 1996). Lower defensibility of old animals makes them better patches for lice. Consequently,

the difference in age composition of the heaviest individuals between wood mice and voles could be manifested in the contrasting patterns of body mass–louse infestation relationship.

The effect of the host's body condition on parasites has been studied in a variety of animals (e.g. Oppliger *et al.* 1996; Brown *et al.* 2000; Krasnov *et al.* 2005b). On the one hand, a host in good condition may provide parasites with resources of a higher quality than a host in poor condition (Dawson and Bortolotti, 1997). On the other hand, parasites may benefit from exploiting hosts of the poorer body condition because their immune system is weaker (Simon *et al.* 2003). It is not surprising, therefore, that studies of the effect of the host's body condition on parasites produced contradictory results with parasite performance in hosts in the good conditions being either better (e.g. Blanco *et al.* 1997) or worse (e.g. Whiteman and Parker, 2004) than in hosts in the poor conditions. Moreover, the opposite patterns of parasite performance in hosts of different nutritional statuses were reported for parasites belonging to the same taxon (fleas; Krasnov *et al.* 2005b vs Tschirren *et al.* 2007). In our study, we found negative relationships between host body mass and the occurrence of lice in three associations and positive relationships in two associations. These opposite patterns could stem from differences in the co-evolutionary history of different host–parasite systems (Tschirren *et al.* 2007). This explanation is indirectly supported by the fact that we found similar patterns in closely-related (among mice or among voles) but different patterns in distantly related hosts (between mice and voles). We also found the same pattern in the same louse (*P. serrata*) parasitic on either *A. agrarius* or *A. flavicollis*. Moreover, the opposite patterns of the relationships between infestation and the host's body condition among host–parasite associations may arise due to either differential immunological responses of the same host to attacks by different parasites or differential responses of the same parasite to the defence efforts of different host or both (e.g. Khokhlova *et al.* 2004).

We conclude that, despite being permanent ectoparasites, the distribution of sucking lice among host individuals was influenced not only by the host-related but also by the environment-related factors. However, the effects of the environment-related factors could be mediated via life history parameters of a host such as reproductive and dispersal patterns, social behaviour and spatial distribution.

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REFERENCES

- Archer, E. K., Bennett, N. C., Ueckermann, E. A. and Lutermann, H. (2014). Ectoparasite burdens of the common mole-rat (*Cryptomys hottentotus hottentotus*) from the Cape provinces of South Africa. *Journal of Parasitology* **100**, 79–84.
- Balashov, Y. S., Bochkov, A. V., Vashchenok, V. S., Grigor'eva, L. A. and Tret'akov, K. A. (2002). Structure and seasonal dynamics of the biotic community ectoparasites of the bank vole in the Il'men'-Volkhov lowland. *Parazitologiya* **36**, 433–446. (in Russian).
- Barton, K. (2014). *MuMIn: Multi-model inference*. R package version 1.10.5. <http://CRAN.R-project.org/package=MuMIn>
- Bashenina, N. V. (1962). *The Ecology of the Common Vole*. Moscow University Press, Moscow, USSR (in Russian).
- Bates, D., Maechler, M., Bolker, B. and Walker, S. (2014a). *lme4: Linear mixed-effects models using Eigen and S4*. R package version 1.1–7, <http://CRAN.R-project.org/package=lme4>
- Bates, D., Maechler, M., Bolker, B. and Walker, S. (2014b). *lme4: Linear mixed-effects models using Eigen and S4*. ArXiv e-print; submitted to *Journal of Statistical Software* <http://arxiv.org/abs/1406.5823>
- Blanco, G., Tella, J. L. and Potti, J. (1997). Feather mites on group-living Red-billed Choughs: a non-parasitic interaction? *Journal of Avian Biology* **28**, 197–206.
- Brown, M. J. F., Loosli, R. and Schmid-Hempel, P. (2000). Condition-dependent expression of virulence in a trypanosome infecting bumblebees. *Oikos* **91**, 421–427.
- Bryja, J., Patzenhauerová, H., Albrecht, T., Mošanský, L., Stanko, M. and Stopka, P. (2008). Varying levels of female promiscuity in four *Apodemus* mice species. *Behavioral Ecology and Sociobiology* **63**, 251–260.
- Calvete, C., Estrada, R., Lucientes, J. and Estrada, A. (2003). Ectoparasite ticks and chewing lice of red-legged partridge, *Alectoris rufa*, in Spain. *Medical and Veterinary Entomology* **17**, 33–37.
- Chełkowska, H. (1978). Variations in number and social factors in a population of field voles. *Acta Theriologica* **23**, 213–238.
- Colwell, D. D. (2014). Life history parameters of the cattle long-nosed sucking louse, *Linognathus vituli*. *Medical and Veterinary Entomology* **28**, 432–437.
- Dawson, R. D. and Bortolotti, G. R. (1997). Ecology of parasitism of nestling American Kestrels by *Carnus hemapterus* (Diptera, Carnidae). *Canadian Journal of Zoology* **75**, 2021–2026.
- Durden, L. A. and Eckerlin, R. P. (2001). *Polyplax guatemalensis* sp. n. (Phthiraptera: Anoplura), a new sucking louse from *Peromyscus grandis*, a montane cloud forest rodent from Guatemala. *Folia Parasitologica* **48**, 69–72.
- Durden, L. A. and Timm, R. M. (2001). *Hoplopleura janzeni* n. sp. (Phthiraptera: Anoplura), a new sucking louse from a Central American swimming mouse. *Journal of Parasitology* **87**, 1409–1413.
- Durden, L. A., Kollars, T. M., Jr., Patton, S. and Gerhardt, R. R. (1997). Sucking lice (Anoplura) of mammals of Tennessee. *Journal of Vector Ecology* **22**, 71–76.
- Eccard, J. A. and Herde, A. (2013). Seasonal variation in the behaviour of a short-lived rodent. *BMC Ecology* **13**, 43.
- Fernandes, F. R., Cruz, L. D. and Linhares, A. X. (2012). Effects of sex and locality on the abundance of lice on the wild rodent *Oligoryzomys nigripes*. *Parasitology Research* **111**, 1701–1706.
- Fernández-Salvador, R., García-Perea, R. and Ventura, J. (2001). Reproduction and postnatal growth of the Cabrera vole, *Microtus cabrerae*, in captivity. *Canadian Journal of Zoology* **79**, 2080–2085.
- Fuller, W. A. (1967). Winter ecology of lemmings and fluctuations of their populations. *Terre et la Vie* **2**, 97–115.

- Gaufré, B., Petit, E., Brodier, S., Bretagnolle, V. and Cosson, J. F.** (2009). Sex-biased dispersal patterns depend on the spatial scale in a social rodent. *Proceedings of the Royal Society of London B* **276**, 3487–3494.
- Goater, C. P. and Ward, P. I.** (1992). Negative effects of *Rhabdias bufonis* (Nematoda) on the growth and survival of toads (*Bufo bufo*). *Oecologia* **89**, 161–165.
- Gromov, V. S. and Voznesenskaya, V. V.** (2010). Parental care, aggressiveness, and testosterone secretion in male common voles (*Microtus arvalis*) and steppe lemmings (*Lagurus lagurus*). *Doklady Biological Sciences* **431**, 86–88.
- Haitlinger, R.** (1983). Invertebrates associated with the bank vole. Arthropod communities. *Acta Theriologica* **28**, 55–68.
- Hudson, P. J. and Dobson, A. P.** (1995). Macroparasites: observed patterns. In *Ecology of Infectious Diseases in Natural Populations* (eds. Grenfell, B. T. and Dobson, A. P.), pp. 144–176. Cambridge University Press, Cambridge.
- Jore, S., Vanwambeke, S. O., Viljugrein, H., Isaksen, K., Kristoffersen, A. B., Woldehiwet, Z., Johansen, B., Brun, E., Brun-Hansen, H., Westermann, S., Larsen, I.-L., Ytrehus, B. and Hofshagen, M.** (2014). Climate and environmental change drives *Ixodes ricinus* geographical expansion at the northern range margin. *Parasites and Vectors* **7**, 11.
- Khokhlova, I. S., Spinu, M., Krasnov, B. R. and Degen, A. A.** (2004). Immune responses to fleas in two rodent species differing in natural prevalence of infestation and diversity of flea assemblages. *Parasitology Research* **94**, 304–311.
- Kiffner, C., Stanko, M., Morand, S., Khokhlova, I. S., Shenbrot, G. I., Laudisoit, A., Leirs, H., Hawlena, H. and Krasnov, B. R.** (2013). Sex-biased parasitism is not universal: evidence from rodent–flea associations from three biomes. *Oecologia* **173**, 1009–1022.
- Kiffner, C., Stanko, M., Morand, S., Khokhlova, I. S., Shenbrot, G. I., Laudisoit, A., Leirs, H., Hawlena, H. and Krasnov, B. R.** (2014). Variable effects of host characteristics on species richness of flea infracommunities in rodents from three continents. *Parasitology Research* **113**, 2777–2788.
- Korslund, L. and Steen, H.** (2006). Small rodent winter survival: snow conditions limit access to food resources. *Journal of Animal Ecology* **75**, 156–166.
- Krasnov, B. R. and Matthee, S.** (2010). Spatial variation in gender-biased parasitism: host-related, parasite-related and environment-related effects. *Parasitology* **137**, 1526–1537.
- Krasnov, B. R., Morand, S., Hawlena, H., Khokhlova, I. S. and Shenbrot, G. I.** (2005a). Sex-biased parasitism, seasonality and sexual size dimorphism in desert rodents. *Oecologia* **146**, 209–217.
- Krasnov, B. R., Khokhlova, I. S., Arakelyan, M. S. and Degen, A. A.** (2005b). Is a starving host tastier? Reproduction in fleas parasitizing food-limited rodents. *Functional Ecology* **19**, 625–631.
- Krasnov, B. R., Stanko, M. and Morand, S.** (2006a). Age-dependent flea (Siphonaptera) parasitism in rodents: a host's life history matters. *Journal of Parasitology* **92**, 242–248.
- Krasnov, B. R., Stanko, M. and Morand, S.** (2006b). Are ectoparasite communities structured? Species co-occurrence, temporal variation and null models. *Journal of Animal Ecology* **75**, 1330–1339.
- Krasnov, B. R., Stanko, M. and Morand, S.** (2007). Host community structure and infestation by ixodid ticks: repeatability, dilution effect and ecological specialization. *Oecologia* **154**, 185–194.
- Krasnov, B. R., Stanko, M. and Morand, S.** (2010). Competition, facilitation or mediation via host? Patterns of infestation of small European mammals by two taxa of haematophagous arthropods. *Ecological Entomology* **35**, 37–44.
- Krasnov, B. R., Bordes, F., Khokhlova, I. S. and Morand, S.** (2012). Gender-biased parasitism in small mammals: patterns, mechanisms, consequences. *Mammalia* **76**, 1–13.
- Krištofik, J. and Lysy, J.** (1982). Seasonal dynamics of sucking lice (Anoplura) in small mammals (Insectivora, Rodentia) in the natural foci of infections in south-west Slovakia. *Biologia (Bratislava)* **47**, 605–617.
- Leeson, H. S.** (1941). The effect of temperature upon the hatching of the eggs of *Pediculus humanus corporis* De Geer (Anoplura). *Parasitology* **33**, 243–249.
- Lehane, M.** (2005). *The Biology of Blood-Sucking in Insects*, 2nd edn. Cambridge University Press, Cambridge.
- Leonardi, M. S. and Palma, R. L.** (2013). Review of the systematics, biology and ecology of lice from pinnipeds and river otters (Insecta: Phthiraptera: Anoplura: Echinophthiriidae). *Zootaxa* **3630**, 445–466.
- Lin, L. K., Nishino, T. and Shiraishi, S.** (1993). Postnatal growth and development of the Formosan wood mouse *Apodemus semiotus*. *Journal of the Mammalogical Society of Japan* **18**, 1–18.
- Linardi, P. M. and Krasnov, B. R.** (2013). Patterns of diversity and abundance of fleas (Insecta: Siphonaptera) and mites (Acari: Mesostigmata) in the Neotropics: host-related, parasite-related and environment-related factors. *Medical and Veterinary Entomology* **27**, 49–58.
- Lopucki, R.** (2007). Social relationships in a bank vole *Clethrionomys glareolus* (Schreber 1780) population: video monitoring under field conditions. *Polish Journal of Ecology* **55**, 543–558.
- Marshall, A. D.** (1981). *The Ecology of Ectoparasitic Insects*. Academic Press, London.
- Matthee, S., McGeoch, M. A. and Krasnov, B. R.** (2010). Parasite-specific variation and the extent of male-biased parasitism; an example with a South African rodent and ectoparasitic arthropods. *Parasitology* **137**, 651–660.
- Mazur, E. and Jakal, J.** (1982). *Atlas Slovenskej Socialistickej Republiky*. Slovenska Akademia Vied, Bratislava (in Slovak).
- Miller, R. A.** (1996). The aging immune system: primer and prospectus. *Science* **273**, 70–74.
- Mize, E. L., Tsao, J. I. and Maurer, B. A.** (2011). Habitat correlates with the spatial distribution of ectoparasites on *Peromyscus leucopus* in southern Michigan. *Journal of Vector Ecology* **36**, 308–320.
- Moyer, B. R., Drown, D. D. and Clayton, D. H.** (2002). Low humidity reduces ectoparasite pressure: implications for host life history evolution. *Oikos* **97**, 223–228.
- Musser, G. G., Durden, L. A., Holden, M. E. and Light, J. E.** (2010). Systematic review of endemic Sulawesi squirrels (Rodentia, Sciuridae), with descriptions of new species of associated sucking lice (Insecta, Anoplura), and phylogenetic and zoogeographic assessments of sciurid lice. *Bulletin of the American Museum of Natural History* **339**, 1–260.
- Nakagawa, S. and Schielzeth, H.** (2013). A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution* **4**, 133–142.
- Nakatsu, A.** (1975). Some observations on the Japanese field vole, *Microtus montebelli* (Milne-Edwards) in captivity. I. Postnatal growth and development. *Bulletin of the Government Forest Experiment Station* **276**, 23–29.
- Oguge, N. O., Durden, L. A., Keirans, J. E., Balami, H. D. and Schwan, T. G.** (2009). Ectoparasites (sucking lice, fleas and ticks) of small mammals in southeastern Kenya. *Medical and Veterinary Entomology* **23**, 387–392.
- Oppliger, A., Christe, P. and Richner, H.** (1996). Clutch size and malaria resistance. *Nature* **381**, 565.
- Pacala, S. W. and Dobson, A. P.** (1988). The relation between the number of parasites/host and host age: population dynamic causes and maximum likelihood estimation. *Parasitology* **96**, 197–210.
- Pruitt, W. O.** (1984). *Snow and small mammals*. In *Winter Ecology of Small Mammals* (ed. Merritt, J. F.), pp. 1–8. Carnegie Museum of Natural History, Pittsburgh.
- R Core Team** (2013). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>
- Reiczigel, J.** (2003). Confidence intervals for the binomial parameter: some new considerations. *Statistics in Medicine* **22**, 611–621.
- Rózsa, L., Reiczigel, J. and Majoros, G.** (2000). Quantifying parasites in samples of hosts. *Journal of Parasitology* **86**, 228–232.
- Scantlebury, M., Maher McWilliams, M., Marks, N. J., Dick, J. T. A., Edgar, H. and Lutermann, H.** (2010). Effects of life-history traits on parasite load in grey squirrels. *Journal of Zoology* **282**, 246–255.
- Schrader, G., Schmolz, E., Könnig, M. and Dahl, R.** (2008). Survival and reproduction of a laboratory strain of body lice (Phthiraptera: Pediculidae) at different ambient temperatures. In *Proceedings of the Sixth International Conference on Urban Pests* (ed. Robinson, W. H. and Bajomi, D.), pp. 307–314. OOK-Press Kft., Veszprém, Hungary.
- Simon, A., Thomas, D. W., Blondel, J., Lambrechts, M. M. and Perret, P.** (2003). Within-brood distribution of ectoparasite attacks on nestling blue tits: a test of the tasty chick hypothesis using inulin as a tracer. *Oikos* **102**, 551–558.
- Smith, V. S., Light, J. E. and Durden, L. A.** (2008). Rodent louse diversity, phylogeny, and cospeciation in the Manu Biosphere Reserve, Peru. *Biological Journal of the Linnean Society* **95**, 598–610.
- Sosnina, E. F., Nazarova, I. V. and Sadekova, L. K.** (1981). Sucking lice of small mammals from the Volga-Kama State Reserve. *Parazitologiya* **15**, 157–162. (in Russian).
- Stanko, M.** (1988). Fleas (Siphonaptera) of small mammals in eastern part of Volovské vrchy mountains. *Acta Rerum Naturalium Musei Nationalis Slovaci* **34**, 29–40. (in Slovakian).
- Stanko, M.** (1994). Fleas synusy (Siphonaptera) of small mammals from the central part of the East-Slovakian lowlands. *Biologia (Bratislava)* **49**, 239–246.

- Stanko, M., Miklisová, D., Göüy de Bellocq, J. and Morand, S.** (2002). Mammal density and patterns of ectoparasite species richness and abundance. *Oecologia* **131**, 289–295.
- Stanko, M., Krasnov, B. R., Miklisová, D. and Morand, S.** (2007). Simple epidemiological model predicts the relationships between prevalence and abundance in ixodid ticks. *Parasitology* **134**, 59–68.
- Štefka, J. and Hypša, V.** (2008). Host specificity and genealogy of the louse *Polyplax serrata* on field mice, *Apodemus* species: a case of parasite duplication or colonisation? *International Journal for Parasitology* **38**, 731–741.
- Tschirren, B., Bischoff, L. L., Saladin, V. and Richner, H.** (2007). Host condition and host immunity affect parasite fitness in a bird-ectoparasite system. *Functional Ecology* **21**, 372–378.
- Viljoen, H., Bennett, N. C., Ueckermann, E. A. and Lutermann, H.** (2011). The role of host traits, season and group size on parasite burdens in a cooperative mammal. *PLoS ONE* **6**, e27003.
- Whiteman, N. K. and Parker, P. G.** (2004). Body condition and parasite load predict territory ownership in the Galapagos hawk. *The Condor* **106**, 915–921.
- Wilson, N. A., Telford, S. R. and Forrester, D. J.** (1991). Ectoparasites of a population of urban gray squirrels in northern Florida. *Journal of Medical Entomology* **28**, 461–464.
- Zuk, M. and McKean, K. A.** (1996). Sex differences in parasite infections: patterns and processes. *International Journal for Parasitology* **26**, 1009–1024.