Prediction of prevalence from mean abundance via a simple epidemiological model in mesostigmate mites from two geographical regions

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SUMMARY

We analysed data on the abundance and distribution of 26 species of mesostigmate mites with different feeding habits collected from bodies of small mammalian hosts in 2 geographical regions (West Siberia and Argentina). We tested whether prevalence of a mite can be reliably predicted from a simple epidemiological model that takes into account mean abundance and its variance. We theorized that the difference between prevalence predicted from the model and observed prevalence would be smallest in obligatory haematophagous mites, intermediate in facultatively haematophagous mites and greatest in non-haematophagous mites. We also theorized that prevalence of mites from the region with sharp seasonality (Siberia) would be predicted accurately only if host number would be taken into account. We found that the success of a simple epidemiological model to predict prevalence in mites was similar to that reported earlier for other ectoparasitic arthropods. Surprisingly, the model predicted prevalence of obligatory exclusively haematophagous mites less successfully than that of mites with other feeding habits. No difference in the model performance between mites occurring in the 2 geographical regions were found independent of whether the model took the number of hosts into account.

Key words: abundance, epidemiological model, haematophagy, mesostigmate mites, prevalence.

INTRODUCTION

A positive relationship between mean abundance of a parasite and its prevalence is one of the most common patterns in parasite ecology (Shaw and Dobson, 1995; Morand and Guégan, 2000; Krasnov *et al*. 2002; Simkova *et al*. 2002; Matthee and Krasnov, 2009). This pattern is not restricted to parasites but rather represents a manifestation of an even more general pattern, namely a positive relationship between abundance and occupancy which has been reported for various free-living taxa, habitats and biogeographical regions (see Gaston, 2003 for review).

Hypotheses that have been proposed for the explanation of positive abundance-occupancy relationship in free-living taxa (Gaston, 2003) often have involved complicated phenomena such as interspecific differences in niche breadth (Brown, 1984) or position (Hanski *et al*. 1993) or density-dependent habitat selection (O'Connor, 1987). In the pioneering study aimed to test several hypotheses explaining positive abundance-prevalence relationship in parasites, Morand and Guégan (2000) found that in nematodes of mammalian hosts, the relationship appeared to be well explained by demographic and stochastic mechanisms revealed by a simple epidemiological model, so that there was no need to invoke any complicated mechanism. Indeed, prevalence of nematodes was predicted successfully by a model with a minimal number of parameters, namely mean abundance of parasites and its variance. Later, this model was found to predict prevalence in a variety of other parasites such as monogeneans (Simkova *et al*. 2002), fleas (Krasnov *et al*. 2005*a*, *b*; Matthee and Krasnov, 2009), ixodid ticks (Stanko *et al*. 2007; Matthee and Krasnov, 2009), lice (Matthee and Krasnov, 2009) and gamasid mites (Matthee and Krasnov, 2009). Comparison of the results of these studies, however, suggested that the reliability of the

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epidemiological model predicting prevalence of a parasite may differ among parasites due to different tightness of association with their hosts manifested in, for example, different time spent on the host or different necessity of blood feeding (Matthee and Krasnov, 2009).

Earlier studies that aimed to test whether prevalence can be predicted from mean parasite abundance and its variance focused mainly either on permanent parasites (Morand and Guégan, 2000; Simkova *et al*. 2002) or parasites that feed solely on host-produced resources (Krasnov *et al*. 2005*a*, *b*; Stanko *et al*. 2007; Matthee and Krasnov, 2009). It is still unclear whether this model can successfully predict prevalence of facultative parasites, phoretics or commensals. To fill this gap, we tested if prevalence of mesostigmate mites characterized by different feeding modes can be predicted reliably from a model that takes into account the above-mentioned most parsimonious set of parameters. Although this model has been applied to mesostigmates earlier by Matthee and Krasnov (2009), their study involved 2 species only and thus did not provide a clear-cut conclusion regarding the effect of the tightness of parasite-host association (in terms of the necessity of blood feeding) on the performance of an epidemiological model.

Mesostigmate mites represent a convenient taxon for investigating this effect because the interspecific variation in the ecology and feeding mode among mites is large, ranging from predation to endoparasitism (see Radovsky, 1985 for review). We focused on mites collected from host body surfaces. These included both facultative and obligatory haemato- and/or lymphophagous mites as well as predatory, saprophagous and omnivorous species that presumably use a host mainly as a dispersal vehicle rather than a food source. We theorized that the difference between prevalence predicted from the model and observed prevalence would be smallest in obligatory haematophagous mites, intermediate in facultative haematophagous mites and greatest in non-haematophagous mites.

Furthermore, the reliability of the model predicting prevalence of a parasite has been suggested to differ within parasite taxon among geographical regions due to the confounding effect of host environment. Thus some model modification (e.g., including additional information on host number) was required in a region with high environmental fluctuations (Krasnov *et al*. 2005*a* versus Krasnov *et al*. 2005*b*). In particular, this geographical difference was found for fleas, but has never been studied in any other parasite taxon. To investigate further the environmental/geographical dependence of the applicability of the model predicting prevalence from mean abundance and its variance, we analysed data on abundance and distribution of mites from 2 geographical regions, namely Western Siberia and Buenos Aires Province of Argentina. The climate of both regions is temperate, but seasonality in Argentina is less expressed than in Siberia. Consequently, we theorized that the model would predict accurately the prevalence of mites from Siberia only when it takes into account host number, as was reported for ectoparasites from a region with low environmental predictability (Krasnov *et al*. 2005*a*).

MATERIALS AND METHODS

Field data collection

We used data on mites collected from the bodies of small mammalian hosts (rodents and soricomorphs) in West Siberia and Argentina. In Siberia, data were collected in the vicinity of Novosibirsk city from May–June to August–September in 1982–1987. Main habitat types of the study area included cherry and apple orchards, pine forests, and aspen-birch forests alternating with wetlands and grasslands. All mammals (rodents and soricomorphs) were captured using pitfall traps with drift fences arranged in 23 lines, each 50 m in length (with 10 m distance between traps). Pitfall traps were checked daily. Field data were collected by the late A.K. Dobrotvorsky and then transferred for further analyses to the Laboratory of Arthropod-Borne Viral Infections, Omsk Research Institute of Natural Foci Infections under the responsibility of N.P.K.-V. In Argentina, rodents were sampled in 6 localities in the marshlands of Buenos Aires Province in 1990–1991, 1994–1996 and 2000–2001 (2–10 times per locality). The study area was situated in the biogeographic province La Pampa (Morrone, 2001) which constitutes the southern border of the South American subtropical humid forest. Main habitat types included a mixture of graminoid swamps and forested wetlands and xeromorphic and riparian marshlands along river banks. Mammals were captured during 1-day trappings using mesh live-traps (80–180 traps per locality) arranged in 10×10 or 8×10 lines or grids with either 3 or 10 m distance between traps.

Captured mammals were euthanized with sulphur ether, placed in individual pre-marked cloth bags and transferred to a laboratory where each animal was systematically examined under a stereoscopic microscope using forceps to remove ectoparasites. All ectoparasites were counted and identified to species level. Counts of mites included both nymphs and imagoes. Detailed descriptions of the study areas and sampling procedures were reported elsewhere (Dobrotvorsky, 1992; Lareschi, 2000, 2004, 2006; Lareschi *et al*. 2003, 2007).

Data selection, arrangement and calculation of abundance and prevalence

Siberian data were arranged into 23 monthly collections that were considered as trapping sessions.

Table 1. Data on small mammals and mesostigmate mites used in the analyses and host species associated with each mite species used in the analyses

(For each mite species, host species from which at least 30 individual mites were collected (in ascending order). In parentheses at the first mention of each species – feeding mode [for mites; OEH – obligate exclusive haematophage, ONH – obligate non-exclusive haematophage, FH – facultative haematophage, NH – non-haematophage (saprophage, predator or omnivore); see text for explanations)] and number of captured/collected individuals (for mammals and mites). In addition to host species mentioned, mites were collected in (a) Siberia from 39 *Apodemus peninsulae*, 26 *Cricetus cricetus*, 107 *Micromys minutus*, 58 *Mus musculus*, 101 *Myodes glareolus*, 30 *Crocidura leucodon*, 8 *Crocidura sibirica*, 56 *Sorex caecutiens*, and 4 *Sorex roboratus*, and (b) Argentina from 7 *Deltamys kempi* and 10 *Oligoryzomys nigripes*.)

Region	Mite	Main host species
Siberia	*Androlaelaps fahrenholzi* (4058; ONH)	*Microtus gregalis* (873), *Arvicola amphibius* (216), *Microtus oeconomus* (491), *Microtus agrestis* (231), *Microtus arvalis* (196), *Myodes rutilus* (554), *Sorex araneus* (3894), *Apodemus agrarius* (458)
	Eulaelaps stabularis (547; FH)	*S. araneus*, *M. gregalis*, *Sicista betulina* (572), *A. amphibius*, *A. agrarius*, *M. rutilus*
	Haemogamasus ambulans (398; ONH)	*S. araneus*, *M. oeconomus*, *M. rutilus*
	Haemogamasus mandschuricus (367; ONH)	*A. amphibius*, *M. gregalis*
	Haemogamasus nidiformes (70; FH)	*M. gregalis*
	Hirstionyssus eusoricis (2796; OEH)	*S. araneus*, *Neomys fodiens* (249), *Sorex isodon* (274), *M. oeconomus*, *Sorex tundrensis* (148), *S. minutus*, *A. agrarius*
	Hirstionyssus isabellinus (1430; OEH)	*M. gregalis*, *M. rutilus*, *A. amphibius*, *A. agrarius*, *M. arvalis*, *Tamias sibiricus* (39), *M. oeconomus*, *M. agrestis*, *S. araneus*, *Talpa altaica* (39)
	Laelaps clethrionomydis (1918, ONH)	*M. gregalis*, *A. amphibius*, *M. arvalis*, *M. oeconomus*
	Laelaps hilaris (236, ONH)	*M. oeconomus*, *M. arvalis*,
	Laelaps muris (597, ONH)	*A. amphibius*
	Laelaps pavlovskyi (514, ONH)	*A. agrarius*
	Macrocheles glaber (131, NH)	*S. araneus*
	Parasitus consanguineus (711, NH)	*M. gregalis*, *S. araneus*, *A. amphibius*, *A. agrarius*, *M. rutilus*
	Parasitus fimetorum (112, NH)	*A. amphibius*, *M. gregalis*
	Parasitus oudemansi (388, NH)	*S. araneus*, *M. gregalis*, *M. oeconomus*
	Parasitus remberti (149; NH)	*S. araneus*
	Poecilochirus necrophori (2751, NH)	*S. araneus*, *M. rutilus*, *M. oeconomus*, *M. gregalis*, *A. amphibius*, *S. isodon*, *M. gregalis*, *S. betulina*, *M. arvalis*, *Myodes rufocanus* (186), *S. minutus*, *N. fodiens*
	Poecilochirus subterraneus (386, NH)	*S. araneus*, *M. rutilus*, *A. agrarius*, *M. gregalis*
	Proctolaelaps pygmaeus (145; NH)	*S. araneus*
Argentina	*Androlaelaps fahrenholzi* (759; ONH)	*Scapteromys aquaticus* (203), *Oxymycterus rufus* (136), *Akodon azarae* (58), *Oligoryzomys flavescens* (69)
	Androlaelaps rotundus (246; ONH)	*A. azarae*
	Gigantolaelaps wolffsohni (173; ONH)	*O. flavescens*
	Laelaps manguinhosi (4376; ONH)	*S. aquaticus*, *Holochilus brasiliensis* (5), *O. flavescens*
	Laelaps paulistanensis (176; ONH)	*O. flavescens*
	Mysolaelaps microspinosus (205; ONH)	*O. flavescens*
	Ornithonyssus bacoti (978: OEN)	*S. aquaticus*, *O. rufus*

Argentinian data were arranged into 52 one-day trapping sessions. We selected mite species that were recorded in at least 6 trapping sessions in which at least 4 host individuals were captured and at least 2 of them were infested. Most mesostigmate mites are host opportunists (e.g. Radovsky, 1985). Consequently, data on a particular mite species were pooled across all host species in which at least 2 individuals were found to be infested by this mite. Then, we calculated mean abundance, variance of abundance and prevalence of each selected mite species within each trapping session. Parasitological parameters for *Androlaelaps fahrenholzi* that occurred in Siberia and Argentina were calculated separately for each region. In total, we used data on 9208 (24 species) and 488 (7 species) individual mammal hosts from Siberia and Argentina, respectively, from which 17 704 (19 species) and 6913 individual mites (7 species), respectively, were collected. Main mite-host associations are presented in Table 1.

Model

The simple epidemiological model proposed by Anderson and May (1985) predicts that, given a negative binomial distribution of parasites among host individuals, prevalence of infection P is related to the mean number of parasites per individual host M as $P=1-(1+M/k)^{-k}$, where k is the parameter of the negative binomial distribution. Parameter k can be estimated using various methods (see Wilson *et al*.

2001 for review). In particular, it can be calculated from mean abundance and its variance using (a) the Taylor's (1961) power law and (b) the moment estimate of Elliot (1977). The Taylor's power law is a consistent and universal empirical observation that variance in abundance of a species V increases with its mean abundance M following a simple power law as $V = aM^b$ (Taylor, 1961). Parameter of k can be calculated using the Taylor's relationship between mean abundance and its variance as $k = 1/(aM^{b-2} - 1/M)$, where a and b are taken from the above equation (Perry and Taylor, 1986). The moment estimate of k of Elliot (1977) is $k = M^2/(V - M)$. However, this estimate is approximate and may be unreliable if M is large, k is small and sample size is low (Wilson *et al*. 2001). To overcome the latter, Elliot (1977) proposed an estimate that partially corrects for sample size (n), namely $k = [M^2 - (V/N)]/(V - M)$. This corrected moment estimate of k has proven to be the least variable with mean parasite abundance and sample size when compared to other indices of aggregation (Gregory and Woolhouse, 1993).

Data analysis

We calculated k using both of the above methods, namely (a) using parameters a and b of the Taylor's power law and (b) the moment estimate corrected for sample size. Parameters a and b of the Taylor's power law were calculated by regressing log-transformed variance of mite abundance against log-transformed mean mite abundance (both calculated within a trapping session; see above) for each mite species across the entire host spectrum (see above). Then, we calculated predicted prevalence for each mite in each trapping session based on the two estimates of k (PP_1 and PP_2, respectively), and compared predicted prevalence with observed prevalence for each mite species across trapping sessions using linear regressions separately for models with different calculations of k. We used t-tests to test whether the intercepts and slopes of the resulted regressions differed significantly from 1.

To select between the two methods of estimation of k, we applied meta-analyses across mite species using 2 measures of the effect size. Firstly, the measures of the effect size were Pearson's rank correlation coefficients between predicted (from each model) and observed prevalence after Fisher's z-transformations (untransformed values of correlation coefficients are presented in figures for clarity). We used the number of trapping sessions in which a mite was recorded as sample size for each observation. Secondly, the measures of the effect size were slopes of the regressions of predicted on observed prevalence and the respective standard errors. The better model is the one in which (a) the coefficient of correlation between predicted and observed prevalence is higher and (b) the slope of the regression of predicted on observed prevalence is closer to 1. We compared the combined effect sizes yielded by these meta-analyses between the two models using t-tests.

After the better of the two models was selected (see Results section), we asked whether the success of this model in prediction of prevalence from mean abundance and its variance differed between mites (a) from the 2 geographical regions and (b) with different feeding modes. To answer the latter question, we classified mites into 4 categories (a) obligatory exclusively haematophagous species (feed solely on host's blood and other body fluids); (b) obligatory non-exclusively haematophagous species (feed on both host's blood/body fluids and small arthropods); (c) facultatively haematophagous species; and (d) non-haematophaguous (including predatory, omnivorous and saprophagous) species. Information on feeding modes of different mite species was taken from Zemskaya (1973), Krantz (1978), Balashov (1982, 1999, 2000), Radovsky (1985), Tagiltsev *et al*. (1990) and unpublished data of M. L. We carried out meta-analyses of the slopes of the regressions between predicted and observed prevalences across mite species separately for a subset of mites within either each geographical region or each feeding mode category. We assessed the impact of the factor of either geographical region or feeding mode on the slope of the regression between predicted and observed prevalences using meta-analytic analogues of ANOVA.

In each run of meta-analyses, a combined estimate of the effect size was calculated using both fixed effects and random effects algorithms, which produced similar results. To assess heterogeneity among mite species we calculated the inconsistency index I^2 (Higgins and Thompson, 2002; Higgins *et al*. 2003) as $I^2 = [(Q - \mathrm{df})/Q] * 100\%$, where Q is the chi-squared statistic and df is its degrees of freedom. Because substantial heterogeneity among mite species was revealed for either model ($I^2 = 75{\cdot}4$–$92{\cdot}1\%$), we present the results using the random effects algorithm only. Meta-analysis was carried out using the software package Comprehensive Meta-Analysis version 2 (Biostat Inc., Englewood, NJ, USA).

RESULTS

Summary of the regressions of mite prevalences predicted from mean abundances and their variances against observed prevalences using the 2 models is presented in Table 2. The model with parameter k estimated via the Taylor's power relationship successfully predicted prevalence in 13 mite species, whereas it consistently underestimated prevalence in the remaining 16 species (see illustrative examples with *Eulaelaps stabularis* and *Hirstionyssus isabellinus* in Fig. 1A). The model with parameter k estimated

Table 2. Summary of regressions of predicted (PP_1 and PP_2) from the epidemiological model against observed prevalences of mites infesting small mammals in Siberia and Argentina (all are significant, $P<0{\cdot}05$)

(k values for PP_1 and PP_2 were calculated using either Taylor's power law or moment estimate corrected for sample size, respectively. * – slope does not differ significantly from 1 (t-tests, $P>0{\cdot}05$), ** – intercept does not differ significantly from zero (t-tests, $P>0{\cdot}05$). S and A for *A. fahrenholzi* denote the data on this species from Siberia and Argentina, respectively.)

Mite	Intercept $PP_1 \pm$ S.E.	Slope $PP_1 \pm$ S.E.	r^2	Intercept $PP_2 \pm$ S.E.	Slope $PP_2 \pm$ S.E.	r^2
A. fahrenholzi (*S*)	0·009 ± 0·006**	0·73 ± 0·03	0·97	−0·004 ± 0·010**	0·82 ± 0·06	0·90
E. stabularis	0·001 ± 0·003**	0·97 ± 0·05*	0·95	−0·004 ± 0·003**	1·04 ± 0·04*	0·98
H. ambulans	0·005 ± 0·006**	0·91 ± 0·07*	0·90	0·001 ± 0·001**	0·97 ± 0·01*	0·99
H. mandschuricus	0·003 ± 0·004**	0·82 ± 0·05	0·94	0·001 ± 0·001**	0·93 ± 0·06*	0·98
H. nidiformes	0·001 ± 0·005**	0·98 ± 0·07*	0·96	−0·002 ± 0·002**	1·02 ± 0·03*	0·99
H. eusoricis	0·030 ± 0·004	0·35 ± 0·04	0·81	0·020 ± 0·010**	0·54 ± 0·10	0·59
H. isabellinus	0·010 ± 0·006	0·49 ± 0·06	0·79	0·001 ± 0·001**	0·71 ± 0·05	0·91
L. clethrionomydis	−0·003 ± 0·006**	0·99 ± 0·04*	0·98	0·002 ± 0·007**	0·83 ± 0·04	0·99
L. hilaris	0·002 ± 0·009**	1·07 ± 0·28*	0·56	−0·002 ± 0·006**	1·11 ± 0·17*	0·78
L. muris	0·003 ± 0·010**	1·13 ± 0·36*	0·47	0·007 ± 0·005**	0·53 ± 0·12	0·64
L. pavlovskyi	0·003 ± 0·005**	1·14 ± 0·16*	0·80	0·020 ± 0·003**	0·98 ± 0·09*	0·91
M. glaber	0·003 ± 0·055**	0·90 ± 0·17*	0·79	−0·002 ± 0·001**	1·08 ± 0·05*	0·99
P. consanguineus	−0·002 ± 0·006**	1·07 ± 0·09*	0·90	−0·009 ± 0·004	1·17 ± 0·05	0·97
P. fimetorum	−0·002 ± 0·006**	1·29 ± 0·15*	0·90	0·010 ± 0·005**	0·46 ± 0·11	0·67
P. oudemansi	0·007 ± 0·003	0·78 ± 0·07	0·89	0·002 ± 0·003**	0·87 ± 0·07*	0·90
P. remberti	0·008 ± 0·002	0·45 ± 0·09	0·67	−0·001 ± 0·002**	0·94 ± 0·07*	0·94
P. necrophori	0·040 ± 0·004	0·33 ± 0·05	0·68	0·020 ± 0·010**	0·60 ± 0·13	0·51
P. subterraneus	0·010 ± 0·002	0·51 ± 0·09	0·67	0·001 ± 0·002**	0·88 ± 0·05	0·94
P. pygmaeus	0·001 ± 0·003**	0·95 ± 0·13*	0·84	0·003 ± 0·002**	0·72 ± 0·09	0·87
A. fahrenholzi (A)	0·210 ± 0·061	0·66 ± 0·10	0·55	−0·040 ± 0·050**	0·98 ± 0·08*	0·81
A. rotundus	0·230 ± 0·060	0·55 ± 0·16	0·62	−0·500 ± 0·100**	1·06 ± 0·24*	0·72
G. wolffsohni	0·240 ± 0·092	0·55 ± 0·18	0·44	−0·040 ± 0·050**	1·04 ± 0·10*	0·89
L. manguinhosi	0·490 ± 0·060	0·33 ± 0·10	0·24	0·050 ± 0·080**	0·89 ± 0·13*	0·59
L. paulistanensis	0·070 ± 0·170**	1·05 ± 0·46*	0·56	−0·090 ± 0·130	1·43 ± 0·37*	0·79
M. microspinosus	0·260 ± 0·120**	0·71 ± 0·15*	0·72	0·100 ± 0·050**	0·85 ± 0·06	0·96
O. bacoti	0·430 ± 0·060	0·60 ± 0·11	0·57	0·080 ± 0·070**	0·79 ± 0·12*	0·65

via the moment estimate of Elliot (1977), corrected for sample size, successfully predicted prevalence in 15 mite species, underestimated prevalence in 10 species and overestimated prevalence in 1 species (see illustrative examples with *Laelaps pavlovskyi*, *Laelaps muris* and *Parasitus consanguineus* in Fig. 1B). In 21 of 26 mite species, either both (in 7 species) or 1 of the 2 versions of the model (in 14 species) accurately predicted prevalence from mean abundance and its variance.

From first glance, the success in prediction of prevalence from mean abundance and its variance did not substantially differ between the two models. However, results of the meta-analyses demonstrated that the model that used the moment estimate of k predicted mite prevalence better than the model that used Taylor's power relationship. Indeed, meta-analyses of the Fisher's z-transformed Pearson's correlation coefficients yielded the combined effect sizes of 1·81 ± 0·12 (95% confidence interval for the point estimate ranged from 1·58 to 2·05) and 1·42 ± 0·11 (95% confidence interval for the point estimate ranged from 1·21 to 1·64) for the former and the latter model, respectively ($t=2{\cdot}39$, $P<0{\cdot}05$) (Fig. 2). Meta-analyses of the slopes of the regressions demonstrated that the respective combined effect sizes were 0·90 ± 0·03 (95% confidence interval from 0·84 to 0·94) and 0·74 ± 0·06 (95% confidence interval from 0·63 to 0·85) ($t=2{\cdot}38$, $P<0{\cdot}05$) (Fig. 3).

Meta-analyses of the slopes of the regressions of predicted on observed prevalence carried out separately for Siberian and Argentinian mites demonstrated no effect of the geographical region on the success of predicting prevalence of a mite from mean abundance and its variance (Table 3; Q-value = 0·66, D.F. = 1, $P=0{\cdot}42$). In contrast, this success was significantly affected by feeding mode of a mite (Table 3; Q-value = 10·74, D.F. = 3, $P=0{\cdot}01$). Surprisingly, prediction of prevalence from mite's mean abundance and its variance was the least successful for obligate exclusive haematophages, whereas the model predicted prevalence of mites belonging to 3 remaining feeding modes (obligate non-exclusive haematophages, facultative haematophages and non-haematophages) equally well (Table 3). Indeed, when mites characterized by obligate exclusive haematophagy were excluded from the analysis, the effect of feeding mode on the slope of the regression of predicted on observed prevalence became non-significant (Q-value = 2·57, D.F. = 2, $P=0{\cdot}3$).

DISCUSSION

Results of this study demonstrated that (a) the success of a simple epidemiological model to predict

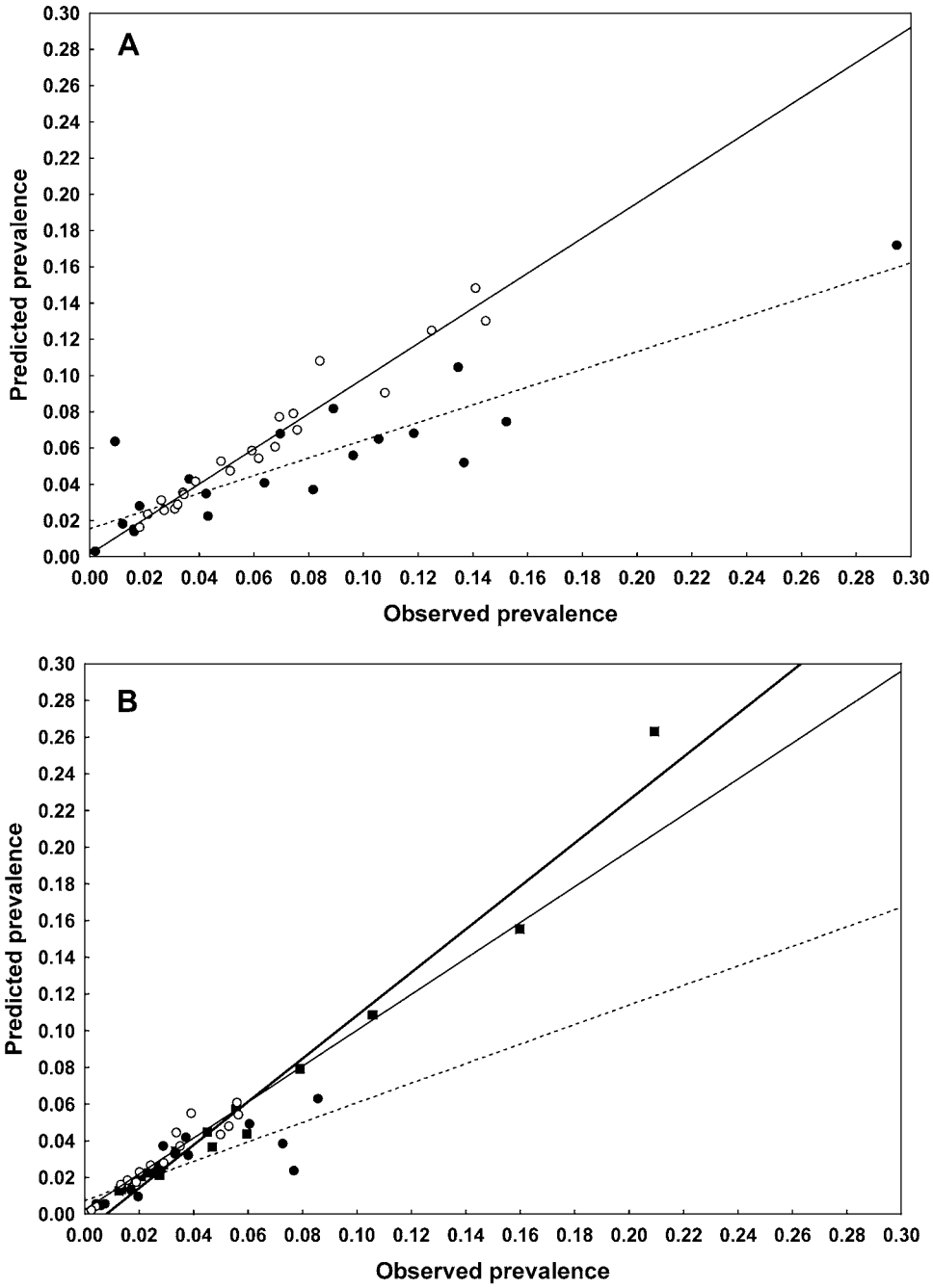

Fig. 1. Relationship between observed and predicted prevalences of mesostigmate mites. (A) Prevalence predicted from the model with parameter k estimated via Taylor's power law; *Eulaelaps stabularis* – open circles, solid line; *Hirstionyssus isabellinus* – closed circles, dashed line. (B) Prevalence predicted from the model with parameter k estimated via moment estimate of Elliot (1977) corrected for sample size; *Laelaps pavlovskyi* – open circles, solid line; *Laelaps muris* – closed circles, dashed line; *Parasitus consanguineus* – squares, bold solid line.

observed prevalence in mites appeared to be similar to that reported for ectoparasitic arthropods that feed solely on host's blood (Krasnov *et al.* 2005*a*, *b*; Stanko *et al.* 2007; Matthee and Krasnov, 2009); (b) surprisingly, the model predicted prevalence of obligatory non-exclusive haematophagous, facultative haematophagous and non-haematophagous mites better than that of obligatory exclusively haematophagous mites; (c) the model successfully predicted observed prevalence of a mite mainly when sample size was taken into account; and (d) in contrast to what was reported for fleas (Krasnov *et al.* 2005*a*, *b*), no difference in the model performance between mites occurring in the two geographical regions were found. Below, we will discuss these results separately.

Performance of epidemiological model among parasite taxa

Our results, together with results of earlier studies, demonstrated that a simple model can successfully

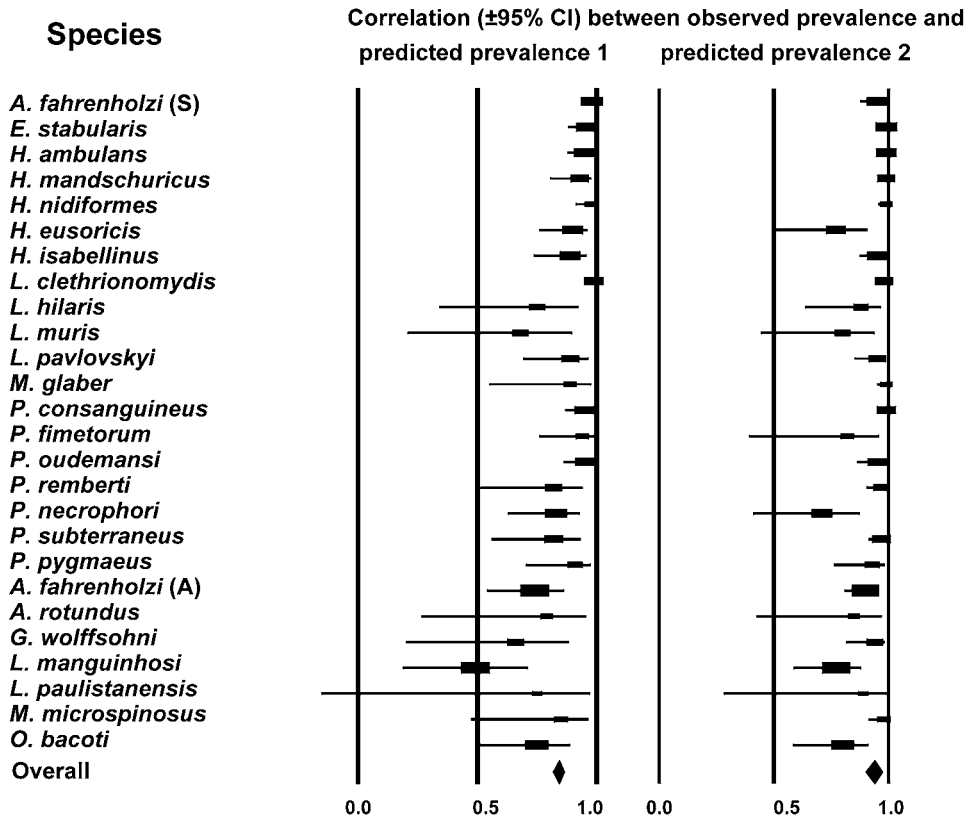

Fig. 2. Forrest plots for the meta-analyses of correlation between prevalence of a mite predicted from the mean abundance and its variance and observed prevalence of this mite across 26 mite species. Predicted prevalence 1 was estimated using calculation of the parameter k of negative binomial via Taylor's power law, whereas predicted prevalence 2 was estimated using moment estimate of k corrected for sample size (see text for explanations). Each square represents the untransformed correlation coefficient and the line indicates the 95% confidence intervals, for each species separately; the size of the square is proportional to the number of trapping sessions in which the mite species was recorded. Diamonds represent the combined effect size. S and A for *Androlaelaps fahrenholzi* denote the data on this species from Siberia and Argentina, respectively.

predict prevalence in a wide range of parasites (including phoretics) that vary greatly with respect to their taxonomic affinity, origin, life-history strategies, geographical distribution and tightness of their association with hosts. Reliability of the model appears to be scale-invariant, so that the model predicted prevalence of parasites equally well whether it was applied within or across host species (Matthee and Krasnov, 2009 versus this study) or within or across parasite species (this study versus Morand and Guégan, 2000).

Performance of epidemiological model within a parasite taxon

In general, either both or one of the two versions of the model accurately predicted prevalence from mean abundance and its variance in 80% of studied mite species. Whenever a model failed to predict prevalence of a mite accurately, prevalence was underestimated, except for a single case when it was overestimated (*Parasitus consanguineus*). In other words, the common situation was that there were more host individuals infested with mites than was predicted from the model. One of the reasons for the observed prevalence being higher than the expected prevalence may be the relatively low level of heterogeneity of host individuals in the face of mite exploitation (be this exploitation parasitism, phoresy or commensalism). Given that many mites are nest-dwellers, the difference among individual hosts in their chances to be exposed to mites may not always be great. However, differences among individuals in their ability to cope with mite exploitation and/or be affected by mite parasitism may be substantial (Møller, 1990*a*, *b*).

Earlier, we used this model to predict prevalences of several parasites exploiting the same host species and found between-species within-higher taxon differences in the model performance (Matthee and Krasnov, 2009). For example, the model accurately predicted observed prevalence in a two-host ixodid, *Hyalomma truncatum*, but underestimated prevalence in a three-host ixodid, *Haemophysalis elliptica*. This suggested that some features of the life history of a species, such as tightness of its associations with the host, might affect the applicability of the model.

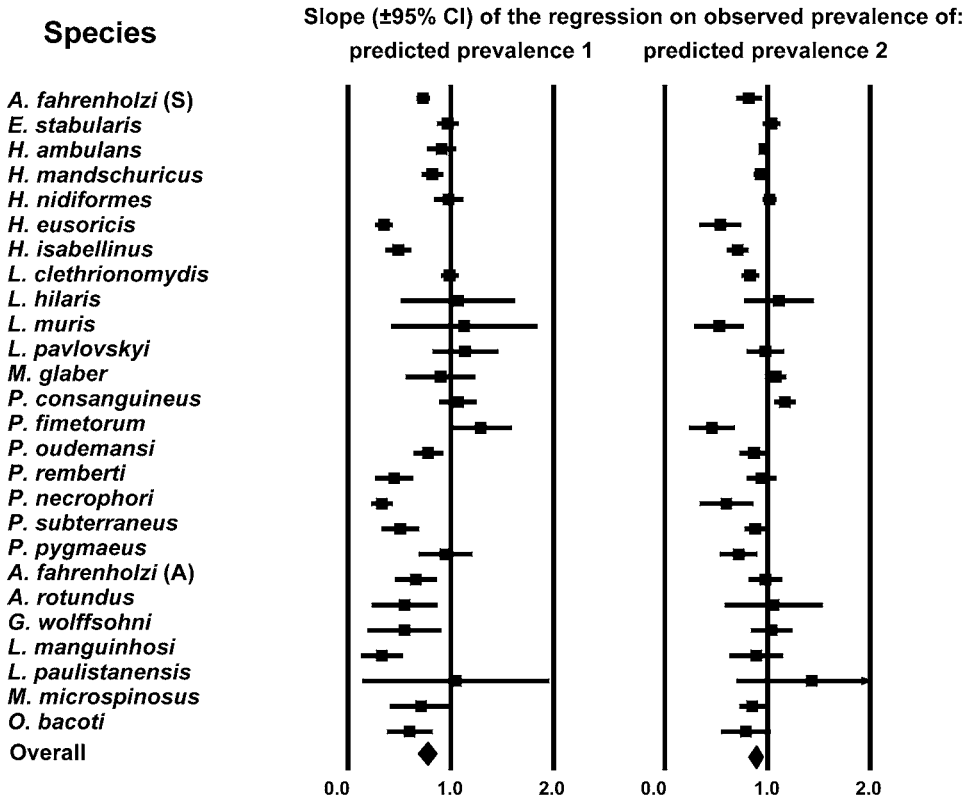

Fig. 3. Forrest plots for the meta-analyses of the slope of the regression of prevalence of a mite predicted from the mean abundance and its variance against observed prevalence of this mite across 26 mite species. See Fig. 2 for explanations of predicted prevalences 1 and 2. Each point represents the slope of the regression of predicted on observed prevalence and the line indicates the 95% confidence intervals, for each species separately; the size of the point is proportional to the number of trapping sessions in which the mite species was recorded. Diamonds represent the combined effect size. S and A for *Androlaelaps fahrenholzi* denote the data on this species from Siberia and Argentina, respectively.

We predicted that the necessity of blood feeding may be an indicator of the tightness of mite-host association and, thus, applicability of the model. Results of this study did not support this idea. For example, blood or lymph feeding is obviously more crucial for obligatory and exclusively haematophagous mites than for mites that only facultatively feed on blood. However, prevalence of the former was the least accurately predicted by the model. It seems that some other features of mite biology are associated with the applicability of the model. For example, all 3 obligatory and exclusively haematophagous species are nidicolous, i.e. they mainly occur in the nest of their hosts rather than on the body (see Krantz, 1978 for *O. bacoti* and Tagiltsev *et al.* 1990 and Korallo, 2009 for *H. eusoricis* and *H. isabellinus*), whereas some facultatively haematophagous or obligatory not-exclusively haematophagous mites spend much more of their life cycle on the body of their hosts (e.g., *L. muris*; Zemskaya, 1969). However, many other facultatively haematophagous, obligatory non-exclusive haematophagous and non-haematophagous mites are also nidicolous (Radovsky, 1985), so that the proportion of life cycle spent on the host body does not appear to be a good indicator of the applicability of the model as well.

Furthermore, necessity of blood feeding in mesostigmate mites appears not to be always associated with direct host exploitation. Some mites that require blood of a vertebrate animal for successful reproduction may obtain blood of a host via predation on other blood-feeding organisms rather than via direct blood sucking. For example, *A. fahrenholzi* and *E. stabularis* have been observed to feed on engorged larvae of ixodid ticks (Tagiltsev, 1957). Moreover, Tagiltsev (1957) argued that the mouth apparatus of *E. stabularis* did not allow it to pierce skin of a rodent host, whereas the thin cuticle of an ixodid larva was easier to penetrate, thus making host's blood consumed by a tick to be available for a mite. Similarly, Tagiltsev (1967) reported that mites *Androlaelaps casalis* in the nests of dormice often attack and devour engorged mites belonging to the genus *Ornithonyssus*. It is unknown, however, whether obligate exclusive haematophages such as *Hirstionyssus* species may obtain blood of a vertebrate via predation on other blood-feeding arthropods. Nevertheless, haematophagy via predation on other haematophages complicates the relationship between

Table 3. Combined effect sizes for meta-analyses of the slope of the regression of prevalence predicted from mean abundance and its variance of a mite on observed prevalence of this mite across mite species

(Meta-analyses were carried out either separately for mites from Siberia and Argentina or separately for mites with different feeding modes. See Table 1 for the abbreviation of feeding modes.)

Mite group	Number of species	Point estimate of slope ± S.E.	Variance	Lower limit	Upper limit
Siberia	19	0·88 ± 0·03	0·001	0·82	0·94
Argentina	7	0·93 ± 0·06	0·004	0·81	1·06
OEH	3	0·68 ± 0·08	0·006	0·52	0·84
ONH	13	0·91 ± 0·04	0·001	0·83	0·98
FH	2	1·03 ± 0·08	0·006	0·88	1·18
NH	8	0·88 ± 0·05	0·002	0·79	0·99

a mite and a host which may negatively affect the applicability of simple models.

The abundance and prevalence of parasites are the net results of the acquisition and loss of parasites by individual hosts. The rates of these processes depend on both hosts and parasites. In particular, they may depend not only on the proportion of a life cycle that a parasite spends on a host, but also on the type of host exploitation by a parasite, i.e. whether a parasite uses its host as either a food source or a dispersal tool or both. It is thus possible that the dynamics of parasite distribution among host individuals and, thus, applicability of any epidemiological model is determined by interplay between these factors. This, undoubtedly, requires further investigation.

Epidemiological model and correction for host number

The model we used involved 2 main factors, namely mean abundance and its variance. Moreover, according to the Taylor' power relationship, mean abundance and its variance are tightly linked (Taylor, 1961; see Shaw and Dobson, 1995 and Morand and Krasnov, 2008 and references therein for parasites). For example, mean abundance explained 96% of the variance in abundance in fleas (Krasnov *et al*. 2005*b*) and 99% in ixodid ticks (Stanko *et al*. 2007). However, this proportion appeared to be lower in mesostigmate mites. Among mite species, coefficients of determination in log-log regressions of variance in abundance against mean abundance ranged from 0·62 to 0·97. When we meta-analysed these coefficients of determination, we found that, in general, mean abundance explained only about 90% of variance in abundance. On the one hand, this suggests that mites are less constrained in the degree of variation observed for any given mean abundance compared with fleas or ticks. On the other hand, this may be the reason behind the necessity to use the version of the model that takes into account the number of host individuals. It is known that host abundance may substantially affect parasite abundance and distribution (e.g., Krasnov *et al*. 2002, for fleas), although the investigations of the effect of the population size or density of hosts and abundance and distribution of parasitic or phoretic mites provided contradictory results (Sorci *et al*. 1997; Lopez, 2005).

Epidemiological model and environmental effect

Ectoparasites in general and mites in particular are affected strongly by the off-host environment (e.g., Maurer and Baumgärtner, 1992). Consequently, environmental factors may affect their abundance and distribution (Zemskaya, 1973). As a result, an epidemiological model that relates abundance and prevalence of a parasite may be expected to behave differently in different environments. For example, Krasnov *et al*. (2005*a*, *b*) found that the applicability of the model differs between fleas inhabiting temperate and arid regions and explained this by differences in the environmental predictability. Later, it was found that applicability of the model may differ also between closely-related parasites inhabiting the same geographical region, suggesting that life-history differences may be more important than geographical differences (Stanko *et al*. 2007; Matthee and Krasnov, 2009). Results of this study did not provide a clear-cut answer about importance of the environment on the reliability of the model. On the one hand, we did not find any difference in efficiency of the model to predict prevalence from mean abundance between Siberian and Argentinian mites. On the other hand, the effect of the environment on the behaviour of the model could be envisaged from comparison of the results of the model application between 2 populations of *A. fahrenholzi*, a cosmopolitan mite species that occurred in both regions. The model accurately predicted the prevalence of *A. fahrenholzi* in a weakly seasonal environment, but underestimated its prevalence in a highly seasonal environment (slope 0·98 ± 0·08 versus slope 0·82 ± 0·06, respectively). Interestingly, an earlier

application of this model using data on a South African population of *A. fahrenholzi* resulted in approximately the same slope of the regression of predicted on observed prevalence as was the case for Argentinian populations ($0{\cdot}81 \pm 0{\cdot}09$; Matthee and Krasnov, 2009).

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