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Ectoparasite infestation patterns of domestic dogs in suburban and rural areas in Borneo

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Abstract Domestic dogs, *Canis lupus*, have been one of the longest companions of humans and have introduced their own menagerie of parasites and pathogens into this relationship. Here, we investigate the parasitic load of 212 domestic dogs with fleas (Siphonaptera) chewing lice (Phthiraptera), and ticks (Acarina) along a gradient from rural areas with near-natural forest cover to suburban areas in Northern

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Borneo (Sabah, Malaysia). We used a spatially-explicit hierarchical Bayesian model that allowed us to impute missing data and to consider spatial structure in modelling dog infestation probability and parasite density. We collected a total of 1,968 fleas of two species, *Ctenocephalides orientis* and *Ctenocephalides felis felis*, from 195 dogs (prevalence, 92 %). Flea density was higher on dogs residing in houses made of bamboo or corrugated metal (increase of 40 % from the average) compared to timber or stone/compound houses. Host-dependent and landscape-level environmental variables and spatial structure only had a weak explanatory power. We found adults of the invasive chewing louse *Heterodoxus spiniger* on 42 dogs (20 %). The effect of housing conditions was opposite to those for fleas; lice were only found on dogs residing in stone or timber houses. We found ticks of the species *Rhipicephalus sanguineus* as well as *Haemaphysalis bispinosa* sp., *Haemaphysalis cornigera*, *Haemaphysalis koenigsbergi*, and *Haemaphysalis semermis* on 36 dogs (17 %). The most common tick species was *R. sanguineus*, recorded from 23 dogs. Tick infestations were highest on dogs using both plantation and forest areas (282 % increase in overall tick density of dogs using all habitat types). The infestation probability of dogs with lice and ticks decreased with elevation, most infestations occurred below 800 m above sea level. However, the density of lice and ticks revealed no spatial structure; infestation probability of dogs with these two groups revealed considerable autocorrelation. Our study shows that environmental conditions on the house level appeared to be more influential on flea and lice density whereas tick density was also influenced by habitat use. Infestation of dogs with *Haemaphysalis* ticks identified an important link between dogs and forest wildlife for potential pathogen transmission.

Introduction

The relationship between mankind and domestic dogs, *Canis lupus*, is unique in that dogs are true companions that share much of the owners' life, be it during resting and at home or during travelling and hunting. This close relationship and intense contact, however, comes at a cost: dogs are widely recognised as playing a role in the transmission of zoonotic parasites and pathogens. In urban areas, dogs may reach high densities and frequent contacts of potentially disease-spreading dogs with others and with omnipresent dog faeces can be of serious health concern (Barutzki and Schaper 2003; Macpherson et al. 2000; Traub et al. 2005; Wang et al. 2006). Dog densities in more rural areas are usually lower and individuals are perhaps less likely to frequently encounter parasites from conspecifics. However, in rural areas, dogs may be more likely to come into contact with wildlife, which may foster the exchange of zoonotic parasites between wildlife, livestock, and humans (Alexander and McNutt 2010; Salb et al. 2008). On a global scale, dogs face as many differences in their environment and socio-economical conditions as human populations, with all the consequences that we experience in geographical differences in disease occurrence and prevalence.

Generally, environment changes are known to intricately alter vertebrate–parasite relationships in many ecosystems and species associations (McCallum and Dobson 2002; Morgan et al. 2004). In Southeast Asia, environmental and socio-economic conditions are changing rapidly with yet unforeseen consequences for environmental resilience and human health (Miettinen et al. 2011; Sodhi et al. 2010). In rural areas, this may for example, include the establishment of new roads that facilitate the fast exchange of people and products, forest and landscape conversions, changes in the time people spend for cultivation and gathering of forest products (traditionally accompanied by dogs), and changes in housing conditions. The effects of environmental conditions of ectoparasites of dogs have been mainly studied in temperate ecosystems (Gracia et al. 2008; Rinaldi et al. 2007; Salb et al. 2008), but considerably less information is available about the diversity of species and epidemiology of ectoparasites in SE Asia and other tropical areas (Irwin and Jefferies 2004; Klimpel et al. 2010). For many areas in the tropics, the challenge for understanding infestation patterns of dogs and other domestic animals with parasites is therefore twofold: basic inventories of which species of ectoparasites infest dogs, and how ectoparasite diversity may differ across (biogeographical) regions, still need to be completed and, further, predicting possible gradients in parasites and disease risk under changing environmental conditions needs fundamental quantitative work.

In this study, we examined the ectoparasite fauna of dogs in Borneo. Because little work on ectoparasites on domestic

animals has been conducted in Borneo to date, we firstly surveyed ectoparasite species diversity. We were further interested in how environmental conditions from the house to landscape scale may impact ectoparasite occurrence and abundance. As Borneo is facing considerable environmental changes due to fast ongoing landscape conversion and socioeconomic development, we expected such changes to impact dog infestation with ectoparasites along our sampled gradient from suburban areas to remote areas adjacent to near-natural forested national parks.

Materials and methods

Study sites and sampling

Our study was conducted in northwestern parts of Borneo in the state of Sabah, Malaysia. We collected samples near the capital town of Kota Kinabalu (latitude, 6.0°; longitude, 116.1°) and in the nearby districts of Keningau, Penampang, Tambunan, Tamparuli, Tuaran, and Ranau (latitude, 4.9–6.1°; longitude, 115.8–116.6°); all sampling locations were near to Crocker Range National Park and Kinabalu National Park. We particularly focused on these areas as this study was part of our initial efforts to investigate possible interactions between wildlife and domestic animals near protected forests. The maximum distance between sampling points was 128 km, elevations ranged from 9 to 1,330 m above sea level (asl).

People encountered in their homes while travelling through the study area were asked for access to their dogs. We sampled one dog per household from those owners who consented; the sampled dog was usually chosen by the house owner based on availability and tameness. All dogs sampled in this study were domiciled dogs, while we did not sample stray dogs or semidomestic dogs typically roaming free but being fed by some individuals or families.

We brushed the dorsal hair coat of dogs from the neck to the tail for 10 min with a flea comb (Trixie, Tarp, Germany, art. no. 23762). All ectoparasites (i.e., fleas, lice, and ticks) were transferred with forceps to a tube containing 99 % ethanol for later counting and identification. Although this sampling was incomplete, we assumed that strict application of the same sampling procedure to all dogs by the same person (KW), gave us a measure of relative ectoparasite densities suitable for quantitative analysis. After brushing, we checked the ears and feet of each dog for the presence of ticks, which were also collected. We measured the length from shoulder to tail as an estimate of body size. We classified age into three categories: 6, 7–12, and >12 months, and noted the gender of each dog. We estimated the local dog density by asking the dog owner about the number of dogs present in his household. We further classified dog habitat use into either house area only, plantation, or plantation and forest. We also noted whether dogs were

involved in hunting or not. Further, we asked house owners if any kind of treatment against parasites was applied to their dog and classified treatments into bathing, bathing with soap, bathing with “dog shampoo” sold for pets, repellent spray, injection of antiparasitics, or none. We considered these treatment categories to provide a coarse measure of increasing care by dog owner; as villagers apply a large variety of products from unknown manufacturers for parasite treatments and we were not able to reproduce product specifications such as the content of acaricide in “dog shampoo”, we are aware that this measure provide only preliminary insights for estimating treatment effect on ectoparasites.

We further classified the type of house into bamboo, timber, stone/compound, and corrugated metal. We classified the ground construction of the house where dogs were assumed to rest into soil and compound. Geographical coordinates and elevation of sampling locations were taken with a handheld GSP device (Garmin GPSmap 62st, Olathe, USA).

Most dog owners were of the local Kadazan–Dusun tribe, but questioning was conducted in the national language, Malay, which is spoken by all local ethnic groups. We further estimated the proportion of forest cover in radii of 2,000 m centred around sampling locations from global land cover data produced by the European Space Agency at a resolution of 300 m (GlobCover 2009, see <http://ionia1.esrin.esa.int/>). We estimated human population density around sampling locations using the LandScan 2007 human population density estimate (UT-Batelle, USA), which estimates population density at ca. 1 km² resolution (Bhaduri et al. 2007). For this dataset, we averaged human population density estimates for all cells covered by the area of 2,000 m

radii centred around sampling locations. Ectoparasites were identified in laboratories where relevant comparative material and expertise was available (fleas, JCB; lice, LD; ticks, TP). Not all fleas were identified to species level, so their abundances were pooled for analysis. For lice, we considered only adults for which the number strongly correlated with the pooled number of all life stages.

Data analysis

Epidemiological studies typically have to deal with spatial data in which nearby individuals are likely to be exposed to similar conditions and parasites. Moreover, the attributes which characterise the sampled units may have complex dependence structures and almost always have missing data. While excluding missing values might lead to considerable loss of information, Bayesian methods may substantially help in solving such problems by allowing all entities to be viewed as random variables, which can be modelled in multilevel structures. Missing outcomes, for example, can be conveniently modelled by randomly imputing missing values while sampling through Markov chain Monte Carlo (MCMC). The possibility to repeatedly impute missing values with combinations of different values derived from the underlying distributions may well reflect our uncertainty about our variables and finally the resulting uncertainty in model coefficient estimates (Gelman et al. 2005).

We assumed a generalized linear regression model for investigating the link between the variability in flea, lice and tick density and the environmental covariates. The model for the number of any of these groups of ectoparasite on different dogs can be described as (see O’Hara 2009):

Number of ectoparasites \sim body size + age + sex + dog density + house type
 + hunting behaviour + treatment + house type + ground + habitat use +
 forest cover + elevation + human density + random noise

with random noise being modelled from a normal distribution. We linked this model to data on a log-linear scale and assumed a Poisson distribution as an observational model (note the combination of assumed Poisson and Gaussian distribution allows the handling of overdispersed data). All environmental variables were scaled for model fitting (dividing centred values by SD).

We used a point-level spatial model to account for spatial effects. Spatial random effects are conceptually similar to other random effects for which variance components are customarily introduced in regression models. The spatial covariance between pairs of points can be estimated through a multivariate normal distribution with a covariance matrix that depends on distance to account for the fact that nearby

points might have similar values due to spatial proximity (Banerjee et al. 2004). The vector of zero-centred spatial random effects *spatial.MVN* is then given as:

$$\text{spatial.MVN} \sim N(0, \sigma^2, H(\Phi))$$

with σ^2 comprising a variance term and $H(\Phi)$ a spatial correlation matrix. The correlation matrix can be derived from an isotropic function of Euclidean distances d_{ij} between points and the scalar parameter Φ . We used the commonly applied exponential function $f(d_{ij}, \Phi) = e^{-\Phi d_{ij}}$. With this background, we partition the “random noise” from the basic model equation in a spatial term and a nonspatial term (referred to as nugget effect in geostatistical models).

From this model, the variance (termed hereafter “var()”) allocated during MCMC updates to each of the different components of the model can be calculated as the squared coefficient estimate multiplied by the variance in the covariate for continuous variables such as body size: $\text{var}(\beta_{\text{bodysize}}) = \beta_{\text{bodysize}}^2 \times \text{var}(\text{bodysize})$; note: as variables are z -transformed, $\text{var}(\text{bodysize})=1$. For categorical variables such as age, we calculate the finite sample variance $\text{var}(\beta_{\text{Age}}^*)$ across all levels, with $\beta_{\text{Age}}^*(i) = \beta_{\text{Age}}(i) - \text{mean}(\sum_i^n \beta_{\text{Age}}(i))$.

Assuming that specific parameters are realisations from common normal distributions (note that the data are modelled on the log scale), we used the following priors: for all missing data i in covariates, we used $\mu(i) \sim N(0,1)$; all variance terms σ^2 for normally distributed coefficient estimates were drawn from uniform distributions with $\sigma^2 \sim \text{Unif}(0,100)$; for the scaling parameter Φ and error terms σ^2 , we used gamma distributions with $\Phi, \sigma^2 \sim \text{Gamma}(1,0.1)$. We applied this model separately to the number of fleas, lice, and ticks found on a subset of 194 out of the 212 sampled dogs, as spatial coordinates were not available for all samples. We tested the possible impact of covariates on infestation probabilities of dogs with these parasites by repeating this model framework as a logistic regression of presence/absence of lice or ticks on any particular dog; results on infestation probabilities are only recorded if there were any differences compared to model output from modelling their density (i.e., spatial effects).

We used the software OpenBUGS 3.1.1 (Lunn et al. 2009) to fit the model separately for fleas and lice. Posteriors were obtained by running 10,000 iterations after discarding 50,000 iterations as a burn-in. Convergence and mixing was checked visually by running two parallel chains. Results are given as the posterior mode and 95 % highest posterior densities as credible intervals (CI). We presented posterior model values for easy reading and estimation of the possible magnitude of effects, while we emphasise that considering uncertainty/CI is as important for inference.

The model code is given in Appendix A1. Further data analyses and summaries were performed in R (R Development Core Team 2011).

Results

Fleas

We collected a total of 1,968 fleas from 195 to 212 examined dogs based on combing each dogs' back for 10 min. Of these, we identified 142 individuals to species level from 15 dogs. We identified the two species *Ctenocephalides orientis* ($N=106$; 32 males and 74 females) and *Ctenocephalides felis felis* ($N=36$; nine males and 27 females). Both species were found to co-

occur on nine of 15 dogs for which fleas have been identified. Fleas were ubiquitously present on dogs throughout the study area (Fig. 1). The total density of fleas on different dogs differed among house types, with most fleas encountered in houses made of bamboo while dogs residing in houses made of stone/compound carried less fleas (posterior mode for deviance from mean for category “bamboo”: 0.33, CI -0.15 to 0.88 ; “stone/compound”: -0.57 , CI -1.05 to -0.07 ; Fig. 2). We estimated that flea density increased by 40 % from the average on dogs residing in bamboo huts and decreased by 43 % from the average on dogs residing in stone/compound houses.

Flea density was higher on smaller dogs with an estimated increase in flea load of 114 % (CI, 57–122 %) per 10 cm decrease in shoulder-tail length. Contrary to our expectations, other covariates, in particular landscape-level estimates, such as forest cover and human density, had no clear impact on flea densities.

There was only weak spatial structure in flea density on different dogs, likely accounting for not more than 3 % (CI, 0–36 %) of variation in flea densities (Fig. 3). While the model allowed us to see which factors are influential on flea densities, it should be noted that in particular the proportion of variance attributed to the different factors included considerable uncertainty (i.e., the proportion of variance explained by covariates such as spatial structure, house type, habitat use, and dog age is likely to be >5 % within 95 CI), highlighting that more intense sampling and perhaps also refinement of covariates would be necessary to more clearly determine the relative importance of different factors. Such large uncertainty was also present in models of lice and ticks.

Lice

We found adults of the invasive chewing louse *Heterodoxus spiniger* on 42 out of the 212 sampled dogs (20 %). We did not find any of the two typically dog-associated lice, the sucking louse *Linognathus setosus* and the chewing louse *Trichodectes canis*. Of the 511 encountered adult lice, 223 were male and 288 female.

All dogs infested with lice resided in either stone/compound or timber houses. We recorded no lice infestations on dogs in houses made of bamboo or corrugated metal. We estimated that lice density decreased by 44 % from the average on dogs residing in bamboo huts and increased as much as 335 % from the average on dogs residing in stone/compound houses (posterior mode for deviance from mean for category “bamboo”: -0.59 , CI -8.34 to 1.48 ; “stone/compound”: 1.48 , CI -0.57 to 5.6 ; Fig. 2). The density of lice was also influenced by elevation with larger densities of lice only found at lower elevations (effect size, -1.68 ; CI, -3.00 to 0.54). This elevation effect was also evident on the infestation probability of dogs with lice (Fig. 4). The infestation probability of dogs with lice revealed considerable spatial structure that explained

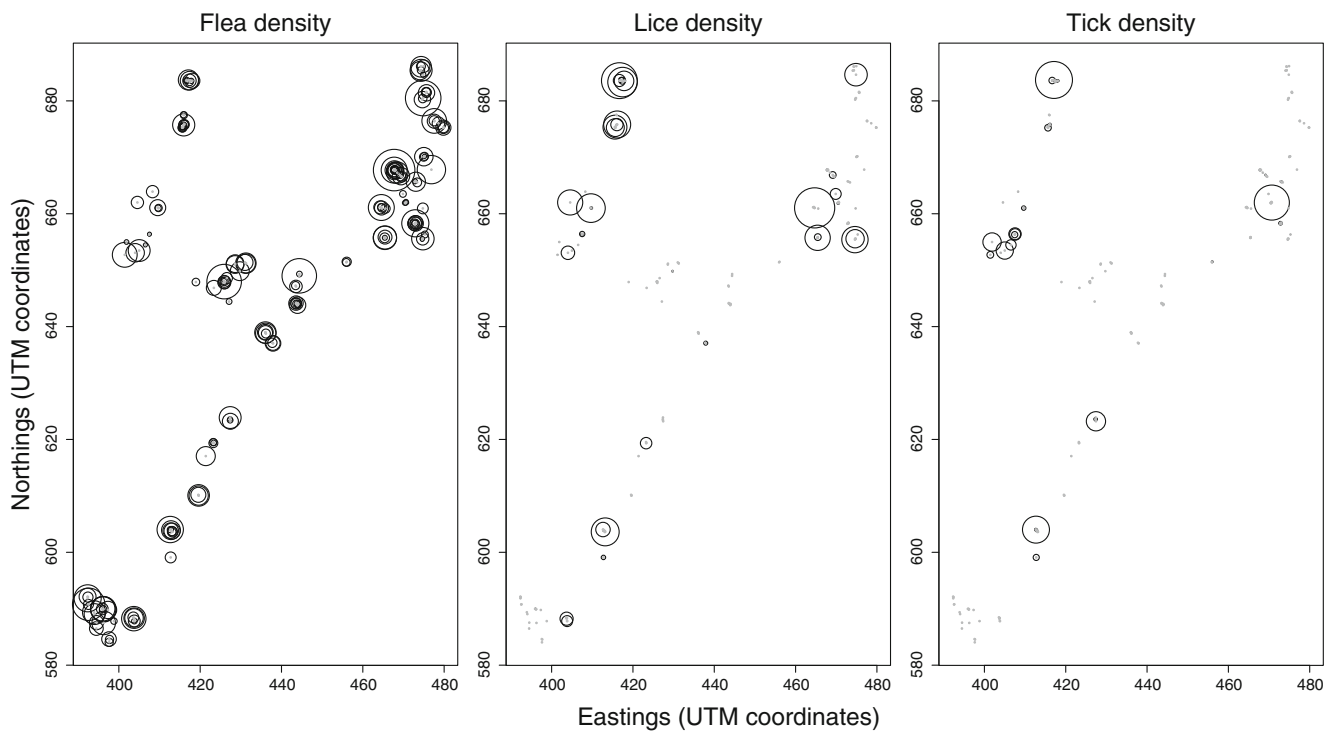


Fig. 1 Density of ectoparasites (flea, lice, and ticks) and their spatial distribution on dogs sampled in Sabah, Northern Borneo. Circle refers to the estimated density of fleas (pooled for the two species *C. orientis* and *C. felis felis*), lice (adults of *H. spiniger*), and ticks (all species) on

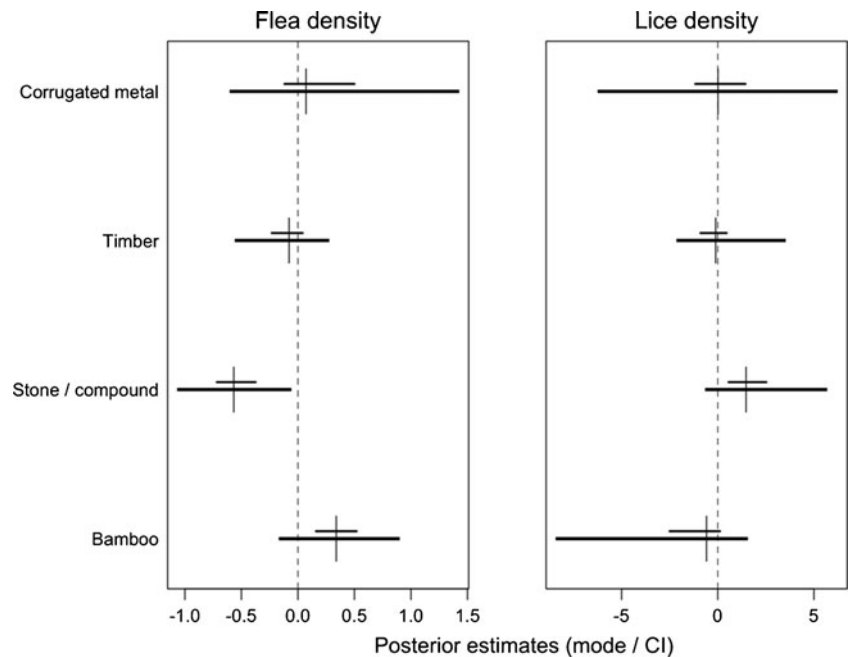
different dogs plotted as square root-transformed posterior modes from model outputs. Grey points refer to the spatial location where dogs were sampled

73 % (CI, 43–86 %; see also Fig. 1) of variation in infestation probability, whereas we found no spatial effect on the density of lice on different dogs. The scalar parameter *F* was estimated as having spatial autocorrelation in lice infestation probability over a spatial extent of ca. 16 km (CI, 5–47 km).

Ticks

We found ticks on 36 (17 %) of the sampled dogs (note that two of the 212 dogs were not completely sampled for ticks due to open wounds and infections in their ears and feet; for

Fig. 2 Differences in mean flea and lice densities on dogs under different housing conditions given as the posterior densities from MCMC sampling. Credible intervals are given as 95 % (lower bars) and 50 % (upper bars) highest posterior densities. Flea densities were highest on dogs in bamboo houses and lowest in stone/compound houses. Note that data were modelled on a log-scale (i.e., deviance of -0.57 from the mean for stone/compound houses refer to a decrease in flea density of 43 % from the average). The effects size of house type on lice density is much larger, but the posterior density distributions show that there is more uncertainty in the effects on house type on lice density



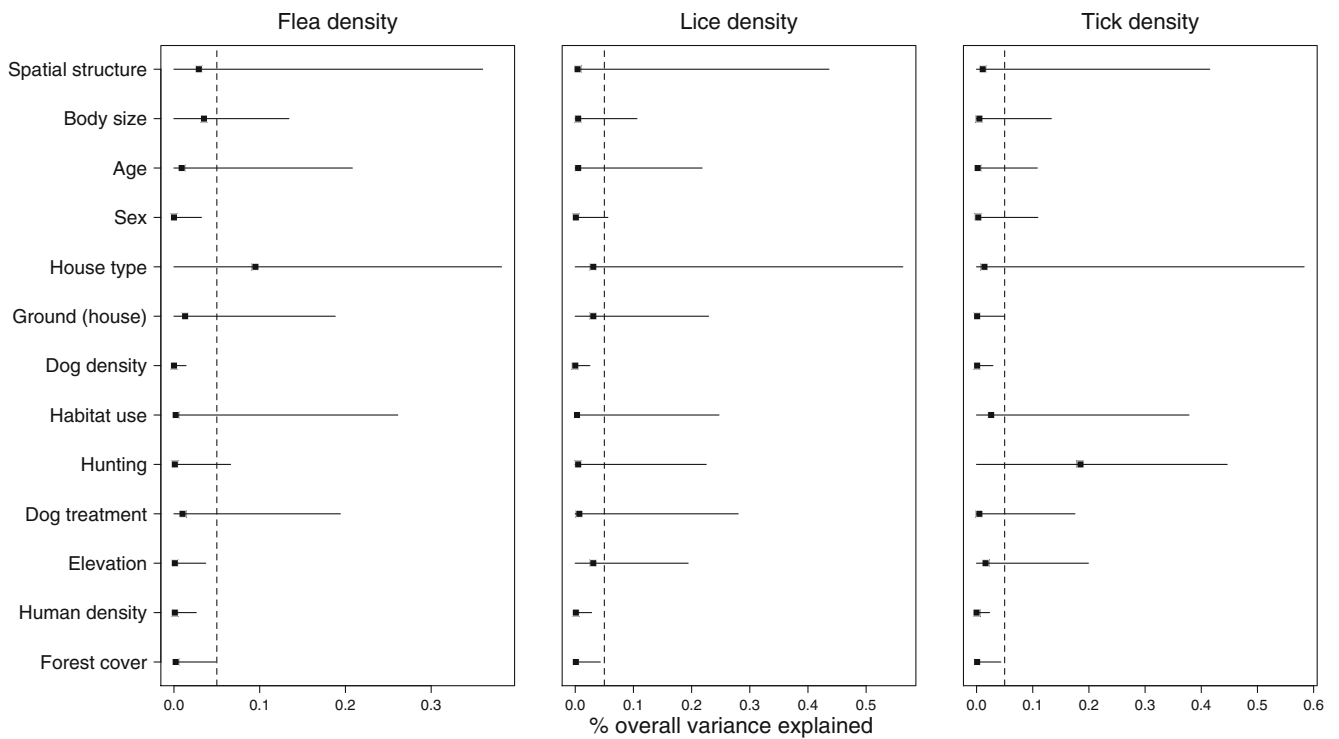


Fig. 3 Variation in ectoparasite density (flea, lice, and ticks) on different dogs explained by environmental variables given as posterior modes and 95 % credible intervals (*bars*)

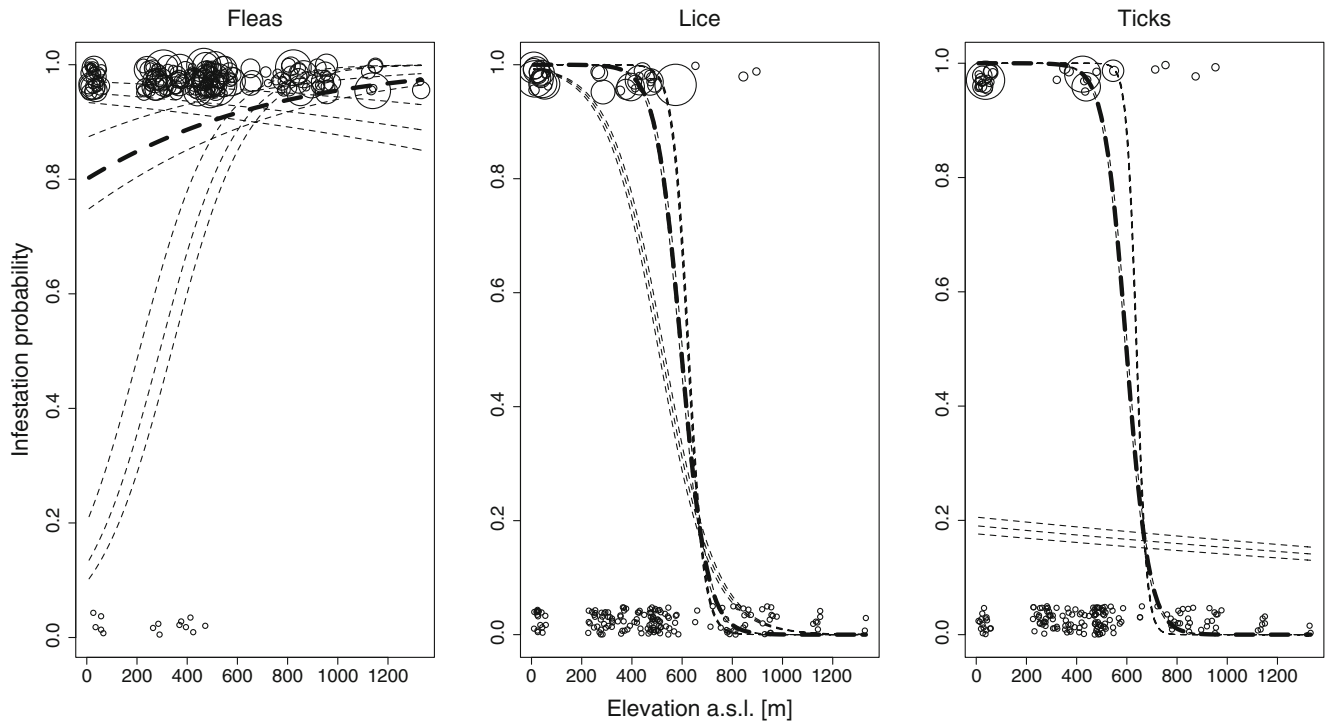


Fig. 4 Occurrence probabilities of fleas, lice, and ticks at different elevations with the posterior mode given as **bold lines**. *Thin lines* represent uncertainty with all combinations of 95 % CI estimates for intercept and slope, demonstrating that a decline in lice and tick occurrence on dogs with

elevation are evident, but effects cannot be precisely estimated from the data. *Circles* represent the observed square root-transformed number of counts with all zero counts at the *bottom*

these individuals, tick densities were modelled as missing data). Most ticks were *Rhipicephalus sanguineus* (63 males, 65 females, 38 nymphs, four larvae), found on 23 dogs. We further recorded *Haemaphysalis bispinosa* group (three males, 10 females, 51 nymphs; six dogs), *Haemaphysalis cornigera* (one female; one dog), *Haemaphysalis koenigsbergi* (two male, two dogs), and *Haemaphysalis semermis* (two males, two dogs).

The largest number of ticks on individual dogs were 53 (*H. bispinosa* group) and 50 (*R. sanguineus*). We found no co-occurring tick species on a single dog, most likely because of the small overall sample size. Overall tick density was considerably higher on dogs that entered both plantations and forest compared to dogs that limited their activity to single habitat types of either plantation or house area only (posterior mode for deviance from mean for category “plantation+forest”, 1.34; CI, -0.25 to 3.68), suggesting a 282 % increase in overall tick density of dogs using all habitat types compared to average densities. Tick density was about four times greater on dogs that were not used for hunting (effect size, 1.61; CI, 0.35 to 3.04) compared to hunting dogs.

There was a negative impact of elevation on tick density (effect size, -1.3; CI, -2.63 to 0.24). Most ticks were found at elevations below 800 m and the infestation probability of dogs with ticks declined with elevation (Fig. 4). In contrast to fleas and lice, there was no clear impact of house type despite the large credible interval (uncertainty) for the variance in tick density due to house type.

Similar to lice, spatial structure explained ca. 54 % (CI, 36–89 %) of the overall variation in infestation probability of dogs with ticks, whereas the density of ticks on dogs revealed no spatial structure, likely explaining only 1 % (CI, 0–42 %) of the overall variation in tick density. The scalar parameter F was estimated as having spatial autocorrelation in tick infestation probability over a spatial extent of ca. 4 km (CI, 1–17 km).

Discussion

In this study, we found fleas of the sympatric species *C. orientis* and *C. felis felis* to be ubiquitously present on dogs. Around 20 % of survey dogs were infested with the chewing louse *H. spiniger* and 17 % were infested with ticks of the five species *R. sanguineus*, *H. cornigera*, *H. koenigsbergi*, *H. semermis*, and *H. bispinosa* group. In light of species diversity, our study extends the number of tick species associated with dogs in SE Asia (Petney and Keirans 1996; Petney et al. 2007; Tanskul et al. 1986). Notably, we found individuals from the species-rich genus *Haemaphysalis* on dogs, which are also known to infest forest wildlife species in Borneo and elsewhere in SE Asia (Hoogstraal and Kim 1985; own

unpublished results). *Haemaphysalis* ticks are among the most important in transmitting disease agents to human and animals; hence, our records identify a possible link for tick-borne disease transmission between dogs and wildlife. The flea and lice species recorded in this study largely resemble the ectoparasite fauna of dogs in surrounding tropical countries in SE Asia (Beaucournu et al. 2001) and elsewhere (e.g., Xhaxhiu et al. 2009; Klimpel et al. 2010), comprising only a few common species. Control and dog treatment against these species may thus follow experience and specific recommendations developed against these species elsewhere (Mehlhorn et al. 2001, 2012).

As in other nearby areas where dog ectoparasites have been sampled to date, the chewing louse *H. spiniger*, which evolved in association with a macropod hosts in Australia and was most likely transferred to other biogeographical areas via dingos and dogs (Marshall 1981) seemed to have largely replaced the dog lice *L. setosus* and *T. canis* that were originally associated with dogs (Durden and Musser 1994). Although *H. spiniger* is still reported from one species of macropodid, the Agile Wallaby (*Macropus agilis*), in Australia (Price et al. 2003), most records of this louse are now from various species of carnivores throughout the world, especially domestic dogs (Marshall 1981; Price et al. 2003). Notably, only a few areas in Borneo and elsewhere in SE Asia remain truly rural as isolated areas with limited road access and large extents of continuous forest cover, but rather large parts of Borneo are increasingly exposed to globalised commerce that also breaks down barriers that had isolated rural human populations and their companion animals. Inhabitants from rural villages in our study area, for example, frequently possessed dogs obtained in other areas, although the construction of paved roads and individual motorised mobility only recently occurred in some of the villages (personal observation). The replacement of the original dog-associated lice with *H. spiniger* may serve as an example of how area-wide spread and homogenization of parasitic fauna is likely to occur.

An interesting finding of our study is that house-level factors were most influential on flea and lice density with contrasting effects, whereas host-dependent or landscape-level environmental covariates were of less explanatory power for these two groups. Relatively higher abundances of the flea *C. felis* on dogs have been also recorded on farms compared to dogs residing in city apartments in a temperate study in Spain (Gracia et al. 2008) and a rural compared to an urban area in Hungary (Farkas et al. 2009), supporting the premise that this flea may benefit from housing conditions where dogs are more exposed to organic matter and unpaved ground. We did not find any effect of host density on fleas, although the number of dogs per household should increase the overall host availability and feeding opportunities for fleas. In contrast to the occasionally recorded

positive relationship between body mass and flea load, which may be because larger body surfaces can accommodate more fleas or because larger dogs can tolerate more fleas per unit body mass (Krasnov 2008), we found fewer fleas on larger dogs. We have no direct explanation for this relationship which may result from a combination of factors: we usually also found relatively high flea densities on small puppies (2–3 months in age), which are mostly stationary with limited stray activity and thus provide constant flea habitat. In contrast, older dogs with larger body surfaces frequently stray in the vicinity of the owners' houses (personal observation) and more often expose their fleas to different conditions, such as intensive solar radiation, while walking around. Larger dogs might be also of more value to house owners for house guarding and hunting and may thus profit from more care that reduces flea density. Disentangling which of these intricately linked factors are most influential on flea density remains unresolved. Certainly, there is a limit to the methodological approach we applied because gathering information about the habitat use of dogs through questionnaires depends on relatively quickly gathering many samples from different areas. However, details of individual dog behaviour which could be only gained if individual dogs were observed over longer time periods remain unknown.

Contrary to our expectation, we found little predictive power of landscape-scale variables such as forest cover and human density on the density of ectoparasites from any of the sampled groups. With increasing human density at the landscape level, the density of dogs and other companion animals is likely to increase at the same scale and hence the probability of flea and lice infection of dogs from other host individuals that use the same landscape. Moreover, increasing human density typically results in more intensive conversion and degradation of the natural environment and thus altered habitat conditions encountered during daily forays of dogs. In a similar fashion, we expected the amount of forest cover to represent an important surrogate for much of the environmental conditions and perhaps also the interaction with wildlife that dogs experienced. While our study suggests that such landscape-scale factors are of little explanatory power for flea and lice density on dogs, it is notable that such landscape-scale impacts on flea infestations patterns have been reported for various kind of wild mammals (Collinge et al. 2005; Thamm et al. 2010). For wild mammals, conditions of resting sites are perhaps not as different from the surrounding environment as for companion animals that rest inside human-made housing areas. Fleas and lice are mostly transmitted from one host individual to another and their off-host environment is largely confined to resting and nesting sites of the host. In fact, lice, especially sucking lice, rarely occur in host resting or nesting sites and cannot survive for extended periods off the host.

Therefore, landscape-scale features may more reflect resting sites of wild mammals that are more or less part of the surrounding landscape but not so in domestic animals that spend considerable time under anthropogenic housing conditions distinct from ambient environmental conditions. Moreover, landscape-scale wide habitat features may also impact regional-carrying capacities and densities of wildlife hosts and the resulting interaction frequencies, but less so for domestic animals feeding mostly in the vicinity of their owners houses. With such a rationale, it seems plausible that dog infestations with fleas and lice are more influenced by household-level factors such as housing conditions that were associated with variable flea and lice density in our study whereas landscape-level factors may have more predictive power on wildlife infestation patterns.

In contrast to fleas and lice, we would expect landscape-scale factors to have most effects on ticks, as their development and survival largely depends on off-host environmental conditions and different proportions of habitat suitable for ticks can be expected under different urban and rural landscape management regimes (Allan et al. 2003; Estrada-Peña 2001; Smith et al. 2011). Such effects, however, were not obvious in our study. Instead, we found that overall tick densities increased with more variety in habitat use, in particular if plantation and forest were accessed in combination. Perhaps using both plantation and forest habitats in combination may also involve the use of ecotones/transition zones, adding another habitat component were tick acquisition could take place. Nonhunting dogs harboured more ticks than hunting dogs, another indicator that behaviour and use of the environment may help us to predict tick infestation patterns. Notably, environmental impact on tick density can be expected to vary among species: while the off-host environment and breeding sites of the tick *R. sanguineus* are largely concentrated at human dwellings, the off-host environment and acquisition sites of other tick species includes forests and other vegetation (Dantas-Torres 2010). While our finding of larger tick density on dogs that used both plantations and forests compared to dogs using only plantations suggests that forest is an important habitat for tick acquisition, we should emphasise that forest conditions in Borneo largely differ among sites, be it through regional conditions or the ever-increasing forest conversion and fragmentation through anthropogenic land use.

Noteworthy, as part of an intensive small mammal survey in different lowland rainforest of Borneo including forest next to our dog study sites (Wells et al. 2007), we found the three tick species *H. cornigera*, *H. koenigsbergi*, and *H. senermis* found on our dogs also to infest treeshrews (Scandentia, Tupaiidae), rodents (Rodentia, Muridae and Sciuridae), and two species of civets (Carnivora, Viverridae), namely *Paradoxurus hermaphroditus* and *Viverra zangalunga* (unpublished results).

The very invasive tick species *R. sanguineus*, in turn, which originated from Africa but now occurs throughout the world, was not found in Borneo ca. 50 years ago (Kohl 1957), suggesting that this tick species may have invaded Borneo afterwards, coinciding with the onset of commercial large-scale forest harvesting.

The overlap in tick species between dogs and a large range of wildlife species may not only have important implications for the transmission and emergence of tick-borne diseases, but also emphasises that ectoparasite diversity and infestation patterns of domestic dogs and other companion animals are not necessarily independent from host–parasite associations of wildlife species occurring in the same area. Such overlaps, for example, leads to questions about the kinds of habitats that are used by tick populations of each species, and thus how the infestation risk of dogs with ticks varies. Tick species survival and population growth may profit from a large range of sympatric host species; for example, infestation of dogs as one host species in particular areas may largely depend on the local wildlife community of potential hosts, which in turn may be influenced by habitat availability and suitability (Keesing et al. 2006; Ostfeld and Holt 2004). Given the intense forest conversion and management in SE Asia (Miettinen et al. 2011; Sodhi et al. 2010) and the reduced small mammal species diversity in altered forests (Wells et al. 2007), it is likely that the infestation of dogs with generalist ticks is largely determined by anthropogenic environmental changes. Developing such concepts further and testing them with empirical research is of significant health concern given that much remains to be learned about the epidemiology and ecology of arthropod-transmitted disease in SE Asia (Irwin and Jefferies 2004; Jones et al. 2008). In fleas collected during this study, for example, molecular screening of 360 fleas revealed the presence of the zoonotic pathogen *Rickettsia felis* in not less than 74 % of fleas and of *Bartonella clarridgeiae* in two fleas (Kernif et al. 2012). The tick *R. sanguineus* has been recently found to transmit canine leishmanioses in Brazil and Italy (Dantas-Torres et al. 2010), but its role in disease transmission in SE Asia remains unknown. Also, pathogen transmission by fleas from commensal and wild rodents may be of considerable health concern (Barbara et al. 2010). Likewise, infestation patterns of commensal rodents are likely to differ with environmental conditions (Chaisiri et al. 2010). In the search for general patterns of how the environment may affect host–parasite associations, it is interesting to note that we found large densities of lice and ticks mostly at elevations below 600 masl, whereas flea density on dogs was not affected by elevation. Lower tick infestation at higher elevations is in agreement with studies from Europe that suggest lower tick abundance of *Ixodes ricinus* at higher altitudes (Gilbert 2010), whereas *R. sanguineus*, which

was the most commonly encountered tick in our study may survive under variable environmental conditions (Dantas-Torres 2010). In contrast to these patterns found on dogs, flea species diversity and density on wild small mammal species (rat, squirrels, and treeshrews) were found to be higher in montane forest above 1,200 masl compared to forests at lower elevations in SE Asia (Adler et al. 2001; Wells et al. 2011). As discussed above, different mechanisms may apply to wildlife versus artificially housed companion animals, for which the relationship to the environment may differ. The considerable and unprecedented land use and climate changes and also the presumably changing abundances of wild and domestic animals which we have to expect during the next decades will most probably alter host–parasite associations for both wildlife and companion animals, with possible consequences for biodiversity and human health (Daszak et al. 2001; Friggens and Beier 2010; Lafferty 2009), suggesting a need for more epidemiological studies.

In summary, our study has provided the first insights into environmental impacts of the ectoparasite fauna of dogs in Borneo and showed that housing conditions may help to predict flea and lice density while habitat use determined tick infestation patterns. Removing uncertainty on how the various environmental factors predict infestation patterns of dogs will require further large-scale studies that consider environmental factors from host- to landscape level over larger geographical space and with replicates in time. Studies investigating the potential processes driving ectoparasite infestation patterns of domestic animals further need also to take interactions with wildlife and land use changes into account.

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