



Interaction of ectoparasites-small mammals in tropical rainforest of Malaysia

A. Madinah^{1,3}, F. Abang¹, A. Mariana², M.T. Abdullah¹ and J. Mohd-Azlan¹

¹ Department of Zoology, Faculty of Resource Science and Technology, Universiti Malaysia Sarawak, 94300 Kota Samarahan, Sarawak, Malaysia

² Unit of Acarology, Infectious Diseases Research Centre, Institute for Medical Research, Jalan Pahang, 50588 Kuala Lumpur, Malaysia

³ Corresponding author: a.madinah@gmail.com, Tel: +6082583180, Fax: +6082583160

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Abstract: The literature regarding the diversity of ectoparasites and their interaction with their hosts remains largely inadequate in Malaysian tropical rainforest. We investigate the interaction patterns and specialization of ectoparasites infesting terrestrial small mammals (rodents and scandents) in Peninsular and Malaysian Borneo from samples made in 16 localities between 2008 and 2010. A total of 3,235 individuals of ectoparasites were collected during field surveys, resulting in an interaction network involving 47 ectoparasites that were distributed on 23 species of small mammals. The overall specialization index H_2' of all ectoparasites and host species was 0.67 which was considered moderate. Ticks appeared to be generalist with specialization index ($H_2' = 0.35$) while lice showed higher specialization ($H_2' = 1$) in selecting host species. The most diverse parasite assemblage was found on *S. muelleri* ($H_{s,w} = 1.96$). Specialization indices among ectoparasite species (d_p) ranged from 0.03 to 1 while the indices among host species (d_h) ranged from 0.20 to 1. Incomplete field data may have contributed to the high specialization indices. This study is significant as it can enhance our understanding the emergence and management of potential zoonotic diseases in Malaysia.

Nomenclature: Standard references throughout this study follow Payne et al. (2005) and Wilson and Reeder (2005) for small mammals, Kohls (1957) for ticks, Strandtmann and Mitchell (1963) for mites, Johnson (1964) for lice, and Nadchatram and Dohany (1974) for chiggers.

Introduction

Malaysia (Peninsular Malaysia and Malaysian Borneo) is one of the 17 countries that have been described as a mega-diversity country. In fact, Malaysia is in one of the four biodiversity hotspots containing high concentrations of endemic species and is experiencing rapid deforestation and habitat degradation (Myers et al. 2000). This includes terrestrial small mammals (mostly rodents and scandents) which are diverse groups of mammals that can be found in a wide variety of habitats (Fleming 1975, Corbet and Hill 1992, Payne et al. 2005, Abdullah et al. 2010). These species play a significant role in maintaining ecosystem functionality as seed dispersal agents and arthropod control, and are medically important as reservoirs of zoonotic diseases (Wells et al. 2007, Nadchatram 2008, Chaisiri et al. 2010). Rodents and scandents are hosts to many ectoparasites and a single host can carry many different species of Acari and Insecta (Nava et al. 2003, Nadchatram 2008).

In general, ectoparasites from rodents and scandents can be classified into five main groups, namely, Mesostigmata (mites), Acarina (ticks), Prostigmata (chiggers), Phthiraptera (lice) and Siphonaptera (fleas) (Paramasvaran et al. 2009). Several studies in Malaysia reported that vertebrate hosts

carry various groups of ectoparasites such as ticks, mesostigmatid mites, listrophorid mites, trombiculid mites (chiggers), lice, fleas, myobiids and cheyletid mites (Shabrina and Salleh 1995, Mariana et al. 2009, Azima et al. 2007, Madinah et al. 2011).

Among the ectoparasites, lice and certain gamasid mites are known as permanent parasites while fleas and certain mites are nest-dwellers. Nest-dwellers only visit the host for feeding and copulation (Thanee et al. 2009). Some ectoparasites are host specific and can only be found on certain rodents and scandents (Bittencourt and Rocha 2003) while others are generalist. The occurrence of a particular ectoparasite species living on more than one host species is a result of complex interactions between the parasites and the host and the co-existence among the parasites (Thanee et al. 2009). This may be related to the intra and interspecific relationships, behaviour and the microhabitats utilised by the host (Bittencourt and Rocha 2003).

The distribution of ectoparasites is influenced by the hosts' microhabitat because ectoparasites may encounter other hosts especially when habitats are disturbed, resulting in the change of the host assemblage (Gettinger and Ernest 1995, Bittencourt and Rocha 2003). Therefore, the diversity and structure of host communities in different environmental

settings can influence ectoparasite dynamics and the transmission of diseases (Suzan et al. 2009, Wells et al. 2011), and the presence of parasites can give important impacts either to host populations or communities (Hudson et al. 2006, Wells et al. 2007, 2011).

Network analysis can be used as a tool to observe patterns and for predicting changes within natural communities consisting of interacting species such as parasites and their hosts (Poulin 2010). Network analysis has been increasingly applied to multiple entity relationships such as parasite ecology (Poulin 2010), plant-animal mutualistic networks (Bascompte and Jordano 2007), the spread of diseases through social networks (Read and Keeling 2003) and more recently, in understanding the relationship between fleas and small mammals (Wells et al. 2011). Additionally, network theory has been applied successfully to explain and predict the spread of parasitic diseases through host populations via social or sexual contact (Eames and Keeling 2002, Drewe 2010). Network analyses in community ecology have been used to describe network properties with introduced new indices (Dormann et al. 2008, 2009). Two types of network are relevant to parasitology: bipartite interaction networks and trophic networks to understand food web relationships (Poulin 2010). Analyses of these networks are powerful tools to represent interactions among species and highlight their interdependence. Additionally, the interaction web allows the visualization of community structure and the ways species depend on one another (Tylianakis et al. 2007).

The association between ectoparasites and small mammals in Malaysia generally lags behind when it comes to ecological network structures of parasitic or mutualistic interactions (Wells et al. 2011). Previous research concentrated on the descriptions of hosts and their ectoparasite species and taxonomic studies in relation to medical and veterinary importance, with little published information on the host-ectoparasite relationship in Malaysia (Muul and Lim 1974, Paramasvaran et al. 2009). This study aims to provide information on tropical parasitology by examining the network structure of small mammals and their ectoparasite associations in Malaysia. This study contributes to a better understanding on the community level of ectoparasite and small mammal interactions in the tropical rainforests of Malaysia. Here we explore ectoparasite composition, the level of associations between ectoparasites and small mammals, the similarity of hosts and specificity of ectoparasite groups.

Materials and methods

Study areas

This study was carried out in 16 localities in both Peninsular and Malaysian Borneo (Figure 1), with 11 locations in Sarawak, four locations in Peninsular Malaysia and one in Sabah from June 2008 until May 2010 (Figure 1). The study sites consisted of seven major types of ecological

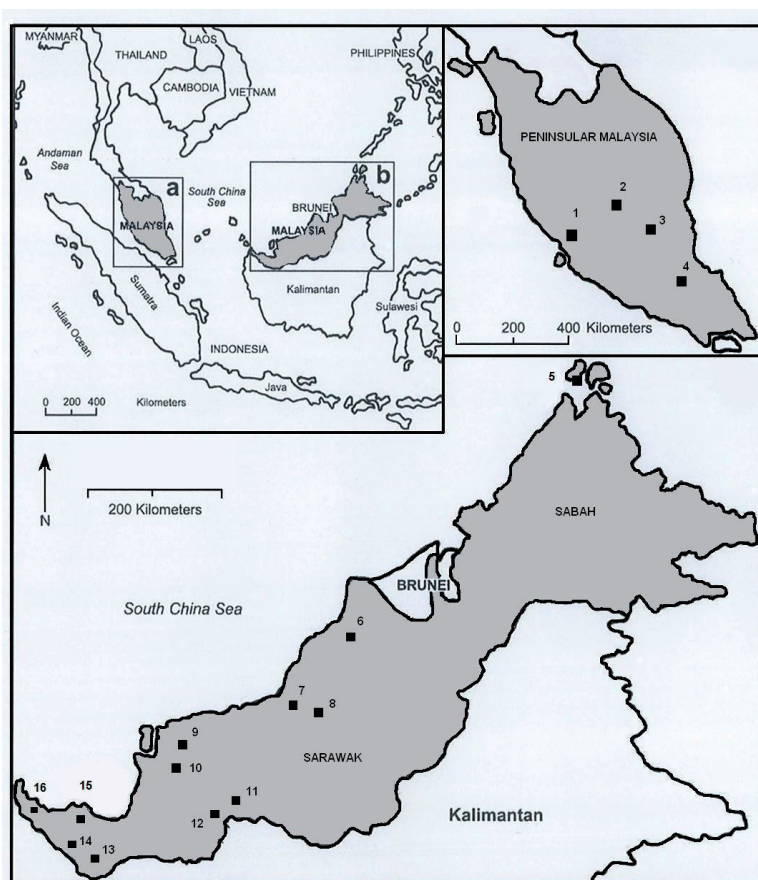


Figure 1. Peninsular and Malaysian Borneo of Sabah and Sarawak and the 16 localities where ectoparasites of rodents and scandents were sampled from 2008-2010. (a) 1: Sungai Dusun Wildlife Reserve, Selangor (SDWR); 2: Lata Bujang Krau Wildlife Reserve, Pahang (LBKWR); 3: Tasek Bera Ramsar Site, Pahang (TBRSS); and 4: Endau Kluang Wildlife Reserve, Johore (EKWR). (b) 5: Balambangan Island, Sabah (BIS); 6: Niah National Park, Miri, Sarawak (NNP); 7: Rumah Temuai Nanga Merit, Kapit, Sarawak (RTNM); 8: Sungai Beletik Nanga Merit, Kapit, Sarawak (SBNM); 9: Bukit Aup Jubilee Park, Sibuluan, Sarawak (BAJP); 10: Human Settlement, Kanowit, Sarawak (HSK); 11: Sungai Bloh Lanjak Entimau Wildlife Sanctuary, Sarawak (SBLEWS); 12: Sungai Menyarin Lanjak Entimau Wildlife Sanctuary, Sarawak (SMLEWS); 13: Gunung Regu Padawan, Sarawak (GRP); 14: Kampung Giam Padawan, Sarawak (KGP); 15: Kubah National Park, Kuching, Sarawak (KNP); and 16: Bukit Pueh, Sematan, Sarawak (BPS).

habitat, namely, (i) secondary forest (ii) lowland dipterocarp forest (iii) riverine forest (iv) peat swamp forest (v) mixed dipterocarp forest (vi) hill dipterocarp forest and (vii) limestone forest.

Collection and analysis methods

Rodentia and Scandentia were sampled using 100 standard cage traps and 20 Sherman traps for five to six consecutive days per site which resulted in 7,900 trap-nights. Cage traps were placed on the ground and in tree branches along the existing trails with approximately five meter intervals. Cage traps were baited with bananas, oil palm fruits, tapioca or salted fish while Sherman traps were baited with peanut butter. All traps were checked twice daily and the baits were replenished twice daily, once in the morning and evening.

Small mammals were identified following Medway (1983), Payne et al. (2005), Wilson and Reeder (2005), and Francis (2008). Each captured animals was marked with a UNIMAS metal tag necklace to assist identification of recaptured animals during the trapping. To prevent contamination of ectoparasites between different host individuals, each individual host was placed in a separate clean cloth bag before anaesthetised with chloroform. The body surface of captured animals was systematically checked for ectoparasites by combing with a fine tooth comb and picking using fine forceps. The ectoparasites found in each individual were preserved in 70% ethanol and stored in labelled individual vials. They were later identified to genera or species level using available keys, published taxonomic drawings and references (Kohls 1957, Domrow 1976, Baker et al. 1962, Strandtmann and Mitchell 1963, Johnson 1964, Jameson 1965, Nadchatram and Dohany 1974, Uchikawa and Suzuki 1980, Durden 1990). Voucher specimens of the hosts were catalogued following Abdullah et al. (2010) and deposited in UNIMAS Zoological Museum.

Data analysis

Records from the 16 localities were pooled in a single network file. Subsequently, the data were sorted and the interactions of each species of ectoparasite and small mammals were quantified into matrices of interaction frequency. Bipartite networks were represented by a matrix in which columns represent the ectoparasites (P1 to P43) and rows the hosts (H1 to H23). Entries in the matrix express the observed links quantitatively. Interaction frequency was defined as the number of host species recorded as carrying a particular ectoparasite species (Wells et al. 2011). We then separated and quantified the interactions of the ectoparasites into three categories, namely, ticks, mites and lice. The deviation from a completely random configuration of ectoparasite and small mammal's relationship was derived from the standardized two-dimensional entropy H_2' at the network level (Wells et al. 2011). At the species level, the d index derived from Kulback-Leibler distance was used to calculate strength of a species specialized index, d_h is a specialized index for ectoparasite species while d_p is a specialized index for host species, and

it calculates how strongly a species deviates from a random sampling of available interacting partners (Blüthgen et al. 2006, Blüthgen 2010). These indices provide a measure of complementary specialization and niche partitioning which ranges from 0 (no specialization) to 1 (perfect specialization) where the increase in d leads to a large number in specialized species, consequently increasing the weighted mean H_2' at the community level (Wells et al. 2011). The indices used in this study, H_2' and d , are least biased by sample size (Blüthgen 2010).

The niche overlap indices were used to determine the value of mean similarities in interaction pattern between ectoparasite species and the infested host. Horn's Index was used in this study to indicate the niche overlap pattern between ectoparasite species, where values near 0 indicate no common use in niches (Horn 1966). Diversity indices are only used in general comparisons of parasites in host groups and species. Shannon-Wiener Diversity Index of host ($H_{s,w}$) which reports the species richness has a moderate ability to discriminate between communities and a low sensitivity to sample size (Magurran 2004). The function *plotweb* draws a bipartite graph, where the rectangles represent species and the width is proportional to the sum of interactions involving these species. Interacting species are linked by lines, whose width is again proportional to the number of interactions. All tests were computed with the *R v2.11* statistical programming language (R Development Core Team 2010). The *bipartite 1.10* (Dormann et al. 2008) and *sna* packages (Butts 2008) were used to calculate these indices. Means are given with \pm standard deviation.

Results

One hundred and forty two individuals of rodents ($n = 124$) and scandents ($n = 18$) belonging to 23 species (16 species of rodents and 7 species of scandents) were trapped in 16 locations (Appendix 1). The highest capture success was recorded for Muller's rat (*Sundamys muelleri*), followed by brown spiny rat (*Maxomys rajah*) and common treeshrew (*Tupaia glis*). Ninety five percent of these small mammals were infested with ectoparasites. Among the infested animals, 10 out of 16 species of rodents and four out of seven species of scandents were noted to carry more than one group of ectoparasites (Appendix 1). Muller's rat *S. muelleri* had the most diverse ectoparasite assemblage ($H_{s,w} = 1.96$) followed by *Maxomys ochraceiventer* ($H_{s,w} = 1.77$), suggesting that these species can accommodate variety of ectoparasites (Appendix 2). The ectoparasite load on rodents are significantly different from scandents ($t = 3.04, p < 0.01$) (Appendix 2).

A total of 3,235 individuals of ectoparasites from two orders (Acarina and Anoplura) and seven families (Ixodidae, Laelapidae, Trombiculidae, Atopomelidae, Sarcoptidae, Hoplopleuridae and Polyplacidae) belonging to three main groups; ticks, mites (mesostigmatids, listrophorids, chiggers or trombiculid mites, astigmatid mites) and lice were identified. This can be further categorized into 23 genera and 47 species of ectoparasites. From the 47 species, six species be-

Table 1. Numbers of ectoparasite groups and structure of ectoparasite-small mammals web indices. Network web for overall interaction is illustrated in Figure 2.

	No. of hosts	No. of ectoparasite species	Matrix size	Lx	Msh	N_0	H_2'	H_{s_w}
Overall	23	47	1081	3.72	0.66	0.20	0.67	3.37
Tick	13	6	78	3.17	0.77	0.75	0.35	2.58
Mites	20	36	720	3.18	0.54	0.17	0.69	3.13
Lice	6	5	30	1.04	0.07	0	1	1.51

Lx = Linkage density, Msh = Mean number of shared host, N_0 = Niche overlap, H_2' = Specialization on network level and H_{s_w} = Shannon-Wiener Diversity Index

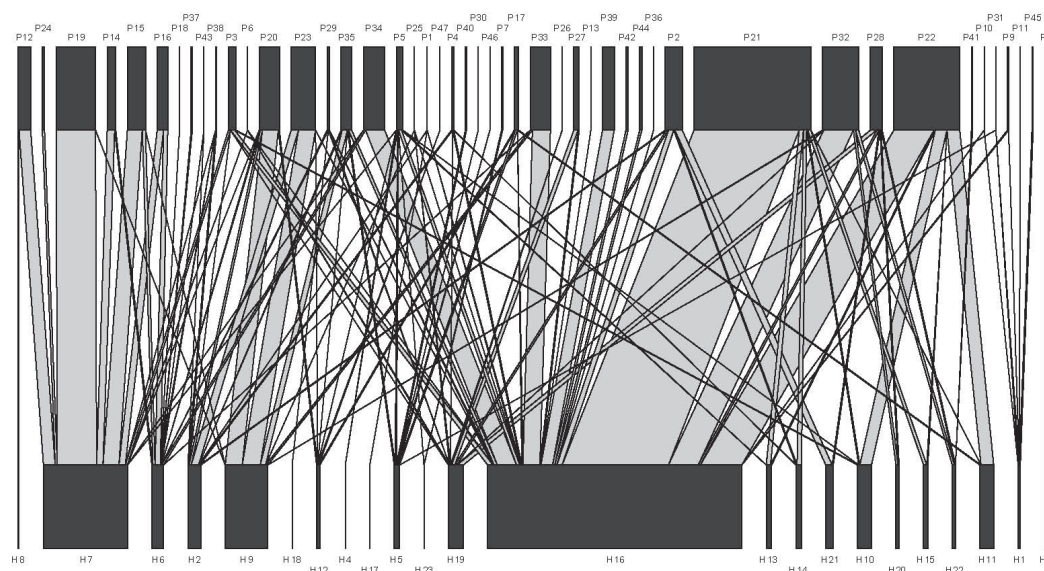


Figure 2. Quantitative ectoparasite small mammal networks for tropical rainforest in Malaysia. For each web, the width of the lower bars represents proportional small mammal host (Rodentia and Scandentia) and the width of the upper bar represents ectoparasites abundance, while the linkage width indicates the frequency of interaction. Upper and lower bars species acronyms are in Appendix 2.

long to the ticks group, 36 species belong to the mites group, and five species belong to the lice group. The mites group was found to contain several more sub-groups, which are mesostigmatid mites (18 species), chiggers (8 species), listrophorid mites (9 species) and astigmatid mites (one species) (Appendix 2). The infestation rates (prevalences) of the ectoparasites groups varied considerably. Mesostigmatid mites were the most diverse ($H_{s_w} = 1.95$, $n = 2,165$) and prevalent group (71.8%), followed by ticks (30.9%) and listrophorids (20.4%) while the lowest prevalence was observed in the itch mites group (1.4%) (Appendix 1). Among the ectoparasites species, *Laelaps sedlaceki* represented the highest number of ectoparasites recorded (23.9%), followed by *L. turkestanicus* (13.6%) and *L. sanguisugus* (7.9%) (Appendix 1).

A total of 122 ecological relationships between ectoparasites and small mammals were observed during this study (Figure 2). The overall complementary specialization index H_2' of the database network was 0.67, suggesting moderate specialization. Lice assemblage showed the highest specialization ($H_2' = 1$) while ticks appeared to be generalist ($H_2' =$

0.35), suggesting lack of specialization compared to other groups (Table 1). Niche overlap (N_0) significantly declined when network specialization (H_2') increased (Linear regression: $F_{1,3} = 16.7$, $P = 0.05$, $R^2 = 0.89$). The niche overlap declined when there were more specialized ectoparasite species in an assemblage. Among the three groups of ectoparasites, ticks showed the highest niche overlap ($N_0 = 0.75$) (Table 1). Mites groups showed the most diverse of ectoparasites species recorded compared to ticks and lice group with $H_{s_w} = 3.13$ (Table 1).

Specialization indices for ectoparasite species (d_p) ranged from 0.03 to 1 while for host species (d_h) the range was from 0.20 to 1 (Appendix 2). The two most commonly found ectoparasite species, *L. sedlaceki* ($d_p = 0.41$) and *L. turkestanicus* ($d_p = 0.40$), exhibited moderate host specificity, infesting both rodents and scandents (Appendix 2). The tick *Ixodes granulatus* was found on 7 out of 16 rodent species (rats) and on *Tupaia tana* (Scandentia), exhibiting low host specificity ($d_p = 0.23$). *Haemolaelaps audyi* was only recorded in *Sundasciurus lowii* and vice versa; showing high specificity

(d_p and $d_h = 1$) for both species. Twenty nine ectoparasites shared more than one host and approximately 17% of the ectoparasites ($n = 18$) were singletons, suggesting that additional samplings may provide a more comprehensive network on parasite ecology.

Discussion

This study contributes to the growing literature on parasite and host association especially in the Southeast Asian region. The network analysis provided more information on how interactions are structured besides providing descriptive ectoparasite accounts which are largely lacking in this region. Due to limitations stemming from the difficulty of covering wide geographical areas for sampling and limited current knowledge of the hosts and ectoparasites involved, the data from the present study may be less comprehensive than it ideally should. Nonetheless, we strongly believe that our longitudinal effort to illustrate the interactions between ectoparasites and terrestrial small mammals in Malaysia is novel on its own. This finding can provide some preliminary insight into how interactions or relationships between ectoparasite and small mammals are structured beyond single species records.

It was evident from our findings that, *S. muelleri* was one of the most frequently caught species in secondary forest with the greatest range of diverse ectoparasite assemblage. This species was often found near streams and also occur deep inside the forest, near the forest edge and human modified landscapes (Payne et al. 2005). Different ecological habitats in Malaysia may harbour different taxonomic composition of host species (Tuen et al. 2000, Tuen et al. 2002, Karim et al. 2004, Abdullah et al. 2006, Khan et al. 2008, Besar et al. 2009, Eileen et al. 2012, Tingga et al. 2012). Paramasvaran et al. (2009) showed that *Rattus rattus diardii* from urban area had the most diverse assemblage of ectoparasites. It is evident that the level of habitat disturbance may increase the prevalence of hosts and ectoparasites. Habitat disturbance may also affect the structure of micromammal communities and thus induce parasite host-switches (Gettinger and Ernest 1995, Wells et al 2007). As the samplings were carried out in disturbed habitat (fruit orchard and secondary forest) and primary forests, the distribution of ectoparasites may have been influenced by the sampling site selection. The highest infestation rates of ectoparasites on small mammals, serves as ecological labels related to the patterns of distribution and behaviour of the host (Audy 1958).

Most of the ectoparasite groups collected in this study have been found and reported in previous studies in Malaysia (Shabrina and Salleh 1995, Azima et al. 2007, Nadchatram, 2008, Mariana et al. 2009, Paramasvaran et al. 2009, Madinah et al. 2011). Consistent with previous studies, mesostigmatid mites formed the most common and predominant group of ectoparasites infesting small mammals (Muul and Lim 1974, Shabrina et al. 1989, Shabrina and Rafeae 1993, Mariana et al. 2006, 2008, Paramasvaran et al. 2009, Madinah et al. 2011). Mesostigmatids are nest dwellers and are known to have a relatively high prevalence on rodents and scandents (Shabrina et al. 1989). The animal host generally provides

permanent nest for these mites. Mesostigmatid mites live in nests of rodents and scandents and feed intermittently on the host. Most mesostigmatid species are ectoparasitic nidicoles that reproduce in the nests of their hosts (Nadchatram 2008). Chiggers (Trombiculid mites), on the other hand, were most abundant on treeshrews (inside the ears) and squirrels, but were not commonly found on rats except on *S. muelleri*. This finding is also in accordance with Muul and Lim (1974). Lice and ticks were found in this study and this accords with Marshall (1981) because both ectoparasite were known as the groups of ectoparasites that mainly infest mammalian host such as rodents and scandents. Nevertheless, contrary to previous studies conducted in the Malaysian contexts (Abang and Hassan 1988, Marshall 1981, Zahedi et al. 1996, Paramasvaran et al. 2009, Wells et al. 2011), no fleas were recovered in our present study. The reason for the total absence of fleas is unclear and therefore warrants further studies.

Generally, complementary specialization index shows moderate host-ectoparasite specificity ($H_2' = 0.67$) with little difference in specialization among taxa, as 29 ectoparasites shared more than one host. The singleton ectoparasites ($n = 18$) may have influenced the results as they indicate high dependence or specialization, although occasionally, they can represent rare species (Dormann et al. 2009). Overall, it appears that lice are host specific ($H_2' = 1$) in tropical rainforests. However incomplete data due to difficulties of sampling and brief sampling period may have caused biased estimates (Goldwasser and Roughgarden 1997). Anopluran lice are known to be highly specific to their mammalian host. It completes their whole life cycles within the host's pelage, thus, their host specificity is predicted to be higher (Marshall 1976). The autecology of the ectoparasites itself may influence the distribution in its host species, consequently resulting in its specialization. One such example would be *Atopophthirus emersoni* which is host specific to rodents and scandents (Durden and Musser 1994).

Mites showed a relatively higher network specialization ($H_2' = 0.69$) and consisted of both specialists and generalists selecting the host species. Laelapid mites and chiggers were not host specific as observed in this study, a finding which is consistent with previous work by Botelho et al. (1981) and Bittencourt and Rocha (2003). These species are often associated with host species from higher taxonomic level (genus, family) (Furman 1972). Ticks, on the other hand, appeared to be generalist ($H_2' = 0.35$). However, tick-host relationship can be strongly biased by spatial patterns (Cummings 2004). This is consistent with Wells et al. (2013), who reported that host specificity by ticks was estimated to be similarly low for all ticks in tropical rainforest in Borneo. Based on ticks feeding behaviour, some species of ticks are classified as two-host, three-host and many-host ticks which complete their life cycles on different individuals of host (Audy et al. 1960, Nadchatram 2008). In our findings, the tick *I. granulatus* was known to be largely distributed on various host animals and has been identified as the common species of 3-host tick that completes all three stages of life cycle on three different individuals of rodents, shrews or other small mammals in Malaysia (Audy et al. 1960, Nadchatram 2008). In general

this suggests that ticks are generalist in selecting their host in tropical rainforest.

Host-ectoparasite specificity can also be influenced by other factors such as ecology, distributions and habitat preference by the host, for example, warm, humid climate dipterocarp forests harbour unfavourable conditions in underground burrows for fossorial small mammals such as *S. muelleri* and *Maxomys rajah* (Wells et al. 2011, 2013). Scandentia (Tupaiaidae) showed lower ectoparasite loads compared to Rodentia (Scuridae and Muridae). This is probably due to the behaviour of these species such as irregular usage of the nest (e.g., *Tupaia tana*). Additionally, their fur provides less optimal micro-habitat for ectoparasites (Muul and Lim 1974, Shabrina and Rafae 1993).

The strength of our results and conclusions are limited by the study's relatively small sample size. This study is biased to some extent as some species of ectoparasite and host were observed only once or a few times. Based on Wells et al. (2011), incomplete data in network structures were known to bias inferences on the degree of specialization of rarely collected species, or the connectivity between species and the resulting modularity with the network. Thus, any conclusion on interactions and host specificity based on observed data of interaction pattern in this study need to be performed cautiously. Nonetheless, in our study, the indices H_2' and d_p were the least biased by sample size (Blüthgen 2010), and consequently the network analysis achieved in this study is useful as it can reveal the general patterns of complementary specialization (Wells et al. 2011). The indices from the bipartite network analysis can explain some elements of interactions and the links can be visually observed. Additionally, we found specific specialization indices d_p and d_h , at least for repeatedly recorded species (e.g., the host *S. muelleri*, *M. rajah* and *M. ochraceiventer* and the ectoparasite *I. granulatus*, *L. sedlaceki*, *L. turkestanicus*) in both types of dataset, thus representing reliable trends.

Information on host-parasite-pathogen interaction is important as it is related to management of zoonotic diseases. This study sheds some light on how these interactions are structured and it can potentially be applied in predicting possible emergence of zoonotic diseases in Malaysia. Approximately 21% of ectoparasite species recorded in this study is of known medical importance. These species could be potential vectors of diseases such as the ticks typhus and Q-fever (e.g., *I. granulatus*), scrub typhus (e.g., *Leptotrombidium deliense*) and murine typhus (e.g., *Polypax spinulosa* and *Hoplopleura dissicula*) (Mariana et al. 2005, Azima et al. 2007, Nadchatram 2008, Paramasvaran et al. 2009, Madinah et al. 2011).

Peninsular Malaysia and Malaysian Borneo are undergoing rapid deforestation and land development resulting in environmental degradation (e.g., plantation, urbanisation, and settlement) and demographic changes due to population increase and rural migration (Sodhi et al. 2004, Mohd-Azlan and Lawes 2011). The current ecosystem and landscape changes may alter the natural ecology, behaviour and distribution pattern of ectoparasites and their hosts. Therefore, a

deeper insight on the variation and intensity of host-ectoparasite associations and interactions is vital to facilitate and improve our knowledge on epidemiology and disease transmissions. It is suggested that future studies should concentrate more on descriptive research on the diversity of ectoparasites and their hosts as they provide baseline information on potential vectors of zoonotic diseases which can be used as a predictive tool to analyse the trend of epidemiology due to environmental changes from anthropogenic activities. The focus should not be merely to document a comprehensive host-parasites network, but on the strength of host-parasite interactions between Peninsular and Borneo, and the fundamental environmental factors that drive the dynamics of these ecological relationships.

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Electronic supplement

Appendix 1. Ectoparasite infestation rates and habitat types caught of rodents and scandents.

Appendix 2. Interaction frequencies of ectoparasites and their hosts compiled from 16 localities in Malaysia.

The file may be downloaded from the web site of the publisher at www.akademai.com.