

Research Article

Distribution and Ecological Niches of Gamasid Mites (Acari: Mesostigmata) on Small Mammals in Southwest China

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The ectoparasitic gamasid mites found on small mammals are important arthropods in the field of medical entomology. This paper studied the distribution and ecological niches of ectoparasitic gamasid mites on small mammal hosts in Yunnan Province of southwest China. Levins' niche breadth and Colwell-Futuyma's method were used to quantitatively evaluate host-specificity and similarity of host selection, and hierarchical analysis was used to illustrate niche overlap among gamasid mite species. Species diversity of both small mammals and gamasid mites was lower in indoor habitats than that in outdoor habitats. Most gamasid mite species were found on the body surface of the host species and niche breadths varied from species to species. A species with low niche breadth indicates high host specificity and most gamasid mites showed a relatively low niche overlap. The results suggest that a coevolutionary relationship may exist between some species of gamasid mites and their small mammal hosts.

1. Introduction

Ectoparasitic gamasid mites (Acari: Mesostigmata) on the body surface of small mammals (especially rodents and insectivores) are generally regarded as an important group of medical arthropods because some are suspected as potential vectors of more than 20 zoonoses. Besides dermatitis caused by feeding ectoparasitic gamasid mites, it has been proved that some gamasid mites could be vectors of rickettsial pox and hemorrhagic fever with renal syndrome (HFRS) [1–3]. Yunnan Province in southwest China (Figure 1) has been a persistent focal point for HFRS in recent years [4]. It is therefore deemed meaningful to investigate the distribution of ectoparasitic gamasid mites on small mammals in Yunnan Province. In recent years, Guo and his colleagues have made a series of studies on gamasid mites parasitic on small mammals in Yunnan, their research covered the fauna, geographical distribution, community structure, and other related issues concerning gamasid mites in that region [5–8]. Our intention was to expand on the distribution and ecological niches of ectoparasitic gamasid mites on small mammals ignored in Guo's former reports

by quantitatively evaluating host specificity and the possible coevolutionary relationship between ectoparasitic gamasid mites and their small mammal hosts. Mite ectoparasitism is a complicated phenomenon involving mutual adaptations between parasites and their hosts. As a result of long-term evolutionary and ecological processes, these complicated mutual interactions have important ecological and evolutionary implications [9, 10]. Parasitic species with high host specificity implies coevolution between parasites and hosts from an ecological view. Yet, host specificity is an ambiguous term that is difficult to quantitatively evaluate. We, therefore, introduce the concept of using the ecological niche to quantitatively evaluate host specificity of ectoparasitic gamasid mites [11–13]. On the basis of evaluating ecological niche and overlap, this paper also discusses co-evolution between selected, dominant species of ectoparasitic gamasid mites and their small mammal hosts in Yunnan Province.

2. Methods

2.1. Investigation Sites. The investigation compiled data came from 28 counties (28 investigation sites) in Yunnan

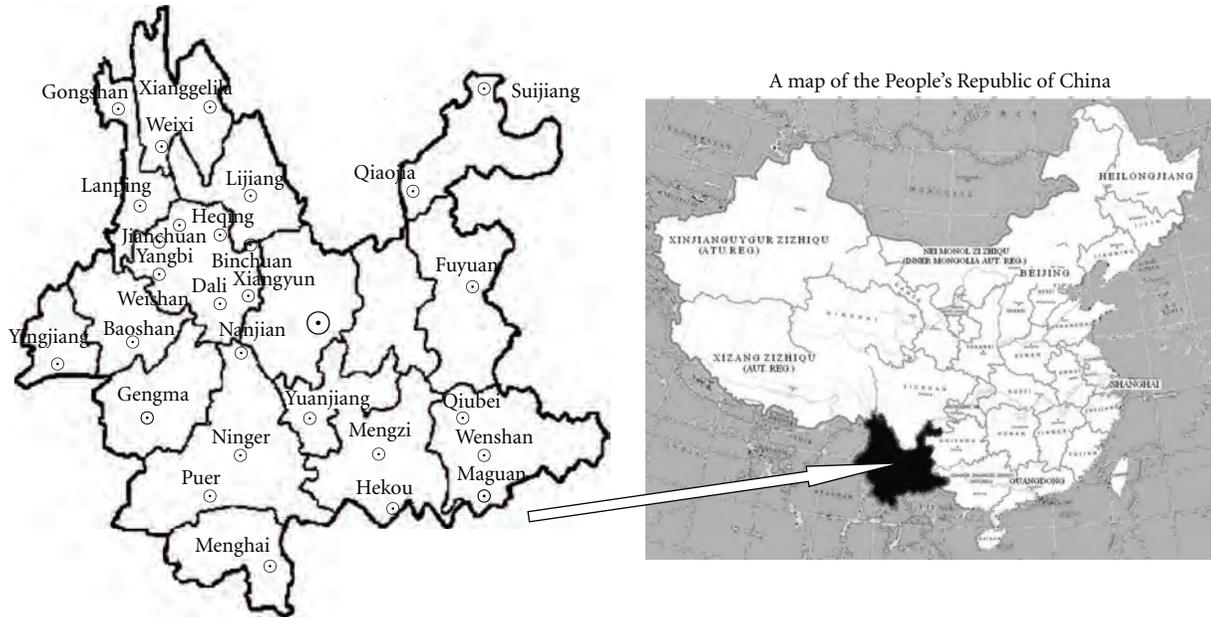


FIGURE 1: A map of Yunnan Province of China, showing the 28 investigated sites (28 counties).

Province ($97^{\circ}31'39'' \sim 106^{\circ}11'47''$ East longitude, $21^{\circ}8'32'' \sim 29^{\circ}15'8''$ North latitude), China. In the field investigation, small mammals were sampled yearly from 1990 to 2008 and surveys were conducted mainly from June to August each year. The 28 investigated sites (the animals captured from each county) included the counties of Baoshan (107), Yangbi (132), Jianchuan (668), Lijiang (377), Heqing (61), Xianggelila (317), Gongshan (795), Weishan (210), Nanjian (201), Puer (634), Ninger (113), Weixi (1560), Lanping (587), Dali (4142), Binchuan (523), Xiangyun (325), Wenshan (111), Qiubei (306), Mengzi (274), Yuanjiang (692), Fuyuan (450), Qiaojia (172), Suijiang (24), Yingjiang (116), Gengma (475), Maguan (112), Hekou (65), and Menghai (995) (Figure 1).

2.2. Trapping, Collection and Identification of Small Mammals, and Gamasid Mites. Small mammals (rodents, shrews, moles, sciurids, and lagomorphs) were captured with mousetraps or mouse cages ($10 \text{ cm} \times 11 \text{ cm} \times 24 \text{ cm}$) made by Guixi Mousetrap Apparatus Factory, Guixi, Jiangxi, China. In each investigated site, mousetraps were set in two different types of habitats, indoors (houses, stables, and stalls, etc.) and outdoors (garden, plowland, bush area, and forests). Each mousetrap was baited with a section cob of corn in the outdoors or a single oil-fried peanut in the indoors. The mousetraps randomly placed in a chosen habitat in the afternoon or evening and checked at dawn the next morning. Captured small mammal hosts were removed from traps, transferred to a white cloth bag in the field, and brought to the laboratory for mite inspection. In the laboratory, small mammals were inspected for mites after anesthetized with ether over a white tray. All gamasid mites found on the body surface of each host were collected and preserved in 70% ethanol. After gamasid mite inspection,

individual small mammal hosts were identified to species on the basis of morphological characteristics [14]. After the sample was processed, all instruments were cleaned with disposable paper towels to reduce the chance of cross contamination. After the investigation at one site, preserved individual mite samples were washed several times in water to remove the alcohol and mounted with Hoyer's medium on microscope slides. After clearing and drying, each mite specimen was identified to species under a microscope according to published keys [15].

2.3. Voucher Specimens. Representative voucher specimens of small mammal and gamasid mite were deposited in the specimen repository of Institute of Pathogens and Vectors, Dali University, China.

2.4. Distribution of Gamasid Mites. The constituent ratios (C_r) of every captured small mammal species and their associated gamasid mite species were calculated. We defined dominant species by the higher constituent ratio compared to common or rare species. Species that accounted for more than 0.1% of the constituent ratio in a community were determined as dominant. Together with the constituent ratio (C_r) of gamasid mites on a certain species of small mammal, mite infestation rates (the percentage of infested hosts with gamasid mites) and the mite abundance (MA , mean number of gamasid mites per host examined) were also calculated for each host species. The data were analyzed by using the Chi-square test.

2.5. Measurement of Ecological Niche and Overlap. Based on the constituent ratios of collected gamasid mites, 30 dominant mite species were chosen as the target mites for measurement of ecological niche and overlap. The total

constituent ratio of the 30 dominant mite species (target mite species) reached 97.68% and the rest 82 rare mite species were not considered because they were so rare. The 67 species of small mammals were regarded as 67 series of potential host resources. The individual distribution proportion (ratio) of each mite species on all 67 series of host resources was then calculated and regarded as the utilization proportion on host resources. Based on the utilization proportions, Levins' niche breadth was used to evaluate the host-specificity [16–18]:

$$B_i = \frac{1}{S \sum_{i=1}^s p_{in}^2}, \quad (1)$$

where B_i is Levins' niche breadth for mite species i while P_{in} is the utilization proportion of mite species i on host resource n (actually individual distribution proportion of mite species i on host resource n), and S the total series of host resources ($S = 67$ here, that is 67 species of small mammal hosts). A higher value of B_i for a certain gamasid mite species means a lower host specificity, and *vice versa*.

The following proportional similarity of niche by Colwell-Futuyma was used to measure niche overlap between two species of gamasid mites [19–21]:

$$C_{ij} = 1 - \frac{1}{2} \sum_{n=1}^S |P_{in} - P_{jn}|. \quad (2)$$

C_{ij} represents the proportional similarity of niche between every two species of gamasid mites (species i and j), P_{in} and P_{jn} are the utilization proportion of mite species i and j on host resource n , and S is the same as the previous formula. Values of C_{ij} range from 0 (no niche overlap) to 1 (complete overlap). Hierarchical analysis under SPSS 16.0 statistical software was used to illustrate the overall niche overlap among 30 gamasid mite species. Between-groups linkage method was used in the clustering process of hierarchical analysis, and the dendrogram was used to illustrate the clustering result.

All analyses were carried out in SPSS 16.0 for Windows (SPSS Inc., Chicago, IL, 2006).

3. Results

3.1. Collected Small Mammals and Gamasid Mites. A total of 14,544 individual small mammals were captured from 1990 to 2008 in the 28 counties (28 sampled sites) and identified as representing 10 families, 35 genera, and 67 species in five orders (Rodentia, Insectivora, Scandentia, Lagomorpha, and Carnivora). We collected 80,791 individual gamasid mites that were identified as 10 families, 33 genera, and 112 species.

3.2. Habitat Distribution of Small Mammals and Gamasid Mites. Species diversities of small mammals were much lower indoors than outdoors; that is, much fewer species were found in indoors than in outdoors ($\chi^2 = 55.537$, $df = 1$, $P < .001$). The individual abundance of small mammal hosts and gamasid mites, however, was much higher indoors than in outdoor habitats (i.e., much more individuals were found indoors than outdoors). Of 67 species of small mammal

hosts captured, for instance, only three species, *Rattus tanezumi*, *Rattus norvegicus*, and *Mus musculus*, dominated the indoor habitat, but their constituent ratios are relatively high (especially in *Rattus tanezumi*). The remaining 64 species of small mammal hosts were mainly distributed in outdoor habitats, but most of them had a relatively low constituent ratio (Table 1).

3.3. Mite Infestation of Small Mammals. The number of mite species on mammals varies from host species to species (from 3 to 50 species, $\chi^2 = 286.1$, $df = 33$, $P < .001$) and most mite species can parasitize a very wide range of hosts (from 2 to 31 species, $\chi^2 = 109.0$, $df = 29$, $P < .001$). The mite abundance of different host species also showed significant difference ($\chi^2 = 575.3$, $df = 33$, $P < .001$). Some species of small mammals were infested with a great number of gamasid mite individuals (high individual abundance) but lacked rich mite species (low species richness). Other hosts, however, harbored large numbers of gamasid mite species (high species richness), but had low overall numbers of mites (low individual abundance). For example, 50 species of gamasid mites (high mite species richness) were collected from a rodent host, *Apodemus chevrieri*, but infested individuals displayed low mite abundance (1.61 individual mites per host). The opposite situation, relatively low species richness of gamasid mites (16, 11, 29, 18, and 4 species of the mites, resp.) with high individual abundance of mites, happened in the following small mammal hosts: *Dremomys pernyi*, *Niviventer excelsior*, *Niviventer fulvescens*, *Berylmys bowersi* and *Niviventer eha* (Table 1).

Although some small mammals harbored large numbers of mite species, most individuals had one or more mite species as the dominant ectoparasitics. For example, *Mus pahari* is usually infested with *Laelaps guizhouensis* (80.92%), *Laelaps paucisetosa* (49.64%), and *Laelaps xingyiensis* (43.47%), while *Mus caroli* is usually infested with *Laelaps algericus* (52.13%) and the genus *Eothenomys* often harbors *Laelaps chini* (Table 3).

3.4. Distribution and Host Selection of Gamasid Mites. In this paper, only 30 dominant species of gamasid mites were chosen as target species and they accounted for 97.68% of the total mite species collected. The distribution and host selection of gamasid mites varied from species to species. Some gamasid mite species often parasitized one or two species of mammal hosts and examples include the following mite species: *L. paucisetosa*, *L. xingyiensis*, *Dipolaelaps anourosorecis*, and *Laelaps liui*. Other mite species, however, tended to select a wide range of hosts, and *L. turkestanicus* and *L. nuttalli* are examples (Table 2).

In our study, we found that some species achieve maximum individual abundant on certain host species, that is *L. liui* (97.86%) on the host *Berylmys bowersi* and *L. algericus* (97.10%) on the host *Mus caroli*, while *L. guizhouensis*, *L. paucisetosa*, and *L. xingyiensis* (97.92%, 98.48%, and 95.71%, resp.) were found on the same host *M. pahari* (Table 4). The results suggest that the distribution of gamasid mite species among different host species is quite uneven. Although most

TABLE 1: Dominant small mammal hosts captured and number of gamasid mite species collected in Yunnan Province of southwest China.

Names of dominant small mammal hosts	Number of hosts collected	Constituent ratios of the hosts (%)	Number of mite species	Number of mite individuals	Mite abundance	Habitat distribution of the hosts
<i>Rattus tanezumi</i>	3859	26.53	43	18459	4.78	Indoor
<i>Apodemus chevrieri</i>	1870	12.86	50	3018	1.61	Outdoor
<i>Eothenomys miletus</i>	1802	12.39	41	2258	1.25	Outdoor
<i>Rattus norvegicus</i>	1262	8.68	31	6102	4.84	Indoor
<i>Mus pahari</i>	697	4.79	34	13559	19.45	Outdoor
<i>Rattus nitidus</i>	580	3.99	32	11765	20.28	Outdoor
<i>Apodemus draco</i>	540	3.71	26	562	1.04	Outdoor
<i>Niviventer confucianus</i>	464	3.19	44	5394	11.63	Outdoor
<i>Mus caroli</i>	376	2.59	33	2258	6.01	Outdoor
<i>Apodemus sylvaticus</i>	280	1.93	20	501	1.79	Outdoor
<i>Apodemus latronum</i>	278	1.91	18	204	0.73	Outdoor
<i>Suncus murinus</i>	254	1.75	25	196	0.77	Outdoor
<i>Rattus rattus slandeni</i>	253	1.74	37	842	3.33	Outdoor
<i>Tupaia belangeri</i>	237	1.63	19	159	0.67	Outdoor
<i>Crocidura attenuata</i>	235	1.62	22	139	0.59	Outdoor
<i>Mus musculus</i>	210	1.44	12	156	0.74	Indoor
<i>Niviventer fulvescens</i>	197	1.35	29	7058	35.83	Outdoor
<i>Anourosorex squamipes</i>	151	1.04	24	2445	16.19	Outdoor
<i>Apodemus peninsulae</i>	105	0.72	13	75	5.77	Outdoor
<i>Dremomys pernyi</i>	96	0.66	16	880	55.00	Outdoor
<i>Micromys minutus</i>	83	0.57	13	133	10.23	Outdoor
<i>Callosciurus erythraeus</i>	72	0.50	11	140	12.73	Outdoor
<i>Eothenomys eleusjs</i>	67	0.46	13	326	25.08	Outdoor
<i>Eothenomys sp</i>	64	0.44	5	28	5.60	Outdoor
<i>Niviventer excelsior</i>	54	0.37	11	594	54.00	Outdoor
<i>Berylmys bowersi</i>	45	0.31	18	603	33.50	Outdoor
<i>Eothenomys protidor</i>	44	0.30	3	12	4.00	Outdoor
<i>Eothenomys custos</i>	38	0.26	12	245	20.42	Outdoor
<i>Nasillus gracilis</i>	33	0.23	15	165	11.00	Outdoor
<i>Sorex excelsus</i>	28	0.19	4	4	1.00	Outdoor
<i>Niviventer eha</i>	26	0.18	4	126	31.50	Outdoor
<i>Sciurotamias forresti</i>	23	0.16	4	16	4.00	Outdoor

TABLE 1: Continued.

Names of dominant small mammal hosts	Number of hosts collected	Constituent ratios of the hosts (%)	Number of mite species	Number of mite individuals	Mite abundance	Habitat distribution of the hosts
<i>Tamiops swinhoei</i>	18	0.12	3	39	13.00	Outdoor
<i>Ochotona thibetana</i>	14	0.10	5	6	1.20	Outdoor

Annotation: The remaining small mammal hosts whose constituent ratios were lower than 0.1% and are not included in Table 1 and had an outdoor distribution. The hosts not included in Table 1 are *Ochotona forresti*, *Trogopterus xanthipes*, *Crocidura dracula*, *Petaurista elegans*, *Pteromys volans*, *Soriculus caudatus*, *Bandicota indica*, *Eothenomys melanogaster*, *Microtus clarkei*, *Ochotona gaoligongensis*, *Soriculus leucops*, *Sorex bedfordiae*, *Callosciurus quinquestratus*, *Neotetracus sinensis*, *Apodemus agrarius*, *Pemurista atbiventer*, *Hylope alboniger*, *Arctonyx collaris*, *Parascaptor leucurus*, *Sorex cylindricalcauda*, *Mustela kathiah*, *Petaurista sp.*, *Niviventer andersoni*, *Belomys pearsoni*, *Petaurista xanthotis*, *Necmgale elegans*, *Dremomys lokriah*, *Tamias sibiricus*, *Ochotona Daurica*, *Vandeleuria oleracea*, *Vernaya fulva*, *Scaptonyx fuscicaudus* and Muridae spp.

TABLE 2: Host ranges and niche breadth of 30 dominant gamasid mites species on 67 species of small mammal hosts.

Dominant gamasid mite species	Codes of the mites species	Number of mite individuals	Constituent ratios of the mites (%)	Number of infested host species (host ranges)	Niche breadths
<i>Laelaps nuttalli</i>	1	20248	25.06	28	0.0397
<i>Laelaps echidninus</i>	2	15840	19.61	23	0.0622
<i>Laelaps guizhouensis</i>	3	10444	12.93	17	0.0156
<i>Laelaps turkestanicus</i>	4	6429	7.96	31	0.0402
<i>Laelaps traubi</i>	5	4165	5.16	25	0.0448
<i>Ornithonyssus bacoti</i>	6	3340	4.13	15	0.0360
<i>Laelaps chini</i>	7	2734	3.38	28	0.0450
<i>Dipolaelaps anourosorecis</i>	8	2358	2.92	15	0.0165
<i>Laelaps paucisetosa</i>	9	1979	2.45	9	0.0154
<i>Laelaps algericus</i>	10	1933	2.39	6	0.0158
<i>Hirstionyssus sunci</i>	11	1099	1.36	27	0.0880
<i>Laelaps xingyiensis</i>	12	955	1.18	8	0.0163
<i>Laelaps fukienensis</i>	13	923	1.14	10	0.0343
<i>Eulaelaps dremomydis</i>	14	832	1.03	13	0.0163
<i>Eulaelaps shanghaiensis</i>	15	815	1.01	9	0.0175
<i>Proctolaelaps pygmaeus</i>	16	689	0.85	24	0.0842
<i>Haemogamasus oliviformis</i>	17	651	0.81	23	0.1475
<i>Laelaps jettmari</i>	18	422	0.52	11	0.0186
<i>Laelaps jingdongensis</i>	19	410	0.51	12	0.0381
<i>Hypoaspis pavlovskii</i>	20	391	0.48	27	0.1646
<i>Laelaps liui</i>	21	374	0.46	2	0.0156
<i>Eulaelaps substabularis</i>	22	369	0.46	19	0.0606
<i>Haemolaelaps glasgowi</i>	23	290	0.36	14	0.1027
<i>Tricholaelaps myonyssognathus</i>	24	273	0.34	11	0.0230
<i>Liponyssoides muris</i>	25	244	0.30	7	0.0191
<i>Eulaelaps huzhuensis</i>	26	154	0.19	11	0.0731
<i>Haemogamasus dorsalis</i>	27	149	0.18	8	0.0429
<i>Hypoaspis miles</i>	28	138	0.17	17	0.0765
<i>Hypoaspis lubrica</i>	29	134	0.17	16	0.0420
<i>Androlaelaps singularis</i>	30	131	0.16	19	0.1566

of the gamasid mite species can parasitize many species of hosts, others have relatively fixed principal host specie.

3.5. Niche Breadth of Gamasid Mites. In the measurement of ecological niche, the individual distribution proportion (ratio) of each mite species on 67 series of host resources was used to calculate the breadth of gamasid mites. Most gamasid mite species could be found on the body surface of several host species (more than two host species at least) and niche breadths ranged from 0.0154 to 0.1646. Of the 30 mite species studied, *L. turkestanicus* was found on 31 species of small mammal hosts displaying the widest host range while *L. liui*, found on only two species of hosts, had the narrowest host range. The niche breadth of *H. pavlovskii* was the highest (0.1646) followed by *A. singularis* (0.1566) and *H. oliviformis* (0.1475). *L. paucisetosa* showed the narrowest niche breadth (0.0154). Niche breadth for the genus *Laelaps* was much narrower than the genus *Haemogamasus*. Although *L. turkestanicus* had the widest host range (found on 31 species of hosts), its niche breadth was relatively low (0.0402). In contrast, the host range of *A. singularis* was relatively narrow (on 18 host species), but its niche breadth was relatively high (0.1566). The niche breadth of gamasid mites does not seem to match their respective host range (Table 2).

3.6. Niche Overlap of Gamasid Mites. Three species of gamasid mites (*L. guizhouensis*, *L. paucisetosa*, and *L. xingyiensis*) tended to choose the same mammal species (*Mus pahari*) as their principle host. Those three mite species showed niche values with a high degree of overlap (from 0.96 to 0.99). Comparison of gamasid mites species showed a relatively low niche value overlap (≤ 0.50). The higher overlapping values beyond 0.50 only happened in 8.28% of the mite species. Some niche overlaps were almost zero, which happened in *D. anourosorecis*, *L. algericus*, *E. dremomydis*, *L. liui*, and so forth (Table 5). A low niche overlap usually indicates that the compared species have formed a niche separation in host selection. The complicated niche overlaps among 30 of the gamasid mite species we studied were illustrated by hierarchical clustering analysis. The 30 species of gamasid mites were classified into 15 niche overlapping groups when $\lambda = 5.0$ in the clustering dendrogram (Figure 2, Table 6). The gamasid mites within the same group tended to parasitize the same hosts (Table 6).

4. Discussion

4.1. Species of Ectoparasitic Gamasid Mites. Mite assemblages on small mammalian hosts are strongly influenced by the ecological habitat of their hosts [22]. Generally speaking, broad-ranging mammals should acquire more species of ectoparasites because a larger geographical range implies occupation of different habitats, a higher probability of contact with a larger number of other species, and this should lead to higher parasite species richness [23]. Additionally, from the parasite perspective, a large geographic range should indicate that a parasitic species has a larger number of

possible hosts, increasing the likelihood that more parasites become established [24]. Yunnan Province is a big province with accompanying altitude gradients and topographical variation providing complicated ecological landscapes and habitats. Plant and animal resources are abundant in Yunnan Province, which is often described as “the kingdom of plants and animals” in China. Although the field investigation in this paper involved 28 counties in Yunnan Province, it is impossible to cover all the complicated situations in all areas and habitats. As a broad-ranging investigation, we have accumulatively captured 67 species and 14,544 individual small mammals. From those 67 mammal species, 80,791 individual gamasid mites belonging to 10 families, 33 genera, and 112 species were collected. These numbers imply a high species diversity of gamasid mites in Yunnan Province. Thirty of the 112 gamasid mite were determined as dominant species. When the investigation is further extended, the individuals of some rare hosts will increased and therefore some rare species of gamasid mites on them will be probably found. The major dominant species of gamasid mites, however, should be stable and unchangeable because of the big host samples (14 544 individual small mammals). The results imply that Yunnan Province of China is rich in species of gamasid mites with high species diversity and it is a valuable research place. The outdoor habitats provided richer species diversity of both small mammals and gamasid mites compared to the indoor habitats. The species diversity of ectoparasitic gamasid mites is prominently influenced by the species diversity of their small mammal hosts.

4.2. Ecological Niche and Host Specificity of Gamasid Mites. Small mammals are the food resource of ectoparasitic gamasid mites that consume the blood or body fluids from their hosts. The host range and Levins' niche breadth should provide values opposite host specificity for ectoparasitic gamasid mites that use the hosts as their principle food resource [11–13]. The host range is defined as the number of host species parasitized by a particular ectoparasitic gamasid mite species. The host range could reflect the host specificity to some degree, but it only reflects the number of host species and does not consider the distribution of mite individuals among host species, which can cause some bias in the evaluation of specificity. In comparison with the host range, Levins' niche breadth is much more accurate for evaluation of ectoparasitic host specificity [12, 13]. A higher niche breadth usually indicates a lower host specificity, and *vice versa*. Ectoparasitic gamasid mites with low host specificity will naturally increase the opportunity of transmitting zoonoses assuming that they frequently change feeding sites (new host).

4.3. Ecological Niche and Coevolution. Host specificity is the result of co-evolution between the parasite and their host and a high specificity often indicates a high degree of co-evolution. Therefore the niche breadth can also be used to demonstrate co-evolution between ectoparasites and their hosts [25]. A narrow niche breadth indicates a higher degree of co-evolution between the mite and their host,

TABLE 3: The mite infestation rates of small mammals with 30 dominant gamasid mite species.

Dominant host species	Infestation rate of 30 dominant mite species (%)																														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	
<i>Rattus tanezumii</i>	22.49	26.79	0.08	0.10	0.10	7.62	0.05	0.00	0.00	0.05	1.68	0.03	0.00	0.00	0.00	1.55	0.00	0.00	0.00	0.31	0.00	0.00	0.13	2.23	1.22	0.00	0.03	0.75	0.88	0.16	
<i>Apodemus chevrieri</i>	1.66	1.39	0.43	0.96	0.96	0.16	1.18	0.32	0.21	0.00	6.04	0.05	0.00	0.00	4.33	1.98	3.37	5.99	2.57	2.19	0.00	2.94	0.64	0.16	0.00	0.70	0.00	0.43	0.37	0.43	
<i>Eothenomys nitidus</i>	0.39	0.44	0.55	0.61	1.28	0.06	28.25	0.00	0.39	0.00	0.89	0.00	0.06	0.06	0.44	1.55	5.38	0.22	0.50	2.55	0.00	0.78	1.17	0.00	0.00	1.78	0.33	0.39	0.06	0.28	
<i>Rattus norvegicus</i>	16.64	20.44	0.16	0.32	0.32	10.70	0.48	0.00	0.08	0.32	3.25	0.16	0.00	0.08	2.14	0.24	0.08	0.16	0.55	0.00	0.16	0.24	0.63	0.24	0.08	0.00	0.08	0.16	0.40	0.40	
<i>Mus pahari</i>	0.00	1.00	80.92	1.58	0.00	0.00	0.72	0.14	49.64	0.72	2.44	43.47	0.14	0.14	0.00	1.87	1.00	0.14	0.00	1.72	0.00	0.29	0.00	0.00	0.00	0.00	1.15	2.15	0.57	1.15	
<i>Rattus nitidus</i>	47.07	67.76	0.17	1.03	0.34	0.52	0.69	0.00	0.17	0.00	8.97	0.00	0.17	0.00	8.28	0.34	0.00	0.00	2.24	0.00	0.17	0.34	1.38	0.52	0.00	0.00	0.34	0.34	1.21	1.21	
<i>Apodemus draco</i>	0.19	0.19	0.00	2.41	5.00	0.56	5.37	0.00	0.00	0.00	0.37	0.00	0.00	0.00	0.19	0.56	8.33	0.00	22.04	1.48	0.00	3.33	0.00	0.00	0.00	5.74	0.00	0.00	0.00	0.19	
<i>Niviventer confucianus</i>	1.29	26.08	0.65	50.43	40.95	0.22	1.94	0.22	0.00	0.00	1.51	0.22	4.09	0.43	0.22	2.37	3.88	0.00	1.72	5.17	0.65	0.65	0.22	0.43	0.00	1.29	0.00	0.43	0.65	1.29	
<i>Mus caroli</i>	4.79	0.80	2.13	1.33	0.00	0.27	0.80	0.00	0.53	52.13	0.53	2.13	0.00	0.00	0.00	3.19	0.00	0.53	0.00	1.06	0.00	5.32	0.27	1.06	0.00	0.00	0.00	4.26	0.53	0.80	
<i>Apodemus sylvaticus</i>	10.36	2.14	1.43	2.14	0.71	0.00	1.43	0.71	0.00	0.00	2.14	0.00	0.00	0.00	0.00	1.07	6.43	4.29	6.07	2.86	0.00	5.36	0.71	0.00	0.00	3.57	0.36	0.00	0.00	0.36	
<i>Apodemus latronum</i>	3.96	0.36	0.00	0.00	0.36	0.00	1.08	0.00	0.36	0.00	3.60	0.00	0.00	0.36	1.44	0.00	5.76	1.08	10.43	1.08	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Suncus murinus</i>	9.06	1.97	0.39	0.39	0.00	2.36	0.79	1.18	0.00	0.00	1.57	0.00	0.00	0.00	0.00	3.54	0.39	0.00	0.00	2.36	0.00	0.00	0.00	1.57	0.00	0.00	0.00	2.36	2.36	2.36	
<i>Rattus rattus</i>	20.16	15.02	1.19	6.32	1.98	2.77	0.40	0.40	0.00	0.00	8.30	0.00	0.00	0.00	0.79	3.16	1.98	0.00	0.00	3.16	0.00	1.19	0.79	0.40	0.79	0.00	0.00	2.37	1.58	3.56	
<i>standeni</i>	0.84	1.69	0.42	0.84	1.69	0.84	0.42	0.42	0.00	0.00	2.11	0.00	0.00	0.42	0.00	0.00	0.00	0.00	0.84	0.00	0.00	0.00	0.00	0.42	0.00	0.00	0.00	0.42	0.42	0.42	
<i>Tupaia belangeri</i>	3.83	2.13	0.43	0.43	0.00	2.98	0.43	0.85	0.00	0.00	3.40	0.00	0.00	0.00	0.00	0.85	0.00	0.43	0.00	0.85	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.43	0.43	0.43	
<i>Crocodyra attenuata</i>	1.43	2.86	0.95	0.48	0.00	4.76	0.00	0.00	0.48	0.95	0.00	0.00	0.00	0.00	0.00	0.95	0.00	0.00	0.00	0.00	0.00	0.00	0.48	0.00	0.48	0.00	0.00	0.48	0.48	0.00	
<i>Mus musculus</i>	5.08	56.35	0.00	67.01	40.61	0.00	0.00	0.00	0.51	0.00	4.57	0.51	5.08	0.00	0.00	2.54	1.02	0.00	0.00	1.52	0.00	1.02	0.51	0.00	0.00	0.00	0.00	0.51	0.51	0.00	0.00
<i>Niviventer fulvescens</i>	1.32	3.31	0.00	0.66	0.00	0.00	0.66	35.76	0.00	0.00	3.97	0.00	0.00	0.00	0.00	0.66	3.31	0.00	0.00	4.64	0.00	0.00	1.32	0.00	0.00	0.00	0.00	0.66	0.00	2.65	
<i>Anourosorex squamipes</i>	0.95	0.00	0.00	2.86	0.00	0.95	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.95	0.95	4.76	12.38	0.00	10.48	0.95	0.00	2.86	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Apodemus peninsulae</i>	0.00	0.00	0.00	4.17	5.21	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	53.13	0.00	0.00	1.04	0.00	2.08	1.04	0.00	0.00	0.00	0.00	0.00	0.00	3.13	0.00	1.04	1.04
<i>Dromomys pernyi</i>	4.82	7.23	3.61	2.41	0.00	0.00	2.41	0.00	0.00	1.20	1.20	10.84	0.00	0.00	2.41	1.20	1.20	2.41	0.00	0.00	0.00	0.00	0.00	4.82	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Micromys minutus</i>	1.39	0.00	0.00	0.00	12.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.56	0.00	0.00	2.78	0.00	1.39	0.00	0.00	0.00	0.00	0.00	0.00	1.39	0.00	0.00	0.00	0.00
<i>Callosciurus erythraeus</i>	1.49	0.00	0.00	0.00	1.49	0.00	43.28	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.48	1.49	2.99	1.49	2.99	0.00	4.48	0.00	0.00	0.00	0.00	1.49	1.49	0.00	0.00	0.00
<i>Eothenomys clevisi</i>	0.00	0.00	0.00	0.00	0.00	0.00	1.56	0.00	0.00	0.00	1.56	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.13	0.00	0.00	0.00	1.56	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Eothenomys sp</i>	3.70	16.67	0.00	44.44	51.85	1.85	3.70	0.00	0.00	0.00	1.85	0.00	12.96	0.00	0.00	0.00	0.00	0.00	0.00	5.56	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.85	0.00	0.00	0.00
<i>Niviventer excelsior</i>	0.00	2.22	4.44	8.89	4.44	0.00	0.00	8.89	0.00	0.00	6.67	0.00	0.00	0.00	0.00	6.67	0.00	0.00	0.00	6.67	66.67	0.00	0.00	0.00	0.00	0.00	0.00	2.22	0.00	4.44	4.44
<i>Berythius bowersi</i>	0.00	0.00	0.00	0.00	0.00	0.00	4.55	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.55	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Eothenomys protidior</i>	2.63	0.00	0.00	0.00	0.00	52.63	2.63	0.00	0.00	2.63	0.00	0.00	0.00	0.00	0.00	15.79	0.00	0.00	0.00	0.00	2.63	0.00	0.00	0.00	0.00	0.00	13.16	0.00	0.00	0.00	0.00
<i>Eothenomys custos</i>	6.06	0.00	0.00	0.00	0.00	3.03	9.09	0.00	0.00	3.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.57	0.00	3.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Nasillus gracilis</i>	0.00	0.00	0.00	0.00	0.00	3.57	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.57	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Sorex excelsus</i>	0.00	0.00	0.00	0.00	15.38	3.85	0.00	3.85	0.00	0.00	0.00	0.00	34.62	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Niviventer eha</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Sciurotamias forresti</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.35	8.70	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.35	4.35
<i>Tamias swinhoei</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	22.22	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Ochotona thibetana</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	7.14	0.00	0.00	0.00	0.00	7.14	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Annotation: The rest small mammal hosts whose constituent ratios lower than 0.1% were not included in Table 2. The species codes of 30 dominant gamasid mite species are the same as those in Table 2.

TABLE 4: The distribution of 30 dominant species of gamasid mites on dominant small mammal hosts.

Dominant host species	Constituent ratios of 30 dominant mite species (%)																														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	
<i>Rattus tanezumii</i>	52.83	32.75	0.04	1.07	2.06	41.74	0.11	0.00	0.00	0.10	11.92	0.10	0.00	0.00	0.00	23.95	0.00	0.00	0.00	3.58	0.00	0.00	3.79	79.85	88.11	0.00	0.67	33.33	57.46	6.87	
<i>Apodemus chevrieri</i>	0.75	1.98	0.47	2.29	1.34	0.15	2.21	0.38	0.30	0.00	33.58	0.10	0.00	0.00	92.27	5.81	20.89	89.34	26.59	17.65	0.00	35.50	21.03	1.10	0.00	11.04	0.00	9.42	8.96	10.69	
<i>Eothenomys miletus</i>	0.03	0.39	0.05	0.23	0.89	0.03	55.72	0.00	0.15	0.00	2.09	0.00	0.33	0.48	2.45	2.03	20.28	1.18	3.90	16.88	0.00	0.54	12.07	0.00	0.00	24.68	55.70	4.35	0.75	5.34	
<i>Rattus norvegicus</i>	12.08	10.32	0.05	0.20	0.12	48.71	0.72	0.00	0.10	0.47	11.46	0.42	0.00	0.00	0.25	12.48	2.00	0.24	0.49	2.81	0.00	0.54	1.03	3.66	1.23	0.65	0.00	0.72	5.97	9.16	
<i>Mus pahari</i>	0.00	0.14	97.92	0.59	0.00	0.00	1.30	0.08	98.48	1.09	5.64	95.71	0.22	2.04	0.00	2.61	1.84	0.00	0.00	3.58	0.00	0.81	0.00	0.00	0.00	0.00	17.45	15.94	2.99	14.50	
<i>Rattus nitidus</i>	28.62	32.94	0.12	0.11	0.19	4.07	0.20	0.00	0.25	0.00	12.74	0.00	3.79	0.00	0.00	31.06	0.46	0.24	0.00	6.65	0.00	0.27	28.97	6.59	1.64	0.00	0.00	1.45	2.99	9.16	
<i>Apodemus draco</i>	0.04	0.01	0.00	0.44	0.96	0.30	1.30	0.00	0.00	0.00	0.18	0.00	0.00	0.00	0.37	0.87	8.76	0.00	53.66	3.07	10.84	0.00	0.00	0.00	0.00	32.47	0.00	0.00	0.76		
<i>Niviventer confucianus</i>	0.17	7.46	0.11	37.74	32.03	0.09	0.43	0.04	0.00	0.00	1.18	0.10	23.62	0.24	0.12	2.32	3.07	0.00	2.20	6.91	2.14	0.54	0.34	0.73	0.00	5.19	0.00	2.17	3.73	6.11	
<i>Mis caroli</i>	0.89	0.04	0.26	0.50	0.00	0.03	0.07	0.00	0.35	97.10	0.36	2.20	0.00	0.00	0.00	2.61	0.00	1.18	0.00	1.02	0.00	0.00	0.69	1.83	0.00	0.00	0.00	20.29	1.49	3.05	
<i>Apodemus sylvaticus</i>	0.60	0.28	0.48	0.48	0.05	0.00	0.00	0.21	0.00	0.00	0.55	0.00	0.00	0.00	0.00	0.44	4.61	5.45	9.76	3.07	0.00	31.71	0.69	0.00	0.00	0.00	0.67	0.00	0.00	0.76	
<i>Apodemus latronum</i>	0.14	0.01	0.00	0.00	0.05	0.00	0.18	0.00	0.05	0.00	1.82	0.00	0.00	0.12	1.23	0.00	5.22	0.95	13.90	1.02	0.00	8.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
<i>Sorex murinus</i>	0.23	0.06	0.01	0.03	0.00	0.39	0.11	0.38	0.00	0.00	0.91	0.00	0.00	0.00	0.00	2.03	0.15	0.00	0.00	2.81	0.00	0.00	0.00	5.13	0.00	0.00	0.00	4.35	8.21	6.11	
<i>Rattus rattus slandeni</i>	1.19	1.17	0.04	2.58	0.19	0.42	0.04	0.04	0.00	0.00	8.55	0.00	0.00	0.00	0.25	1.89	1.23	0.00	0.00	5.37	0.00	1.08	0.69	0.37	2.05	0.00	0.00	5.80	4.48	16.79	
<i>Tupia belangeri</i>	0.01	0.03	0.01	0.08	0.58	0.24	0.04	0.00	0.00	0.00	1.00	0.00	0.00	0.60	0.00	0.00	0.00	0.00	0.77	0.00	0.00	0.00	0.00	0.00	6.15	0.00	0.00	0.00	0.75	0.76	
<i>Crocidura ateruata</i>	0.14	0.10	0.02	0.08	0.00	0.30	0.11	0.17	0.00	0.00	1.09	0.00	0.00	0.00	0.00	3.05	0.00	0.71	0.00	0.51	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.72	0.75	1.53	
<i>Mis musculus</i>	0.05	0.06	0.02	0.02	0.00	3.08	0.00	0.00	0.05	1.19	0.00	0.00	0.00	0.00	0.00	0.29	0.00	0.00	0.00	0.00	0.00	0.34	0.00	0.41	0.00	0.00	0.00	0.00	0.75	0.00	
<i>Niviventer fulvescens</i>	0.08	8.64	0.00	47.51	47.32	0.00	0.00	0.00	0.05	0.00	0.36	0.10	60.78	0.00	0.00	1.31	0.92	0.00	0.00	0.77	0.00	3.25	1.03	0.00	0.00	0.00	0.67	0.72	3.73	0.00	
<i>Anourosorex squamipes</i>	0.16	0.32	0.00	0.02	0.00	0.00	0.51	95.12	0.00	0.00	3.91	0.00	0.00	0.00	0.00	0.29	0.92	0.00	0.00	2.05	0.00	0.00	1.38	0.00	0.00	0.00	0.00	0.72	0.00	3.05	
<i>Apodemus peninsulae</i>	0.00	0.00	0.00	0.05	0.00	0.03	0.18	0.00	0.00	0.00	0.00	0.00	0.00	0.12	0.12	0.87	2.15	0.00	4.15	0.26	0.00	0.81	0.00	0.00	0.00	11.69	0.00	0.00	0.00	0.00	
<i>Dremomys pernyi</i>	0.00	0.00	0.00	0.20	0.19	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	95.79	0.00	0.00	0.15	0.00	0.49	2.05	0.00	0.00	0.00	0.00	0.00	0.00	2.68	0.00	0.75	1.53
<i>Micromys minutus</i>	0.24	0.13	0.06	0.00	0.00	0.00	0.07	0.00	0.00	0.05	0.09	1.36	0.00	0.00	2.94	0.15	0.15	0.47	0.00	0.00	0.00	0.00	0.00	4.40	0.00	0.00	0.00	0.00	0.00	0.00	
<i>Callosciurus erythraeus</i>	0.01	0.00	0.00	0.03	1.22	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.84	0.00	0.00	0.31	0.00	0.00	0.26	0.00	0.00	0.00	0.00	0.00	0.00	0.67	0.00	0.00	0.00	
<i>Eothenomys eleusis</i>	0.00	0.00	0.00	0.00	0.05	0.00	0.00	9.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.29	0.15	0.24	0.24	0.51	0.00	0.54	0.00	0.00	0.00	0.00	0.00	0.72	0.75	0.00	
<i>Eothenomys sp</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.80	0.00	0.00	0.27	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.26	0.00	0.00	0.00	0.37	0.00	0.00	0.00	0.00	0.00	0.00	
<i>Niviventer excelsior</i>	0.03	0.14	0.00	3.92	6.87	0.00	0.36	0.04	0.00	0.00	0.09	0.00	0.65	0.00	0.00	0.00	0.00	0.00	0.00	1.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.72	0.00	0.00	
<i>Berythius bowersi</i>	0.00	0.17	0.02	0.22	0.05	0.00	0.00	0.68	0.00	0.00	0.64	0.00	0.00	0.00	0.00	0.58	0.00	0.00	0.00	10.74	97.86	0.00	0.00	0.00	0.00	0.00	0.00	0.72	0.00	1.53	
<i>Eothenomys protidori</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.18	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.07	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
<i>Eothenomys custos</i>	0.00	0.00	0.00	0.00	0.00	0.00	6.44	0.55	0.00	0.00	0.09	0.00	0.00	0.00	0.00	0.00	3.38	0.00	0.00	0.00	0.54	0.00	0.00	0.00	0.00	0.00	8.05	0.00	0.00	0.00	
<i>Nasillus gracilis</i>	0.01	0.00	0.00	0.00	0.00	0.00	0.36	0.51	0.00	0.00	0.18	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.26	0.00	0.27	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
<i>Sorex excelsus</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.26	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
<i>Niviventer eha</i>	0.00	0.00	0.00	0.61	0.02	0.00	0.04	0.00	0.00	0.00	0.00	0.00	9.21	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
<i>Sciurotamias forresti</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.11	0.24	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.76	
<i>Tamopsis swinhoeti</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.60	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
<i>Ochetona tibetana</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.15	0.00	0.00	0.00	0.27	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	

Annotation: The species codes of 30 dominant gamasid mite species are the same as those in Table 2.

TABLE 5: Niche overlaps among 30 species of gamasid mites.

Gamasid Code	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30						
1	<i>Laelaps nuttalli</i>	1																																		
2	<i>Laelaps</i>	0.77	1																																	
3	<i>Laelaps</i>	0.03	0.03	1																																
4	<i>Laelaps</i>	0.06	0.23	0.03	1																															
5	<i>Laelaps</i>	0.06	0.23	0.02	0.89	1																														
6	<i>Laelaps</i>	0.60	0.50	0.01	0.03	0.05	1																													
7	<i>Laelaps</i>	0.11	0.14	0.10	0.13	0.14	0.10	1																												
8	<i>Laelaps</i>	0.02	0.03	0.02	0.02	0.02	0.01	0.11	1																											
9	<i>Laelaps</i>	0.02	0.03	<u>0.99</u>	0.02	0.02	0.01	0.10	0.01	1																										
10	<i>Laelaps</i>	0.02	0.02	0.02	0.02	0.01	0.02	0.10	0.01	0.02	1																									
11	<i>Laelaps</i>	0.41	0.43	0.08	0.11	0.09	0.30	0.17	0.07	0.07	0.02	1																								
12	<i>Laelaps</i>	0.03	0.02	<u>0.96</u>	0.02	0.02	0.01	0.10	0.01	<u>0.96</u>	0.04	0.07	1																							
13	<i>Laelaps</i>	0.05	0.22	0.01	0.73	0.73	0.04	0.10	0.01	0.01	0.00	0.06	0.00	1																						
14	<i>Laelaps</i>	0.01	0.02	0.00	0.01	0.04	0.01	0.09	0.01	0.00	0.00	0.02	0.00	0.01	1																					
15	<i>Laelaps</i>	0.03	0.04	0.01	0.04	0.04	0.01	0.14	0.01	0.01	0.00	0.38	0.02	0.01	0.01	1																				
16	<i>Laelaps</i>	0.72	0.77	0.07	0.14	0.13	0.45	0.20	0.05	0.07	0.07	0.56	0.08	0.11	0.03	0.12	1																			
17	<i>Laelaps</i>	0.19	0.25	0.16	0.23	0.23	0.16	0.48	0.15	0.15	0.14	0.47	0.15	0.18	0.14	0.38	0.35	1																		
18	<i>Laelaps</i>	0.04	0.05	0.02	0.04	0.04	0.01	0.12	0.01	0.01	0.01	0.38	0.02	0.01	0.01	0.92	0.13	0.41	1																	
19	<i>Laelaps</i>	0.04	0.01	0.06	0.01	0.01	0.06	0.06	0.07	0.07	0.24	0.07	0.05	0.06	0.21	0.06	0.50	0.26	1																	
20	<i>Laelaps</i>	0.26	0.35	0.13	0.26	0.26	0.20	0.42	0.12	0.13	0.11	0.58	0.13	0.21	0.12	0.30	0.45	0.74	0.33	0.29	1															
21	<i>Laelaps</i>	0.01	0.04	0.00	0.02	0.03	0.00	0.08	0.01	0.00	0.00	0.02	0.00	0.02	0.00	0.00	0.05	0.15	0.00	0.05	0.10	1														
22	<i>Laelaps</i>	0.06	0.12	0.04	0.11	0.10	0.04	0.18	0.04	0.04	0.03	0.43	0.03	0.06	0.03	0.40	0.18	0.60	0.45	0.52	0.40	0.02	1													
23	<i>Laelaps</i>	0.51	0.54	0.15	0.20	0.21	0.23	0.38	0.16	0.15	0.15	0.58	0.15	0.19	0.14	0.37	0.61	0.64	0.37	0.29	0.67	0.14	0.40	1												
24	<i>Laelaps</i>	0.64	0.44	0.01	0.02	0.03	0.48	0.08	0.01	0.01	0.00	0.24	0.01	0.02	0.02	0.41	0.15	0.01	0.07	0.25	0.02	0.02	0.25	1												
25	<i>Laelaps</i>	0.58	0.38	0.00	0.04	0.04	0.46	0.09	0.01	0.01	0.18	0.00	0.02	0.01	0.00	0.32	0.15	0.00	0.07	0.17	0.00	0.04	0.21	0.81	1											
26	<i>Laelaps</i>	0.02	0.10	0.01	0.09	0.10	0.01	0.37	0.01	0.01	0.00	0.15	0.01	0.06	0.01	0.14	0.15	0.58	0.12	0.44	0.45	0.02	0.26	0.37	0.00	0.01	1									
27	<i>Laelaps</i>	0.09	0.10	0.25	0.10	0.11	0.07	0.78	0.08	0.24	0.08	0.16	0.24	0.08	0.11	0.09	0.16	0.43	0.08	0.01	0.39	0.07	0.12	0.34	0.05	0.07	0.31	1								
28	<i>Laelaps</i>	0.38	0.42	0.15	0.11	0.09	0.35	0.17	0.01	0.15	0.20	0.40	0.17	0.04	0.01	0.11	0.48	0.34	0.11	0.03	0.45	0.01	0.14	0.34	0.40	0.36	0.15	0.27	1							
29	<i>Laelaps</i>	0.65	0.53	0.03	0.14	0.12	0.52	0.12	0.00	0.03	0.02	0.40	0.04	0.09	0.00	0.08	0.52	0.30	0.10	0.03	0.43	0.01	0.16	0.32	0.69	0.62	0.12	0.10	0.58	1						
30	<i>Laelaps</i>	0.31	0.39	0.18	0.17	0.16	0.24	0.22	0.07	0.18	0.07	0.62	0.19	0.12	0.05	0.16	0.52	0.41	0.16	0.09	0.63	0.04	0.19	0.48	0.26	0.14	0.25	0.31	0.54	0.46	1					

TABLE 6: Niche overlapping groups of gamasid mites.

Niche overlapping groups	Species of gamasid mites (Code)	Corresponding main hosts
Group 1	<i>L. guizhouensis</i> (3), <i>L. paucisetosa</i> (9), <i>L. xingyiensis</i> (12)	<i>M. pahari</i>
Group 2	<i>D. anourosorecis</i> (8)	<i>A. squamipes</i>
Group 3	<i>E. dremomydis</i> (14)	<i>D. pernyi</i>
Group 4	<i>L. liui</i> (21)	<i>B. bowersi</i>
Group 5	<i>L. algericus</i> (10)	<i>M. caroli</i>
Group 6	<i>L. turkestanicus</i> (4), <i>L. traubi</i> (5), <i>L. fukienensis</i> (13)	<i>N. fulvescens</i> <i>N. confucianus</i>
Group 7	<i>L. echidninus</i> (2), <i>P. pygmaeus</i> (16), <i>L. nuttalli</i> (1)	<i>R. nitidus</i> <i>R. tanezumi</i> <i>R. norvegicus</i>
Group 8	<i>T. myonysofnathus</i> (24), <i>L. muris</i> (25), <i>H. lubrica</i> (29), <i>O. bacoti</i> (6)	<i>R. tanezumi</i>
Group 9	<i>H. oliviformis</i> (17), <i>H. pavlovskii</i> (20), <i>H. glasgowi</i> (23)	<i>A. chevrieri</i> <i>E. miletus</i>
Group 10	<i>H. sunci</i> (11), <i>A. singularis</i> (30)	<i>A. chevrieri</i>
Group 11	<i>H. miles</i> (28)	<i>R. tanezumi</i> <i>M. caroli</i>
Group 12	<i>L. chini</i> (7), <i>H. dorsalis</i> (27)	<i>E. miletus</i>
Group 13	<i>E. shanghaiensis</i> (15), <i>L. jettmari</i> (18)	<i>A. chevrieri</i>
Group 14	<i>L. jingdongensis</i> (19), <i>E. substabularis</i> (22)	Genus <i>Apodemus</i>
Group 15	<i>E. huzhuensis</i> (26)	<i>A. draco</i>

and *vice versa*. A few species of ectoparasitic gamasid mites have developed an adequate co-evolutionary relationship with their hosts because of the high host specificity. The specificity of most ectoparasitic gamasid mites, however, is relatively low and it suggests that the co-evolution between gamasid mites and their hosts has not well developed. Most gamasid mite species in genus *Laelaps* prefer to live on the body surface of the host while species in genus *Haemogamasus* tends to live in the host nests. The niche breadths of *Laelaps* were much narrower than those of *Haemogamasus*, suggesting a high degree of co-evolution between the host-living *Laelaps* compared with the nest dwelling *Haemogamasus*. Examples of nest dwelling mites in genus *Haemogamasus* are *H. pavlovskii*, *H. oliviformis*, and *H. glasgowi*, and they show broad niche breadths.

4.4. Niche Overlap and Host Selection. Niche overlap estimates can approximate the degree that certain species partition resources within a certain community. Niche

overlap measures the degree to which two different species share a particular resource and it reflects, in the case of gamasid mites, on small mammal hosts similarities of host resource utilization between two mites species in a certain community. When the host species are regarded as the food resource, a high niche overlap between any two mite species means that these species tend to choose the same or similar small mammal species, especially their dominant hosts. In contrast, a low niche overlap between any two mite species usually indicates a low similarity in host selection. The results showed that *L. guizhouensis*, *L. paucisetosa*, and *L. xingyiensis* had a high niche overlap values that indicated similar host selection. The common dominant host of *L. guizhouensis*, *L. paucisetosa*, and *L. xingyiensis* was *M. pahari*. The 30 species of gamasid mites were classified into 15 niche overlapping groups using the value of $\lambda = 5.0$ in the clustering dendrogram. Gamasid mites within the same group tended to parasitize the same hosts, especially the dominant ones. Most species of gamasid mites, however, showed relatively

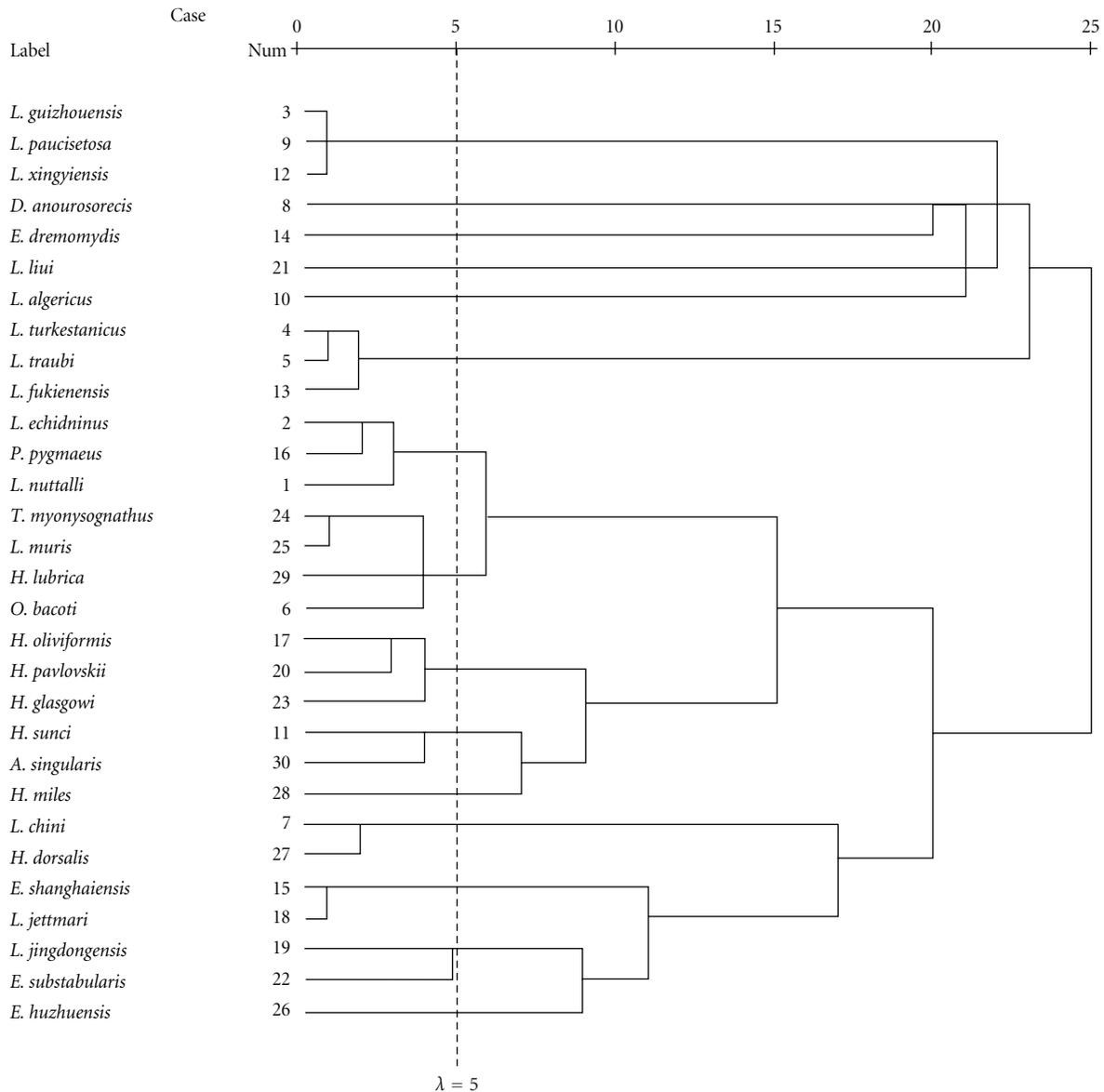


FIGURE 2: The hierarchical cluster dendrogram of 30 mite species based on the Euclidean distance.

low niche overlaps, and higher overlapping values (beyond 0.50) only happened in 8.28% of the mite species. Some niche overlaps were almost zero, as in *D. anourosorecis*, *L. algericus*, *E. dremomydis*, and *L. liui*. The results indicate that some species of gamasid mites have developed a mechanism of niche separation to avoid competition for the same host resources. Those gamasid mites tend to be parasitic on a distinct host species, leading to the niche separation. Niche separation is actually the process of natural selection, which drives competing species into using different hosts. High niche overlap often results from strong competition or repellency; yet the end result of niche separation can be an observed decrease in competition or avoidance. Some species with high overlap values should interact as competitors or intraguild predators, while other species with low pairwise overlap values are nonetheless vulnerable to the effects of

diffuse competition [26]. In considering the relationship between niche overlap and competition, niche overlap should not be taken as a sufficient condition for competition. Many factors may prevent or diminish competition between populations with similar resource utilization patterns. The typically opposing forces of intraspecific and interspecific competition need to be simultaneously considered, for it is the balance between them that in large part determines niche boundaries [27]. But what drives species to overlap or partition? The mechanism remains to be further studied.

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