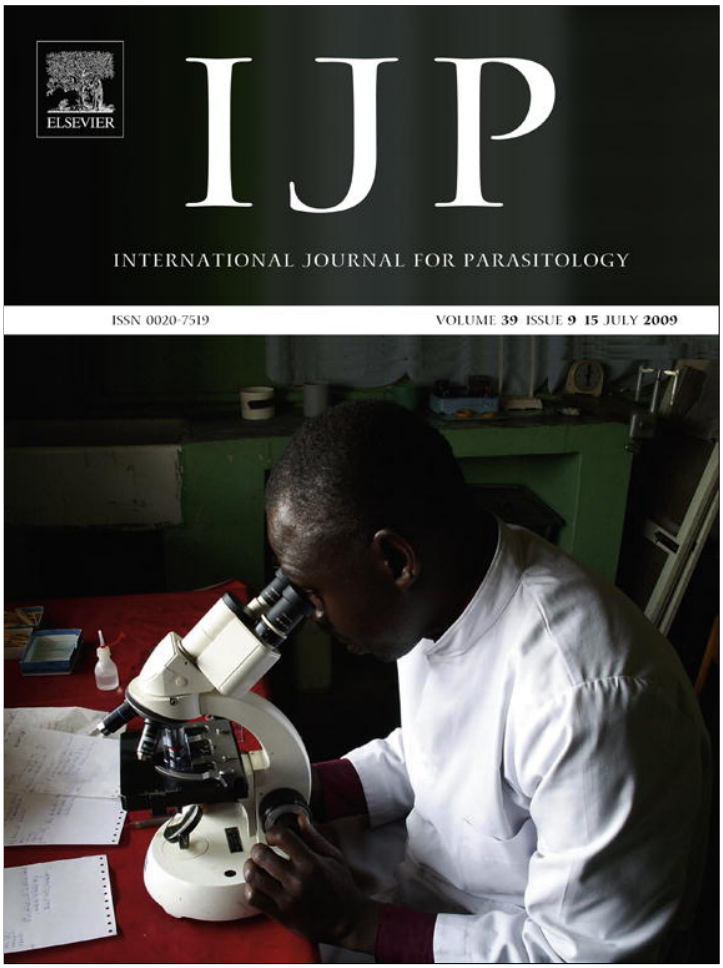

International Journal for Parasitology 39 (2009) 995–1002

Contents lists available at ScienceDirect

International Journal for Parasitology

journal homepage: www.elsevier.com/locate/ijpara

Host specificity in bat ectoparasites: A natural experiment

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ARTICLE INFO

Article history:
Received 12 September 2008
Received in revised form 19 November 2008
Accepted 18 December 2008

Keywords:
Bat parasites
Cave roost
Chiroptera
Co-evolution
Host–parasite associations
Host specificity
Sri Lanka

ABSTRACT

We undertook a field study to determine patterns of specialisation of ectoparasites in cave-dwelling bats in Sri Lanka. The hypothesis tested was that strict host specificity (monoxeny) could evolve through the development of differential species preferences through association with the different host groups. Three species of cave-dwelling bats were chosen to represent a wide range of host–parasite associations (monoxeny to polyxeny), and both sympatric and allopatric roosting assemblages. Of the eight caves selected, six caves were "allopatric" roosts where two of each housed only one of the three host species examined: *Rousettus leschenaulti* (Pteropodidae), *Rhinolophus rouxi* and *Hipposideros speoris* (Rhinolophidae). The remaining two caves were "sympatric" roosts and housed all three host species. Thirty bats of each species were examined for ectoparasites in each cave, which resulted in a collection of nycteribiid and streblid flies, an ischnopsyllid bat flea, argasid and ixodid ticks, and mites belonging to three families. The host specificity of bat parasites showed a trend to monoxeny in which 70% of the 30 species reported were monoxenous. Odds ratios derived from χ^2-tests revealed two levels of host preferences in less-specific parasites (i) the parasite was found on two host species under conditions of both host sympatry and host allopatry, with a preference for a single host in the case of host sympatry and (ii) the preference for a single host was very high, hence under conditions of host sympatry, it was confined to the preferred host only. However, under conditions of host allopatry, it utilized both hosts. There appears to be an increasing prevalence in host preferences of the parasites toward confinement to a single host species. The ecological isolation of the bat hosts and a long history of host–parasite co-existence could have contributed to an overall tendency of bat ectoparasites to become specialists, here reflected in the high percentage of monoxeny.

1. Introduction

Host specificity is the tendency of a parasite to occur on one or a few host species and is a product of co-existence between both parasite and host lineages (Brooks and McLennan, 1993; Patterson et al., 1998; Timms and Read, 1999; Poulin, 2007). A generalist is able to expand its geographical range beyond its host's range (Tripet and Richner, 1997; Poulin 2007). A specialist, on the other hand, is able to exploit the phenology and life history of the host effectively and reduce competition (Brooks and McLennan, 1993; Timms and Read, 1999; ter Hofstede and Fenton, 2005; Poulin, 2007). Bats (Mammalia: Chiroptera) harbor a rich fauna of ectoparasites representing various groups of Arthropoda (Marshall, 1981, 1982; Whitaker, 1988; Kettle, 1995). Their parasites are traditionally considered to be host specific, as a result of the ecological isolation of bats and/or the associated life history strategies of the parasites (Maa, 1965; Wenzel and Tipton, 1966; Shatrov, 1992; Dick et al., 2003; Dick and Patterson, 2007). Members of the families Nycteribiidae, Streblidae (bat flies), Polyctenidae (bat bugs), Ischnopsyllidae (bat fleas), and certain Acarina are exclusively found on bats (Maa, 1965; Usinger, 1966; Marshall, 1981, 1982; Kettle, 1995).

For descriptive purposes, host–parasite associations can be classified into several categories based on the degree of parasite specialization: monoxenous (where a parasite utilizes only a single host species), oligoxenous (utilizing two or more congeneric species), pleioxenous (utilizing two or more host genera in the same family) or polyxenous (utilizing many hosts of different families) (Marshall, 1981, 1982). Host specialization can operate through a combination of several processes: allopatric host distributions (host isolation) can prevent parasites from being exposed to other hosts, lower dispersal ability of the parasite reduces the chance of utilization of other hosts in situations of host sympatry, and there are subsequent physiological, morphological and behavioural adaptations that further reduce the chances of colonization and

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doi:10.1016/j.ijpara.2008.12.009

establishment on a novel host (Caire et al., 1985; Brooks and McLennan, 1993; Reed and Hafner, 1997; Timms and Read, 1999; Tompkins and Clayton, 1999; Dick and Patterson, 2007). Parasites achieve greatest survival on their preferred host, and selection favours the increased utilization of the host or group of hosts that give them the highest fitness (Giorgi et al., 2004). In contrast, exposure to multiple host species could trigger adaptations to utilize these additional hosts (Krasnov et al., 2007 but see Dick and Patterson, 2007). Numerous factors such as the complex life cycle stages of some parasites, host demography, host biogeography and parasite dispersal can further influence these associations (Shatrov, 1992; Marshall, 1981; Patterson et al., 1998; ter Hofstede and Fenton, 2005; Dick, 2007; Dick and Patterson, 2007; Krasnov et al., 2007; Patterson et al., 2007; Reckardt and Kerth, 2007). Host roosting ecology is one such important factor in the bat-ectoparasite system (Kunz, 1982; ter Hofstede and Fenton, 2005; Dick and Patterson, 2007; Reckardt and Kerth, 2007; Patterson et al., 2007).

About 30 species of bats have been recorded from Sri Lanka representing both fruit bats/flying foxes (four species) and insectivorous bats (~26 species; Phillips, 1980; Bates and Harrison, 1997). Scott (1908, 1925) and Phillips (1924) provided the first descriptions of ectoparasites of Sri Lankan bats, and these have been followed by several taxonomic studies (Thompson, 1937; Turk, 1950; Theodor, 1967; Brown et al., 2003). However, no attempts have been made to elucidate the ecology of bat parasites except for the descriptive study of Weerakkody et al. (1999). Recent descriptions of two new species of bat ectoparasites and the recognition of several undescribed species (Brown et al., 2003) accentuate the limits of knowledge of the parasite fauna of the island's Chiroptera.

We undertook a field study to determine the host–parasite associations of selected cave-roosting bat species in Sri Lanka. The primary objective was to understand the effect of a host's roosting behaviour on parasite specialization. We further anticipated that the results would elucidate mechanisms of co-evolution of host and parasite strategies. The hypothesis tested was that strict host specificity (monoxeny) could evolve through the development of differential preferences during association with different host groups. The hypothesis would be supported if parasites showed an increase in host preferences with varying compositions of hosts that eventually lead to strict confinement to a single species. We carefully chose host species that represented all types of host–parasite associations (monoxeny to polyxeny) and represent both sympatric and allopatric host assemblages.

2. Materials and methods

2.1. Chiropteran hosts

Three strictly cave-dwelling bat species that are colonial, which tend to roost both under sympatry and allopatry, and which represent two families were selected, namely two insectivorous species, *Hipposideros speoris* (family Rhinolophidae; Sheilder's leaf-nose bat), *Rhinolophus rouxi* (Rhinolophidae; Rufus horseshoe bat), and a frugivorous species *Rousettus leschenaulti* (Pteropodidae; Fulvous fruit bat) (Phillips 1980; Bates and Harrison 1997; Yapa et al., 2000; Simmons, 2000; Teeling et al., 2005). In the sympatric roosts, two other insectivorous bat species, *Miniopterus schreibersii* (family Vespertilionidae) and *Hipposideros lankadiva* (family Rhinolophidae) were found (Bates and Harrison, 1997; Yapa et al., 2000). Both caves with sympatric populations of bats had a similar host composition (Yapa, 1992; Yapa et al., 2000). Recent molecular phylogenies place Megachiroptera within Microchiroptera as the sister group to superfamily Rhinolophoidea, a clade referred to as either Yinpterochiroptera or Pteropodiformes (Teeling et al., 2002, 2005; but see Gunnell and Simmons, 2005). Hence, we considered *Hipposideros* within the family Rhinolophidae, and megabats (Pteropodidae) within the suborder Yinpterochiroptera.

2.2. Cave roosts

The selection of roosting sites (caves) was based on the species composition, colony size and accessibility. Eight localities, two caves with sympatric roosts and six with single species roosts, that is with two single species roosts for each host species (Fig. 1; Table 1), were selected. The species composition of bats in these caves has been studied previously and known to be constant at least since 1990 (Yapa, 1992; Yapa et al., 2000). All caves were natural caves, however, parts of Induruwa and Hatthikucchi caves have been slightly altered, as they are located in ancient temples.

2.3. Collection and identification

Fieldwork was conducted from February to May, and August to October 2002. Thirty individuals from each bat species were captured from each cave roost using hand nets and mist nets (Finnemore and Richardson, 1999). Mist nets were used in Ridiviharaya, Kanneliya and Waulpane caves to capture bats only on occasions where hand nets failed. Captured bats were placed in separate cloth sacks. A unique cloth sack, a toothbrush and a white copier paper were used for each individual bat. At the capture site, bats were placed on white paper (that was laid on a table) and were briefly exposed to ether soaked cotton wool prior to screening to sedate. All ectoparasites were collected from the dorsal and ventral pelage and wing membranes of semi-torpid bats using toothbrushes, forceps and a mounted magnifying glass (magnification 4×) into separate vials containing 70% ethyl alcohol (Hilton, 1970; Hutson, 1971; Whitaker, 1988). The white paper was searched for parasites under the magnifying glass. About 5 min were spent on each bat. After sampling in one cave location the brushes and sacks were visually inspected for parasites and washed with detergent to remove any live parasites. Bats were marked by clipping a patch of fur on their belly to avoid resampling in the event of recapture and were released to their original roost. Sampath Seneviratne screened the bats for parasites in all sites.

The parasites collected were examined under the stereomicroscope in the laboratory, and specimens were mounted using procedures described by Whitaker (1988) with modifications. Parasite identification was based on descriptions and keys available (Kessel, 1925; Jobling, 1934, 1936; Hiregaudar and Bal, 1956; Maa, 1965, 1971; Usinger, 1966; Theodor, 1967; Advani and Vazirani, 1981; Hutson, 1984; Brown et al., 2003). Several experts helped identify specimens and confirmed our identifications (see Acknowledgements for details).

2.4. Analysis

Parasite population parameters, abundance (mean number of parasites per host), prevalence (the proportion of infested hosts (Jovani and Tella, 2006)), and mean intensity (mean number of parasites per infested host), were computed following Bush et al. (1997). Monoxenous parasites were not subjected to any statistical analysis due to the absence of comparable parasite populations on other hosts. For less-specific parasites, prevalence and mean intensity were used to compare (Jovani and Tella, 2006) hosts, host roosting behaviour and host habitat. Odds ratios (OR) derived from the χ^2-test were used to develop a model to determine the degree of host preference. Statistical analyses were performed using SPSS 11 (SPSS Inc., Chicago, IL, USA) and Epi Info 6 (version 6.04; Center for Disease Control and Prevention, Atlanta, GA, USA) computer programs. Parasite diversity between host species and between cave roosts was ascertained using Shannon Wiener index (Magurran, 1988).

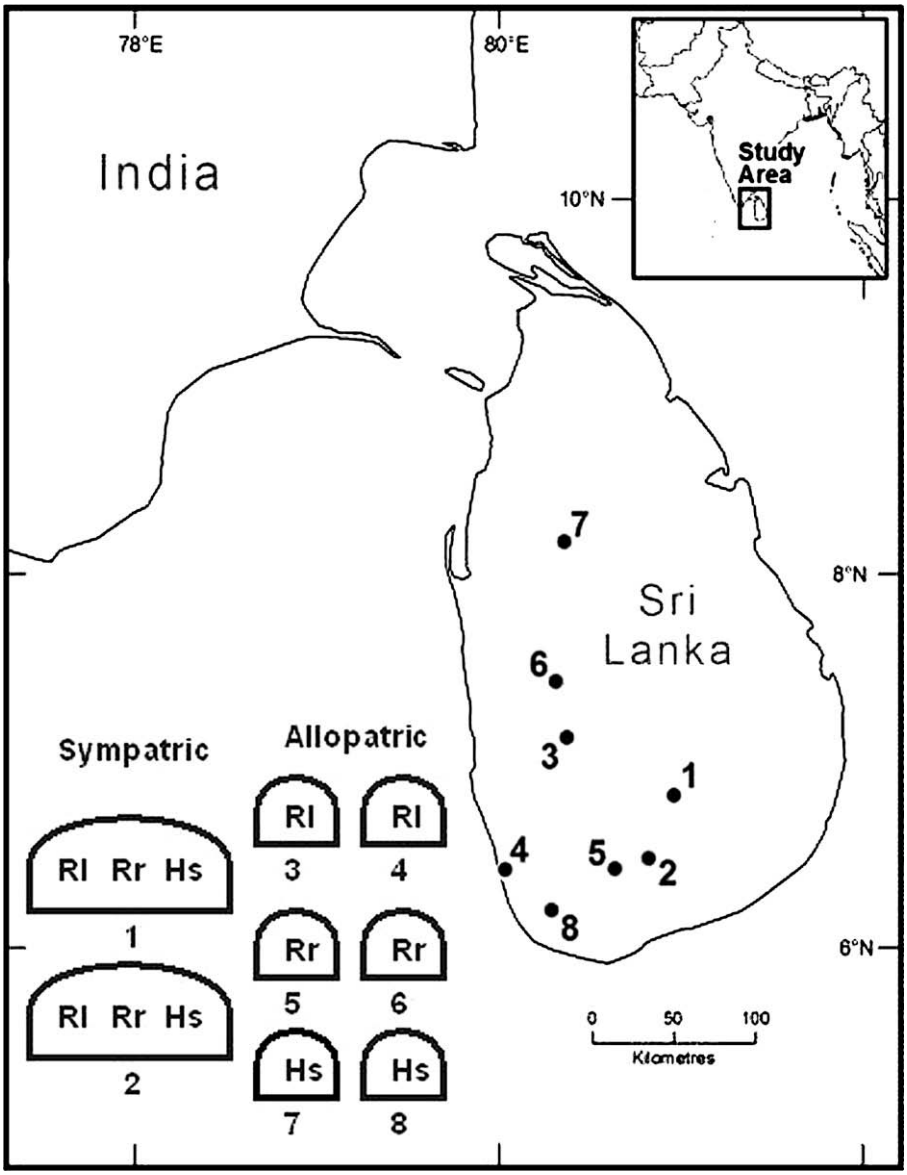

Fig. 1. The distribution of eight cave-roosts studied in Sri Lanka: 1, Waulgalge; 2, Waulpane; 3, Naugala; 4, Induruwa; 5, Wijeriya; 6, Ridiviharaya; 7, Hatthikucchi; 8, Kanneliya. The bat species found in the different cave roosts are shown in the bottom left hand corner. Caves 1 and 2 were sympatric bat roosts; the other six caves (3–8) were occupied by single host species; Rl, *Rousettus leschenaulti*; Rr, *Rhinolophus rouxi*; Hs, *Hipposideros speoris*.

Table 1
The description of cave-roosts studied.

Cave No.	Cave name	Geographic coordinates (°E, °N)	Size (m^3)	Substrate		Number of bats screened				
				Roof/walls	Floor	Rl	Rr	Hs	Hl	Ms
1	Waulgalge	(81.03, 6.43)	45,000	S	Dry	30	30	24	5	9
2	Waulpane	(80.37, 6.27)	50,000	R, L	Wet	30	30	23	4	5
3	Naugala	(80.19, 7.14)	500	R	Dry	30	–	–	–	–
4	Induruwa	(80.01, 6.23)	150	R	Dry	30	–	–	–	–
5	Wijeriya	(80.37, 6.27)	300	R, L, S	Wet	–	30	–	–	–
6	Ridiviharaya	(80.29, 7.32)	600	R	Dry	–	30	–	–	–
7	Hatthikucchi	(80.14, 7.53)	110	R	Dry	–	–	27	–	–
8	Kanneliya	(80.21, 6.16)	350	R, S	Wet	–	–	30	–	–
Total						120	120	104	9	14

Rl, *Rousettus leschenaulti*; Rr, *Rhinolophus rouxi*; Hs, *Hipposideros speoris*; Hl, *Hipposideros lankadiva*; Ms, *Miniopterus schreibersii*; L, Lime; R, Rock; S, Soil. The size of the cave is the estimated volume (average height × length × width). Cave floor is assigned as 'Wet' when a stream is flowing through the cave; the 'Dry' cave floor is characterized by accumulated bat guano.

3. Results

Arthropod ectoparasites ($n = 3,080$) belonging to 30 species were collected from 367 individual hosts (Table 1), including eight nycteribiid species of bat flies (Nycteribiidae), six streblid bat flies (Streblidae), a single bat flea (Ischnopsyllidae), four ticks (Argasidae and Ixodidae) and 11 mites (Leeuwenhoekiidae, Spinturnicidae and Trombiculidae) (Table 2). The mites were the most abundant group with 1,430 individuals collected from the five host species. Nycteribiid flies were the second most abundant (610); fleas were the rarest group with only 76 individuals. Quantitative information was not collected on the microhabitats. The microhabitats of these ectoparasites on the bat host was variable: nycteribiids, small streblids, ticks and fleas occupied the pelage; large streblids were frequently found close to the armpit and on the forearm; mites primarily occupied the ventral patagium; larval ticks were found on the rump, and some streblid flies (*Ascodipteron*) were found exclusively on the proximal edge of the dorsal tail membrane. All specimens, except for the holotypes and paratypes of *Whartonia ratnasooriyai* and *Chiroptella kanneliya*, and the two unidentified species of *Rudnicula* were catalogued and deposited in the parasite collection of the Department of Zoology, University of Colombo, Sri Lanka. The unidentified *Rudnicula* species and the type specimens of the *Whartonia* and *Chiroptella* have been deposited in the U.S. National Museum of Natural History (Brown et al., 2003).

Of the hosts examined, *R. leschenaulti* was the largest host, and showed the highest parasite intensity. Even though the single nycteribiid found on *R. leschenaulti* (*Eucampsipoda latistana*) showed a higher mean intensity (4.12) and prevalence (97.5%), nycteribiids on the other hosts showed a lower mean intensity (1.95 of *R. rouxi* and 3.0 and 1.94 on *H. speoris*), and prevalence (34.17% on *R. rouxi,* and 0.97% and 1.94% on *H. speoris*) (Table 2). *Rousettus leschenaulti* carried only a single individual streblid fly (prevalence 0.83%, mean intensity 1.00) compared with the two streblids at a higher mean intensity observed on *H. speoris* and *R. rouxi* (Table 2). Acarines showed greater affinity to *R. leschenaulti*. The single bat flea species was exclusively found on *R. leschenaulti*.

Twenty-one out of the 30 parasites encountered were strictly host-specific (Table 2, and see the discussion for previous reports of host associations). The flea and *Ascodipteron* (Streblidae) were monoxenous. In addition, monoxenous associations were detected in seven of eight nycteribiids (87.5%), five of six streblids (83.3%), three of four ticks (75%) and five of 11 mites (45.4%) (Table 2). The remaining nine parasites were pleoxenous and polyxenous. Of the less specific species, *Ornithodoros* sp. 1 was polyxenous and remainder were pleoxenous (Table 3). The *Rudnicula* sp. had

Table 2
Ectoparasites and their level of parasitism on five species of bat hosts at the studied cave roosts.

Number	Parasite	Host	Prevalence (%)	Abundance	Mean intensity
Nycteribiidae (Diptera)					
1	*Eucampsipoda latisterna* (Schuurmans and Stekhoven, 1938)	Rl	97.5	4.02	4.12
2	*Phthiridium phillipsi* (Scott, 1925)	Rr	34.17	0.67	1.95
3	*Phthiridium* sp. (sp/z/24)	Hs	1.94	0.019	1.00
4	*Phthiridium ceylonicum* (Theodor, 1967)	Hl	66.67	1.11	1.67
5	*Penicillidia indica* (Scott, 1925)	Ms	35.71	0.78	2.20
6	*Nycteribia allotopa* (Speiser, 1901)	Ms	85.71	2.64	3.08
7	*Nycteribia parvula* (Speiser, 1901)	Ms	28.52	0.43	1.50
8	*Nycteribia* sp. (sp/z/39)	Hs	0.97	0.029	3.00
Streblidae (Diptera)					
9	*Megastrebla parvior* (Maa, 1962)[a]	Rl	0.83	0.008	1.00
10	*Brachytarsina modesta* (Jobling, 1934)	Rr	39.17	0.74	1.89
11	*Brachytarsina amboinensis* (Rondani, 1878)	Ms	85.71	3.14	3.58
12	*Brachytarsina pygialis* (Rondani, 1878)	Hl	66.67	1.33	2.00
13	*Raymondia pagodarum* (Speiser, 1900)	Rr, Hs	58.0	2.24	3.84
14	*Ascodipteron* sp. (sp/z/43)	Hs	25.24	0.25	1.00
Ischnopsyllidae (Siphonaptera)					
15	*Thaumapsylla breviceps* (Rothschild, 1907)	Rl	19.16	0.63	3.30
Argasidae (Acarina)					
16	*Argas* sp. (sp/z/278)	Rl	2.5	0.042	1.67
17	*Ornithodoros* sp. 1 (sp/z/280)	Rl, Rr	8.33	0.117	1.40
18	*Ornithodoros* sp. 2 (sp/z/281)	Rr	1.67	0.017	1.00
Ixodidae (Acarina)					
19	*Haemaphysalis* sp. (sp/z/286)	Rr	21.66	0.46	9.23
Spinturnicidae (Acarina)					
20	*Meristaspis lateralis* (Kolenati, 1856)	Rl	38.33	2.65	6.91
21	*Ancystropus* sp. (sp/z/154)	Rl	3.33	0.0417	1.25
22	*Ancystropus taprobanius* (Turk, 1950)	Hs	4.85	0.086	1.80
23	*Oncoscelus kanheri* (Hiregauder and Bal, 1956)	Rl	24.17	0.717	2.97
24	*Paraperiglischrus rhinolophinus* (Koch, 1841)	Rr, Hs	22.4	0.218	4.9
25	*Paraperiglischrus hipposideros* (Baker and Delfinado, 1964)	Hl	66.67	4.22	6.33
26	*Spinturnix psi* (Kolenati, 1856)[a]	Rr	71.43	3.36	4.70
Trombiculidae (Acarina)					
27	*Rudnicula* sp. 1 (T-1)	Hs, Rr	15.53	1.67	12.5
28	*Rudnicula* sp. 2 (T-2)	Rr	15.6	1.03	8.34
29	*Chiroptella (Neosomia) kanneliya* (Brown et al., 2003)[a]	Hs	7.5	0.117	3.56
Leeuwenhoekiidae (Acarina)					
30	*Whartonia ratnasooriyai* (Brown et al., 2003)[a]	Rr, Hs	1.78	0.0357	2.00

Numbers in brackets represent the temporary catalogue numbers of representative specimens (see text).
Abbreviations for the hosts as in Table 1.
[a] New records for Sri Lanka.

Table 3
χ^2-comparisons and odds ratios (OR) for non-specific ectoparasites.

Parasite	*n*	Prevalence comparison	χ^2	*P*	OR
Ornithodoros sp. 1	480	Between Rl and Rr in sympatry (1,2)	2	0.2	–
		Between Rl (3,4) and Rr (5,6) in allopatry	9.7	0	8.4
		Between Rl and Rr in all roosts	49	0	36
Raymondia pagodarum	503	Between Hs and Rr in sympatry (1,2)	15	0	5.2
		Between Hs (7,8) & Rr (5,6) in allopatry	0.1	0.8	0.9
		Between Hs and Rr in all roosts	6.2	0	2
Paraperiglischrus rhinolophinus	49	Between Rr and Hs in sympatry (1,2)	2.8	0.1	0.2
		Between Rr (5,6) & Hs (7,8) in allpatry	0	1	1
		Between Rr and Hs in all roosts	2.7	0.4	0.6
Rudnicula sp. 1	292	Between Rr and Hs in sympatry (1)	1.3	0.3	–
		Between Rr(5,6) & Hs(7,8) in allopatry	40	0	0
		Between Rr and Hs in all roosts	38	0	0
Whartonia ratnasooriyai	8	Between Rr and Hs in sympatry (2)	0.8	0.4	–
		Between Hs (7,8) & Rr (5,6) in allopatry	2.8	0.9	0.2
		Between Rr and Hs in all roosts	1.3	0.2	0.3

See Fig. 1 for the experimental layout: cave numbers are given within brackets, cave numbers and abbreviations for hosts are as in Fig. 1, $\alpha < 0.05$.

a 25-fold preference for *H. speoris* over *R. rouxi* (OR 0.04, χ^2 38.20, $P < 0.001$; Table 3, Fig. 1). It was not found on *R. rouxi* in instances of host sympatry, but was found on both hosts in host allopatry with a greater affinity to *H. speoris* (OR 0.03, χ^2 39.54, $P < 0.001$; Table 3). Similarly *Ornithodoros* sp. 1 had a 36-fold preference to *R. leschenaulti* over *R. rouxi* (OR 36.43, χ^2 49.37, $P < 0.001$), whereas in sympatric caves it was only found on its preferred host (Table 3). The OR of *Raymondia pagodarum* indicated a five-fold preference for *H. speoris* over *R. rouxi* in sympatry (OR 5.18, χ^2 14.85, $P < 0.001$); in cases of host allopatry, it did not show a clear preference for any particular host (OR 0.91, χ^2 0.06, $P > 0.05$; Table 3). However, *R. pagodarum* showed a two-fold overall preference for *H. speoris* over *R. rouxi* (OR 1.99, χ^2 6.23, $P = 0.0126$; Table 3). Associations of *Paraperiglischrus rhinolophinus* and *W. ratnasooriyai* were not clear due to inadequate sample sizes.

Thirteen parasite species were recorded under both sympatric and allopatric roosting conditions. Of these, only five species showed a significant difference between the two roosting types; nycteribiids, *Phthiridium phillipsi* (OR 2.29, χ^2 4.48, $P = 0.03$); streblids, *Brachytarsina modesta* (OR 0.31, χ^2 9.02, $P = 0.003$); flea, *Thaumapsylla breviceps* (OR 34.16, χ^2 23.72, $P < 0.001$); ticks, *Ornithodoros* sp. 1 (OR 2.79, χ^2 9.87, $P = 0.002$); mites, *Meristaspis lateralis* (OR 0.23, χ^2 14.1, $P < 0.001$). *Phthiridium phillipsi*, *T. breviceps* and *Ornithodoros* sp. 1 had higher prevalences in sympatric roosts, while *B. modesta* and *M. lateralis* were more prevalent in allopatric roosts. Overall, parasite diversity between hosts in the two sympatric caves and between allopatric caves was not different except between the Naugala and the Induruwa caves ($t_{1,701} = 0.66$), Naugala and Kanneliya caves ($t_{1,162} = 1.90$), Induruwa and Kanneliya caves ($t_{1,195} = 1.43$), Wijeriya and Hatthikucchi caves ($t_{1,267} = 0.65$), Wijeriya and Kanneliya caves ($t_{1,311} = 0.88$) and between Hatthikucchi and Kanneliya caves ($t_{1,204} = 0.45$) ($P < 0.05$).

4. Discussion

We believe this is the first study reporting the degree of host specificity of bat parasites in Sri Lanka as well as one of the few inclusive capture efforts to determine host–parasite associations of bats on the island. Twenty-one of the 30 parasites reported in this study were apparently monoxenous. The remainder were less specific, being either pleoxenous or polyxenous. This high level of specificity is comparable with previous studies generally (Wenzel and Tipton, 1966; Marshall, 1981, 1982; Giorgi et al., 2004; Dick, 2005, 2007; Takahashi et al., 2006; Dick and Patterson, 2007) as well as in Sri Lanka (Weerakkody et al., 1999). We did not attempt to cover the entire spectrum of hosts of any of these parasites thus preventing definitive conclusions on monoxeny. However, previous accounts of most of these species support a monoxenous trend. Most bat flies are highly host-specific (Phillips, 1924; Scott, 1925; Maa, 1965; Theodor, 1967; but see Jobling, 1949). Phillips (1924) recorded eight nycteribiid species, of which seven were monoxenous. The streblid flies showed a similar trend (Phillips, 1924; Scott, 1925, 1936; Marshall, 1981; Weerakkody et al., 1999). The host associations of *T. breviceps* (Siphonaptera) are variable in different parts of its range (Hiregaudar and Bal, 1956; Mitchell and Punzo, 1976). In Sri Lanka, the species is exclusively found on *R. leschenaulti* (Thompson, 1937; Weerakkody et al., 1999; Udagama-Randeniya et al., unpublished data). Similarly, bat mites differ greatly in their host associations based on different studies in the Indian region (Hiregaudar and Bal, 1956; Mitchell and Punzo, 1976; Advani and Vazirani, 1981; Fernandes et al., 1989; Fernandes and Kulkarni, 2003; Udagama-Randeniya et al., unpublished data).

All bat flies and the only siphonapteran recorded in this study confirm previous records (Scott, 1908, 1925, 1936; Phillips, 1924; Thompson, 1937; Hiregaudar and Bal, 1956; Theodor, 1967; Mitchell and Punzo, 1976; Bhat et al., 1979; Weerakkody et al., 1999) except that *Megastrebla parviour* is a new addition to Sri Lanka's ectoparasite fauna; it has been reported on *R. leschenaulti* throughout the Indo-pacific region (Hiregaudar and Bal, 1956; Maa, 1965, 1971; Advani and Vazirani, 1981; Kock, 1986). *Eucampsipoda latistana* was harbored only by *R. leschenaulti* (Scott, 1925; Theodor, 1967; Weerakkody et al., 1999). In India it was found on several other frugivorous hosts such as *Cynopterus sphinx*, *C. brachyotis* and *Pteropus* sp. (Bhat et al., 1979). *Phthiridium ceylonicum* is a nycteribiid endemic to Sri Lanka (Scott, 1914; Theodor, 1967). The current records of acarines confirm those of Turk (1950), Hiregaudar and Bal (1956), Seneviratne (1962, 1965), Fernandes and Kulkarni (2003), Brown et al. (2003), and Udagama-Randeniya et al. (unpublished data).

The ecological isolation of the bat hosts could have contributed to generally higher levels of host specificity in the parasites (Wenzel and Tipton, 1966; Krasnov et al., 2007). Island host populations tend to be more restricted geographically; hence, besides the lower host pool available, this could further limit the parasite's exposure to different host species. Therefore even generalists may be restricted by the available pool of hosts, which can lead to monoxeny (Krasnov et al., 2007; Shenbrot et al., 2007). Furthermore, the high level of monoxeny observed in this study could be due to less

cross-species contamination as a result of (i) host screening in single species roosts and (ii) host capture efforts that were exclusively focused on ectoparasite screening, since sample contamination can falsely impute low specificity.

Two levels of host preference in less-specific parasites were identified (i) the parasite was found on two host species under conditions of both host sympatry and host allopatry but with a higher preference for one host (level-1 preference) and (ii) preference for a single host was very high, such that, under conditions of host sympatry, the parasites were confined to the preferred host, while in situations of host allopatry it was found on both hosts (level-2 preference). On this scale, monoxeny (a specialist parasite) can be placed as a level-3 preference and polyxeny at the opposite end (no host preference). *Rudnicula* sp. 1 was found on both *H. speoris* and *R. rouxi* in single species roosts (in host allopatry) with a 30-fold preference for *H. speoris* over *R. rouxi* (Table 3). The parasite has about a 25-fold overall preference for the former host (Table 3). As a result of this strong preference, in host sympatry, it only parasitised *H. speoris* although *R. rouxi* co-existed in close proximity (level-2 preference; Table 3). Polyxenous *Ornithodoros* sp. 1 showed a similar pattern by having a 36-fold overall preference for *R. leschenaulti* over *R. rouxi* (Table 3). A streblid fly, *R. pagodarum* was found on both hosts under both host roosting conditions. However, its preference for *H. speoris* was greater (five-fold) than *R. rouxi* in sympatric roosts where both hosts are available (level-1 preference; Table 3). Under host allopatry *R. pagodarum* did not show a greater preference for either of the two hosts (Table 3).

The less specialized pleoxenous parasites (level-1 preference) occured on both hosts under conditions of host sympatry and host allopatry, suggesting an ability to maintain fitness on both hosts due to the lesser specialization to a single host species. Over time, parasites can acquire greater adaptations to utilize its preferred host as a result of various selective forces (see McCoy et al., 2001; Giorgi et al., 2004; Dick, 2007; Dick and Patterson, 2007). Thus, under conditions of host sympatry, the parasite was restricted to its preferred host, which provides the greatest benefits (level-2 preference; Table 3). The parasite's ability to colonize and establish on hosts other than its preferred host(s) in host allopatry explains its less specialized adaptations to the 'preferred host' than a monoxenous parasite (Dick and Patterson, 2007). In the situation of monoxeny, the parasite's survival is poor on hosts apart from its specific host, preventing establishment on other hosts in both sympatry as well as in allopatry (Fig. 2). We assumed that polyxenous associations would be classed as level-1 preferences

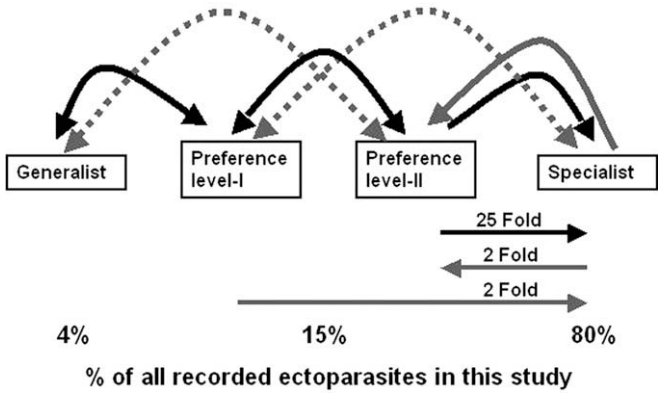

Fig. 2. Possible steps for the development of specificity in bat parasites. The model indicates a trend towards monoxeny. Black curved lines indicate pathways of highest probability; solid grey curved lines indicate pathways of moderate probability; broken lines indicate pathways of lowest probability; arrowheads indicate direction. The direction of preference is indicated by the straight arrows (see Table 3).

or lower (Fig. 2). However, the only polyxenous association reported here (*Ornithodoros* sp. 1) reflected a similar pattern of preference as the other pleoxenous associations (Table 3). This indicates that even generalists can have a significant preference for one or more hosts (McCoy et al., 2001). We have not observed any oligoxenous associations, but it is likely that they would follow the same pattern as that of *Rudnicula* sp. 1. Quantitative information (Tables 2 and 3) and previous parasitological surveys indicate that the overall tendency of a bat ectoparasite to become a specialist is high (McCoy et al., 2001). Especially when a pleoxenous/oligoxenous parasite become monoxenous, we believe, the chances of it reversing back to a less specific state are low (Fig. 2). That is reflected in the very high percentage of monoxeny and high host preferences showed by less-specific parasites (Table 3). The ecological isolation of bats and long history of co-existence of parasite and its host/s (Patterson et al., 1998; Timms and Read, 1999; Dick and Patterson, 2007) could contribute to this general trend.

The adaptations acquired by the parasite increase its chance of survival on the preferred host/s (Clayton et al., 1999; Tompkins and Clayton, 1999; Dick and Patterson, 2007), hence its mean intensity and prevalence is high on the preferred host. However, parasites can increase their chances of finding a suitable mate by aggregating on fewer individual hosts (ter Hofstede et al., 2004). This can lead to a situation where under conditions of host sympatry, generalist species can cluster on fewer hosts regardless of their host preference (Yuval, 1994; ter Hofstede et al., 2004), a potential drawback that could affect on our study. We tried to minimize this drawback by screening a large number of hosts. Mobile ectoparasites such as the parasitic flies theoretically tend to be less specific as they are more likely to encounter new host species (Marshall, 1976, 1981; Reed and Hafner, 1997). However, bat ectoparasites do not show this general trend (Wenzel et al., 1966; Marshall, 1976, 1981; Whitaker, 1988; ter Hofstede et al., 2004; Dick and Patterson, 2007).

Irrespective of the type of roost (Table 1), the parasite diversity on a particular bat host did not vary between caves except in the sympatric caves. However, the prevalence of some ectoparasites differed between caves. A possible reason could be that the greater parasite diversity in sympatric roosts can cause more competition. Particularly mobile (streblid flies) and less-specific parasites (mites) may be subjected to higher levels of competition (Timms and Read, 1999; Dick and Patterson, 2007). In sympatric colonies, different host species tend to roost in monospecific clusters (Kunz, 1982; Hill and Smith, 1985). More crowded roosting in these sympatric roosts (Table 1) can cause individual bats to roost in close proximity to their neighbours than in less crowded single species colonies, which could result in a greater level of competition among monoxenous parasites.

This study elucidates evolutionary pathways of the development of specificity of ectoparasites in colonial Chiroptera, and forms a benchmark study of bat parasite ecology of Sri Lanka. The bat ectoparasites of the island showed a monoxenous trend, with less specialized species showing a gradient in the degree of host specialization. However, phylogenetic relationships of the parasites studied were not accounted here. Detailed future studies including the phylogenetic history of ectoparasites and all closely related hosts will provide a clearer picture of host specificity and associated co-speciation (Barker, 1994; Patterson et al., 1998; Clayton et al., 1999). We did not study bats that utilize other roosting habitats such as tents, crevices, tree cavities, etc., which compose the majority of bat species on the island. To obtain a complete understanding of the nature of possible colonization pathways, it is necessary to study the parasite fauna of all available hosts such as reptiles, birds (e.g., swifts), bats, rodents and other mammals that are sympatrically associated in these cave habitats.

Acknowledgements

We gratefully acknowledge the University of Colombo, Sri Lanka for logistic and financial support and granting permission for the study. W.B. Yapa and P.C.M.B. Digana provided technical support and enthusiastic help throughout the study. S.W. Kotagama and W.D. Ratnasooriya provided the necessary administrative support at the department of Zoology, University of Colombo. Several experts confirmed and helped identify specimens: nycteribiid and streblid flies – D. Kock of Forschungsinstitute Senckenberg, Germany; ticks – N. Wilson, University of Northern Iowa, USA; Trombiculidae and Leeuwanhoekiidae mites – W.A. Brown, University of Hawaii at Manoa, USA; Spincturnicid mites – J. Deunff, University of Rennes, France. We further acknowledge the Department of Wildlife Conservation, and Department of Forestry, Sri Lanka, for granting permission to carry out the fieldwork component. Fig. 1 was prepared for the manuscript by the staff of the Map Room, Queen Elizabeth II Library, Memorial University. S.B. Muzzafar, T. Chapman, I. Beveridge and two anonymous reviewers provided useful comments on the manuscript.

References

Advani, R., Vazirani, T.G., 1981. Studies on ectoparasites of bats of Rajasthan and Gujarat (India). Rec. Zool. Sur. India 22, 1–17.

Barker, S.C., 1994. Phylogeny and classification, origins, and evolution of host associations of lice. J. Parasitol. 24, 1285–1291.

Bates, P.J.J., Harrison, D.L., 1997. Bats of the Indian Subcontinent. Harrison Zoological Museum, Seven Oaks, Kent, UK.

Bhat, H.R., Sreenivasan, M.A., Ilkal, M.A., 1979. Records of Nycteribiidae and Streblidae (Diptera, Pupipara) in Karnataka, India. J. Bombay Nat. Hist. Soc. 76, 268–274.

Brooks, D.R., McLennan, D.A., 1993. Parascript: Parasites and the Language of Evolution. Smithsonian Institution Press, Washington, DC, USA.

Brown, W.A., Udagama-Randeniya, P.V., Seneviratne, S.S., 2003. Two new species of chiggers (Acari: Leeuwenhoekiidae and Trombiculidae) from bats (Chiroptera) collected in the Kanneliya Forest Reserve of Sri Lanka. Int. J. Acarol. 29, 69–73.

Bush, A.O., Lafferty, K.D., Lotz, J.M., Shostak, A.W., 1997. Parasitology meets ecology on its own terms: Margolis et al. revisited. J. Parasitol. 83, 575–583.

Caire, W., Hornuff, L., Sohrabi, N., 1985. Stimuli used by *Trichobius major* (Diptera Streblidae) to locate its bat host *Myotis velifer*. Southwest Nat. 30, 405–412.

Clayton, D.H., Lee, P.L.M., Tompkins, D.M., Brodie Iii, E.D., 1999. Reciprocal natural selection on host–parasite phenotypes. Am. Nat. 154, 261–270.

Dick, C.W., Gannon, M.R., Little, W.E., Patrick, M.J., 2003. Ectoparasite associations of bats from central Pennsylvania. J. Med. Entomol. 40, 813–819.

Dick, C.W., 2005, Ecology and host specificity of bat flies [Diptera: Streblidae] and their chiropteran hosts. Ph.D. Dissertation, Texas Tech University, Lubbock, TX, USA, pp. 253.

Dick, C.W., 2007. High host specificity of obligate ectoparasites. Ecol. Entomol. 32, 446–450.

Dick, C.W., Patterson, B.D., 2007. Against all odds: explaining high host specificity in dispersal-prone parasites. Int. J. Parasitol. 37, 871–876.

Fernandes, S.S., Kulkarni, S.M., 2003. Studies on the trombiculid mite fauna of India. Rec. Zool. Sur. India Occas. Pap. 212, 1–539.

Fernandes, S., Kulkarni, S.M., Bhat, H.R., 1989. Survey of the trombiculid mites from the Himalayan region, India. In: Channabasavanna, G.P., Viraktamath, C.A. (Eds.), Progress in Acarology, vol. 1. Brill Archive, Leiden, Netherland, pp. 107–112.

Finnemore, M., Richardson, P.W., 1999. Catching bats. In: Mitchell-Jones, A.J., McLeish, A.P. (Eds.), The Bat Workers' Manual. Joint Nature Conservation Committee, Peterborough, UK, pp. 33–38.

Giorgi, M., Arlettaz, R., Guillaume, F., Nusslé, S., Ossola, C., Vogel, P., Christe, P., 2004. Causal mechanisms underlying host specificity in bat ectoparasites. Oecologia 138, 648–654.

Gunnell, G., Simmons, N., 2005. Fossil evidence and the origin of bats. J. Mam. Evol. 12, 209–246.

Hill, J.E., Smith, J.D., 1985. Bats: a Natural History. British Museum (Natural History), London, UK.

Hilton, D.F.J., 1970. A technique for collecting ectoparasites from small birds and mammals. Can. J. Zool. 48, 1445–1446.

Hiregaudar, L.S., Bal, D.V., 1956. Some ectoparasites of bats from India. Agra U.J. Res. (Sci.) 5, 1–134.

Hutson, A.M., 1971. Ectoparasites of British bats. Mammal Rev. 1, 143–150.

Hutson, A.M., 1984. Keds, flat-flies and bat-flies. Diptera: Hippoboscidae and Nyceteribiidae, Handbook for the identification of British insects, vol. 10. Royal Entomological Society of London, London, UK. pp. 1–40.

Jobling, B., 1934. Revision of the genus *Nycteribosca* Speiser (Diptera, Pupipara, Streblidae). Parasitology 26, 64–97.

Jobling, B., 1936. A revision of the subfamilies of the Streblidae and the genera of the subfamily Streblinae including a redescription of *Metelasmus pseudopterus* Coquillett and a description of two new species from Africa. Parasitology 28, 355–380.

Jobling, B., 1949. Host–parasite relationship between the American Streblidae and the bats, with a new key to the American genera and a record of the Streblidae from Trinidad, British, West Indies (Diptera). Parasitology 39, 315–329.

Jovani, R., Tella, J.L., 2006. Parasite prevalence and sample size: misconceptions and solutions. Trends Parasitol. 22, 214–218.

Kessel, Q.C., 1925. A synopsis of the Streblidae of the world. J. N.Y. Entomol. Soc. 33, 11–33.

Kettle, D.S. (Ed.), 1995. Medical and Veterinary Entomology. CAB International, Wallington, UK.

Kock, D., 1986. Ectoparasites of bats in Bangladesh (Insecta, Diptera, Nycteribiidae, Hemiptera, Cimicidae). Senck. Biol. 67, 37–42.

Krasnov, B.R., Korine, C., Burdelova, N.V., Khokhlova, I.S., Pinshow, B., 2007. Between-host phylogenetic distance and feeding efficiency in hematophagous ectoparasites: rodent fleas and a bat host. Parasitol. Res. 101, 365–371.

Kunz, T.H., 1982. Roosting ecology of bats. In: Kunz, T.H. (Ed.), Ecology of Bats. Plenum Press, New York, NY, USA, pp. 1–55.

Maa, T.C., 1965. An interim world list of batflies (Diptera: Nycteribiidae and Streblidae). J. Med. Entomol. 1, 377–386.

Maa, T.C., 1971. Studies in Bat Flies (Diptera: Streblidae, Nycteribiidae). Bernice P. Bishop Museum, Entomology Department, Honolulu, Hawaii, USA.

Magurran, A.E., 1988. Ecological Diversity and its Measurement. Princeton University Press, Princeton, NJ, USA.

Marshall, A.G., 1976. Host-specificity amongst arthropods ectoparasitic upon mammals and birds in the New Hebrides. Ecol. Entomol. 1, 189–199.

Marshall, A.G., 1981. The Ecology of Ectoparasitic Insects. Academic Press, London, UK.

Marshall, A.G., 1982. Ecology of insects ectoparasitic on bats. In: Kunz, T.H. (Ed.), Ecology of Bats. Plenum Press, New York, NY, USA, pp. 369–401.

McCoy, K.D., Boulinier, T., Tirard, C., Michalakis, Y., 2001. Host specificity of a generalist parasite: genetic evidence of sympatric host races in the seabird tick *Ixodes uriae*. J. Evol. Biol. 14, 395–405.

Mitchell, R., Punzo, F., 1976. Ectoparasites of bats from Nepal. J. Bombay Nat. Hist. Soc. 73, 84–87.

Patterson, B.D., Ballard, J.W.O., Wenzel, R.L., 1998. Distributional evidence for cospeciation between neotropical bats and their bat fly ectoparasites. Stud. Neotrop. Fauna Environ. 33, 76–84.

Patterson, B.D., Dick, C.W., Dittmar, K., 2007. Roosting habits of bats affect their parasitism by bat flies (Diptera: Streblidae). J. Trop. Ecol. 23, 177–189.

Phillips, W.W.A., 1924. Ecto-parasites of Ceylon bats. Ceylon J. Sci. 13, 65–70.

Phillips, W.W.A., 1980. Manual of the Mammals of Sri Lanka. Wildlife and Nature Protection Society of Sri Lanka, Colombo, Sri Lanka.

Poulin, R., 2007. Evolutionary Ecology of Parasites. Chapman and Hall, London, UK.

Reckardt, K., Kerth, G., 2007. Roost selection and roost switching of female Bechstein's Bats (*Myotis bechsteinii*) as a strategy of parasite avoidance. Oecologia 154, 581–588.

Reed, D.L., Hafner, M.S., 1997. Host specificity of chewing lice on pocket gophers: a potential mechanism for cospeciation. J. Mammal. 78, 655–660.

Scott, H., 1908. On a large series of *Nycteribiidae*, parasitic *Diptera*, from Ceylon. Trans. Entomol. Soc. Lond. 1907, 421–428.

Scott, H., 1914. On some oriental Nycteribiidae. Ann. Mag. Nat. Hist. 8, 209–235.

Scott, H., 1925. Zoogeographical and systematic notes on the Nycteribiidae of India, Ceylon and Burma. Rec. Indian Mus. 27, 351–384.

Scott, H., 1936. Descriptions and records of Nycteribiidae. Zool. J. Linn. Soc. 39, 479–505.

Seneviratne, P., 1962. The Ixodoidea (Ticks) of Ceylon, Part I. Ceylon Vet. J. 10, 30–41.

Seneviratne, P., 1965. The Ixodoidea (Ticks) of Ceylon, Part II and III. Ceylon Vet. J. 13, 28–45.

Shatrov, A.B., 1992. The origin of parasitism in trombiculid mites (Acariformes: Trombiculidae). Parasitology 26, 3–12.

Shenbrot, G., Krasnov, B., Lu, L., 2007. Geographical range size and host specificity in ectoparasites: a case study with Amphipsylla fleas and rodent hosts. J. Biogeogr. 34, 1679–1690.

Simmons, N.B., 2000. Bat phylogeny: an evolutionary context for comparative studies. In: Adams, R.A., Pedersen, S.C. (Eds.), Ontogeny, Functional Ecology, and Evolution of Bats. Cambridge University Press, Cambridge, UK, pp. 9–58.

Takahashi, M., Takahashi, H., Kikuchi, H., 2006. *Whartonia (Fascutonia) natsumei* (Acari: Trombiculidae): a new bat chigger collected from *Plecotus auritus* (Chiroptera: Vespertilionidae) in Japan, with host and distribution records of the genus *Whartonia*. J. Med. Entomol. 43, 128–137.

Teeling, E.C., Madsen, O., Van Den Bussche, R.A., de Jong, W.W., Stanhope, M.J., Springer, M.S., 2002. Microbat paraphyly and the convergent evolution of a key innovation in Old World rhinolophoid microbats. Proc. Natl. Acad. Sci. USA 99, 1431–1436.

Teeling, E.C., Springer, M.S., Madsen, O., Bates, P., O'Brien, S.J., Murphy, W.J., 2005. A molecular phylogeny for bats illuminates biogeography and the fossil record. Science 307, 580–584.

ter Hofstede, H.M., Fenton, M.B., Whitaker Jr., J.O., 2004. Host and host-site specificity of bat flies (Diptera: Streblidae and Nycteribiidae) on Neotropical bats (Chiroptera). Can. J. Zool. 82, 616–626.

ter Hofstede, H.M., Fenton, M.B., 2005. Relationships between roost preferences, ectoparasite density, and grooming behaviour of neotropical bats. J. Zool. 266, 333–340.

Theodor, O., 1967. An Illustrated Catalogue of the Rothschild Collection of Nycteribiidae (Diptera) in the British Museum (Natural History). British Museum (Natural History), London, UK.

Thompson, G.B., 1937. A census of the ectoparasites of some Ceylon bats. J. Anim. Ecol. 6, 337–339.
Timms, R., Read, A.F., 1999. What makes a specialist special? Trends Ecol. Evol. 14, 333–334.
Tompkins, D.M., Clayton, D.H., 1999. Host resources govern the specificity of swiftlet lice: size matters. J. Anim. Ecol. 68, 489–500.
Tripet, F., Richner, H., 1997. The coevolutionary potential of a 'generalist' parasite, the hen flea *Ceratophyllus gallinae*. Parasitol. Res. 115, 419–427.
Turk, F.A., 1950. Studies of acari; parasitic mites from mammalian hosts obtained in Ceylon. Parasitology 40, 63–76.
Usinger, R.L., 1966. Monograph of Cimicidae. Thomas Say Foundation, Entomological Society of America, College Park, MD, USA.
Weerakkody, A.S.A., Randeniya, P.V., Ratnasooriya, W.D., 1999. Ecology of ectoparasites of some cave-dwelling microchiropterans of Sri Lanka. Vidyodaya J. Sci. 8, 189–201.
Wenzel, R.L., Tipton, V.J., 1966. Some relationships between mammal hosts and their ectoparasites. In: Wenzel, R.L., Tipton, V.J. (Eds.), Ectoparasites of Panama. Field Museum of Natural History, Chicago, IL, USA, pp. 677–723.
Whitaker Jr., J.O., 1988. Collecting and preserving ectoparasites for ecological study. In: Kunz, T.H. (Ed.), Ecological and Behavioral Methods for the Study of Bats. Smithsonian Institution Press, Washington, DC, USA, pp. 459–474.
Yapa, W.B., 1992. Ecological and ethological studies on cave dwelling bats in Sri Lanka. M.Sc. Thesis. Department of Zoology, University of Colombo, Colombo, Sri Lanka.
Yapa, W.B., Randeniya, P.V., Digana, P.C.M.B., Ratnasooriya, W.D., 2000. Ecology and biology of Sri Lankan bats: a survey on the distribution of Sri Lankan bats. National Science Foundation, Colombo, Sri Lanka.
Yuval, B., 1994. The vertebrate host as mating encounter site for its ectoparasites: ecological and evolutionary considerations. Bull. Soc. Vect. Ecol. 19, 115–120.