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Transport of bugs of the genus *Cimex* (Heteroptera: Cimicidae) by bats in western Palaearctic

Ondřej BALVÍN[1], Martin ŠEVČÍK[2], Helena JAHELKOVÁ[1], Tomáš BARTONIČKA[3], Maria ORLOVA[4] & Jitka VILÍMOVÁ[1]

[1] *Department of Zoology, Faculty of Science, Charles University, Viničná 7, CZ–128 44 Praha 2, Czech Republic; o.balvin@centrum.cz*
[2] *Slovak Society for Parasitology at Slovak Academy of Sciences, Hlinkova 3, SK–040 01 Košice, Slovakia*
[3] *Department of Botany and Zoology, Faculty of Science, Masaryk University, Kotlářská 2, CZ–611 37 Brno, Czech Republic*
[4] *Institute of Plant and Animal Ecology of Ural Branch of Russian Academy of Science, 8 Marta str. 202, RU–620144 Ekaterinburg, Russia*

Abstract. The study of the dispersal mechanisms of organisms is key to understanding their ecology and diversity. The dispersal of parasites is usually mediated by their host. Cimicidae (Heteroptera) is a family of haematophagous ectoparasites for whom bats are the most common and original host. Cimicids spend most of their time in the bat roost, usually only attaching themselves to the body of their host to feed. Distances between bat roosts are too great for the bugs to cross so their transmissions between them are exclusively passive. In our study we present records of bugs found on bats outside roosts. Since adult bugs are more likely to start a new infestation, their high prevalence among these records suggests that the bugs intentionally remain attached to their host in order to disperse, rather than accidentally leaving the roost while feeding. The vast majority of the records come from the genus *Nyctalus* and some from the genus *Pipistrellus*, whilst only single findings come from other species. It is possible that this disproportion is caused by the different behaviour of bugs on different bat species. The frequency of transmissions of cimicids by particular bat species correlate with the extent of the migratory behaviour of the bats. However, it is also possible that it is caused by an unequal opportunity to fly out attached to the bat due to the different roosting ecology and behaviour of the bat species.

Dispersal ecology, ectoparasites, bats, roosting ecology

Introduction

Due to their complexity, host-parasite systems are valuable study objects in the context of evolutionary ecology. Knowledge of the mode of dispersal of parasites is one of the keys for understanding their ecology as well as their diversity (Poulin 2007). The dispersal of parasites is usually more or less dependant on their hosts.

Bats are highly social animals. During pregnancy and parturition females establish maternity colonies usually in roosts with relatively stable climatic conditions to give birth to their young. Therefore, both their bodies and their shelters provide a suitable environment for insect ectoparasites (cf. Marshall 1982).

Bat bugs (Heteroptera: Cimicidae) are a group of important bat ectoparasites. Though some species or genera are specialized to birds, bats are probably the original and most common hosts of the family (Horváth 1913). As people have shared caves with bats as shelters in the past, populations specialized to humans have developed within three bat-parasitizing species – *Cimex lectularius* Linnaeus, 1758, *C. hemipterus* (Fabricius, 1803) and *Leptocimex boueti* (Brumpt, 1910) (Usinger 1966). However, at least in *C. lectularius*, the original population on bats is isolated from the one

Table 1. Review of published records of bugs of the genus *Cimex* on mist-netted bats in the western Palaearctic. Legend: n1 = number of bats carrying bugs, n2 = total number of bugs; n3 = maximum number of bugs per bat

bat host species	n1	n2	n3	country	reference
Myotis daubentonii	1	1	1	Russia	Orlova et al. (2011)
Nyctalus leisleri	1	1	1	Ireland	Nelson & Smiddy (1997)
Nyctalus leisleri	1	1♀+1♂	2	Germany	Morkel (1999)
Nyctalus noctula	1	1	1	Great Britain	Gilbert (1951)
Nyctalus noctula	6	6	1	Germany	Roer (1975)
Nyctalus noctula	3	2♀♀+1♂	2	Germany	Morkel (1999)
Nyctalus noctula	1	1	1	Italy	Lanza (1999)
Nyctalus noctula	1	♂	1	Bulgaria	Simov et al. (2006)
Nyctalus noctula	4	3♀♀+2♂♂	1	Slovakia	Krištofík & Kaňuch (2006)
Nyctalus noctula	10	9♀♀+2♂♂	2	Slovakia	Krištofík et al. (2012)
Vespertilio murinus	1	♀	1	Russia	Orlova & Pervušina (2010)

on people and has been shown not to constitute any threat to humans (Balvín et al. 2012a). Both the adults and larvae of bat bugs feed on the blood of bats and stay on their body only during the time they spend engorging. Due to the climatic conditions, the bats of Europe usually spend the winter in a different roost to that of the rest of the year (e.g. Anděra & Horáček 2005). The winter roosts usually constitute mines and caves which are too cold for reproducing cimicids; the only record of a bug from an overwintering site was made as far south as Greece (Simov et al. 2006). In contrast, these bugs are very common in summer roosts in Central and Western Europe (e.g. Povolný 1957, Beaucournu 1961, Roer 1969, Zahn & Rupp 2004). Cimicids survive the winter in such roosts and, therefore, they are forced to wait months between blood meals. It is mainly adults which are able to persist (Bartonička & Růžičková 2012) and as their numbers are reduced such a bottleneck in population can cause harm due to inbreeding. The dispersal of bat bugs throughout the roosts of their hosts is necessary not just to maintain the genetic diversity locally, and in the whole population, but also to expand to new or temporarily abandoned roosts. Cimicids are wingless and the bat roosting shelters are usually scattered throughout the country, therefore the transmission of bat bugs between particular roosts is exclusively passive. Unlike the majority of the other bat ectoparasites that spend most of their life on the body of the bat, the findings of bugs on mist-netted bats are rather scarce in western Palaearctic.

Table 1 reviews such records from unspecialized studies. One of the more thorough studies (Rupp et al. 2004) reports bugs found on 15% of the 221 *Nyctalus noctula* (Schreber, 1774) individuals (maximum 4 bugs on each bat) caught in Bavaria, Germany Unfortunately it is not clear whether the bats were mist-netted or caught in their roost but given the type of shelters that *N. noctula* inhabits it is likely that most of bats of the species were mist-netted.

The most specialized study of cimicids on bats in flight (Heise 1988) reports 55 bugs collected from 1631 individuals of *N. noctula*. On at least four occasions the author found bugs in the bags remaining after the capture of *N. noctula*. Two of the bugs were determined as *Cimex lectularius*, whilst the rest were identified as *C. pipistrelli* Jenyns, 1839. All the other studies only recorded the presence of *C. pipistrelli* group.

Considering all the published data, there is a remarkable disproportion between the number of findings of cimicids on *N. noctula* and other bat species caught outside roosts. If mentioned in any of these studies, all bugs reported from mist-netted bats were adults. Heise (1988) believed that the bugs may travel on the body of their hosts for the purpose of dispersal, not just because they did not escape when the bat emerged from the roost while they were feeding.

In this study we present new data on species of the genus *Cimex* found on bats caught outside roosts in the West-Palaearctic region. We discuss the hypotheses that the occurrence of cimicids on the body of bats is (a) random due to the accidental presence of feeding bugs on a bat leaving the roost or (b) intentional and serving for the dispersal of the bugs which is important for the maintenance of a viable and healthy population. We examine the unequal frequency of the transmission of cimicids by different bat species. We discuss whether this is caused (a) by a different and possibly adaptive behaviour of the bugs as a result of the different roosting ecology of each bat species or (b) merely by the different behaviour or ecology of the host bats.

Material and Methods

The specimens of the genus *Cimex* used in this study were collected from 55 mist-netted individuals of bats by the authors or by other bat specialists (localities are given in Table 2). Thorough examinations of mist-netted bats for ectoparasites are carried out by many Czech and Slovak specialists during their field work. Nevertheless, in this study we report the occasions with a positive record of the *Cimex* species. If possible, the number of mist-netted bats, their sex and reproduction status for each species were recorded on each occasion.

The bugs have been preserved in 96% ethanol and deposited in the collections of Ondřej Balvín at Charles University in Prague and Tomáš Bartonička at Masaryk University in Brno. Species determination followed Usinger (1966), but we did not distinguish between species of the *C. pipistrelli* group. According to our own data based on morphology and mitochondrial DNA (Balvín et al. 2012b) there are two distinct haplogroups in the West-Palaearctic region which might represent different species but which are so variable in morphology that they fit to all three species described from the region. Collections 200 and 201 were larvae of 2nd instar; we determined the species using a 658bp long fragment of cytochrome oxydase subunit I.

Results and Discussion

Age of dispersing bat bugs: *is the dispersal intentional or random*?

Altogether we collected 77 cimicids on 55 mist-netted bats of 7 species at 37 localities in the West-Palaearctic region (Table 2). We only report the collections which had a positive record of bugs. All recorded bugs belong to the *Cimex pipistrelli* group; only two collections (426, 428) were identified as *C. lectularius*.

On three occasions more than one bug was collected from one bat individual. For two of these the number was higher than in the published records e.g. by Rupp et al. (2004) or Heise (1988). However, the occurrence of one female, two males and 14 larvae in collection no. 195 (Table 2) was not coincidental. The record comes from a juvenile bat, which was probably sick as it was carried by his mother despite being almost mature enough to fly by itself. According to our experience of bat roosts e.g. offspring of *Myotis myotis* (Borkhausen, 1797) fallen from the colony roost, dying juveniles often attract a large number of many different parasites, including cimicids. We believe that this explains such a high abundance of adult and juvenile bugs on this bat.

Despite that early instars prevail in bat roosts during most of the breeding season (Bartonička & Růžičková 2012) nearly all of the recorded bugs were adult with only three exceptions. The presence of juveniles in the collection 195 is explained above. Samples 200 and 201 are the only collections from *Myotis dasycneme* (Boie, 1825), one from Poland, one from Russia. As these are the only findings from this bat species the presence of bug larvae on their body seems to be a very suspicious coincidence. Unfortunately we can see no explanation to this exception.

As suggested by Heise (1988) the almost exclusive presence of adult cimicids on bats outside their roosts supports the idea that remaining attached to the host is not only an accident during

Table 2. List of records of cimicids on bats caught outside roosts. Legend: IC – identification code of samples in the collection of Ondřej Balvín. Unlabeled collections are deposited in the collection of Tomáš Bartonička; CC – country code (CZ = Czech Republic, FR – France, GE – Germany, HU – Hungary, LB – Lebanon, PL – Poland, RU – Russia, SK – Slovakia, SP – Spain, UA – Ukraine, UK – United Kingdom); HS – host species (*Mdas* – *Myotis dasycneme*, *Mmyo* – *Myotis myotis*, *Nlas* – *Nyctalus lasiopterus*, *Nlei* – *Nyctalus leisleri*, *Nnoc* – *Nyctalus noctula*, *Paur* – *Plecotus auritus*, *Ppyg* – *Pipistrellus pygmaeus*); HAS – host age and sex; BS – bug species (*Clec* – *Cimex lectularius*, *Cpip* – *Cimex pipistrelli*); BN – Sex and number of bugs; j = juvenile, a = adult, ♀ = female, ♂ = male; LG & MG – L. Godlevska & M. Ghazali

IC	CC	locality	coordinates	date	HS	HAS	collector	BS	BN
2	CZ	Příštpo (Třebíč Dist.)	49°04'N, 15°55'E	16 July 1998	*Nnoc*		K. Hůrka	*Cpip*	♀
19m02	CZ	Veselí nad Lužnicí, Švarcemberk fishpond	49°08'N, 14°42'E	5 August 2005	*Nnoc*		H. Jahelková	*Cpip*	♂
19m01	CZ	Veselí nad Lužnicí, Švarcemberk fishpond	49°08'N, 14°42'E	5 August 2005	*Nnoc*		H. Jahelková	*Cpip*	♂
54	LB	Nahr es Safa river	33°42'N, 35°29'E	26 April 2006	*Nnoc*		I. Horáček	*Cpip*	♂
62f02	CZ	Veselí nad Lužnicí, Ruda	49°09'N, 14°41'E	23 August 2006	*Nnoc*	♀j	R. Lučan	*Cpip*	♀
62m01	CZ	Veselí nad Lužnicí, Ruda	49°09'N, 14°41'E	23 August 2006	*Nnoc*	♀j	R. Lučan	*Cpip*	♂
62f01	CZ	Veselí nad Lužnicí, Ruda	49°09'N, 14°41'E	23 August 2006	*Nnoc*	♂j	R. Lučan	*Cpip*	♀
63	CZ	Veselí nad Lužnicí, Švarcemberk fishpond	49°08'N, 14°42'E	14 August 2006	*Nnoc*		A. Zieglerová	*Cpip*	♀
64m01	CZ	Veselí nad Lužnicí, Švarcemberk fishpond	49°08'N, 14°42'E	25 August 2006	*Nnoc*		A. Zieglerová	*Cpip*	♂
64m02	CZ	Veselí nad Lužnicí, Švarcemberk fishpond	49°08'N, 14°42'E	25 August 2006	*Nnoc*		A. Zieglerová	*Cpip*	♂
67	SK	Nitra, city park	48°18'N, 18°04'E	15 July 2006	*Nnoc*	♂	M. Ševčík	*Cpip*	♀
68	SK	Nitra, city park	48°18'N, 18°04'E	21 October 2006	*Nnoc*	♂a	M. Ševčík	*Cpip*	♀
69	SK	Nitra, city park	48°18'N, 18°04'E	21 August 2006	*Nnoc*	♂j	M. Ševčík	*Cpip*	♀
113	CZ	Břeclav	48°45'N, 16°53'E	16 July 2007	*Nnoc*		R. Lučan	*Cpip*	♂
114	CZ	Veselí nad Moravou (Hodonín Dist.)	48°57'N, 17°22'E	18 July 2007	*Nnoc*		R. Lučan	*Cpip*	♀
115	CZ	Líšná (Přerov Dist.)	49°24'N, 17°32'E	6 August 2007	*Nnoc*		R. Lučan	*Cpip*	2♀♀
122	SP	Cortes de la Frontera (Malaga Prov.)	36°31'N, 05°35'E	12 May 2007	*Nlas*		–	*Cpip*	♂
125	CZ	Pavlov (Břeclav Dist.)	48°51'N, 16°38'E	21 July 2007	*Nnoc*	♂	J. Chytil	*Cpip*	♀
126	SK	Trebišov	48°37'N, 21°42'E	3 June 2007	*Nlei*		T. Bartonička	*Cpip*	♀
127	CZ	Mikulov, Sedlec	48°46'N, 16°44'E	18 July 2007	*Nnoc*		J. Chytil	*Cpip*	♀
134	GE	–		30 June 1905	*Nnoc*		M. Kredler	*Cpip*	♀
137	HU	Parád (Heves Dist.)	47°55'N, 20°01'E	26 June 2006	*Nlas*		P. Estók	*Cpip*	♂
138	HU	Eger	47°53'N, 20°22'E	1 April 2006	*Nnoc*		P. Estók	*Cpip*	♀
151	HU	Mánfai-kőlyuk (Baranya Dist.)	46°09'N, 18°12'E	25 August 2007	*Nnoc*		T. Görföl	*Cpip*	♀
152	HU	Béda, Kölked (Baranya Dist.)	45°55'N, 18°44'E	29 July 2008	*Nnoc*		T. Görföl	*Cpip*	♀

153	HU	Baja (Bács-Kiskun Dist.)	46°11’N, 18°53’E	21 July 2007	*Nnoc*	j	T. Görföl	*Cpip*	♀
154	HU	Váralja (Tolna Dist.)	46°12’N, 18°22’E	2 August 2008	*Nnoc*	j	T. Görföl	*Cpip*	♀
155	HU	Váralja (Tolna Dist.)	46°12’N, 18°22’E	2 August 2008	*Nnoc*		T. Görföl	*Cpip*	♀
156	CZ	Hodonín, Hodonínská doubrava	48°53’N, 17°05’E	2008	*Nnoc*		R. Lučan	*Cpip*	♂
192	UK	Herstmonceux, West Sussex	50°53’N, 00°19’E	6 May 2011	*Nnoc*		A. Millar	*Cpip*	♀
194	UA	Kiev	50°21’N, 30°31’E	15 June 2011	*Nnoc*	♀a	L. Godlevska	*Cpip*	♂
195	UA	Verhivnâ (Žitomyr region)	48°49’N, 29°19’E	9 July 2011	*Ppyg*	♀a♂j	L. Godlevska & M. Ghazali	*Cpip*	♀2♂♂ +14jj
196f01	UA	Verhivnâ (Žitomyr region)	48°49’N, 29°19’E	9 July 2011	*Nnoc*	♂j	LG & MG	*Cpip*	♀
196m01	UA	Verhivnâ (Žitomyr region)	48°49’N, 29°19’E	9 July 2011	*Nnoc*		LG & MG	*Cpip*	♂
197	UA	Verhivnâ (Žitomyr region)	48°49’N, 29°19’E	9 July 2011	*Nnoc*	♀j	LG & MG	*Cpip*	♀
198	UA	Verhivnâ (Žitomyr region)	48°49’N, 29°19’E	9 July 2011	*Nnoc*	♀a	LG & MG	*Cpip*	♀
199	PL	Lubnia (Pomorskie Prov.)	53°55’N, 17°45’E	20 June 2011	*Ppyg*	♀a	M. Orlova	*Cpip*	♀
200	PL	Lubnia (Pomorskie Prov.)	53°55’N, 17°45’E	14 July 2009	*Mdas*	♀a	A. Zappart	*Cpip*	j
201	RU	Karabašm (Čelâbinsk region)	55°28’N, 60°19’E	9 July 2011	*Mdas*	♀a	M. Orlova	*Cpip*	j
204	HU	Püspökszentlászló (Baranya Dist.)	46°11’N, 18°21’E	7 July 2011	*Nnoc*	♀j	T. Görföl	*Cpip*	♀
205	HU	Szekszárd (Tolna Dist.)	46°20’N, 18°42’E	7 August 2011	*Nnoc*	♂a	T. Görföl	*Cpip*	♂
206	CZ	Červenohorské sedlo (Jeseník Dist.)	50°07’N, 17°09’E	27 July 2011	*Nnoc*		P. Hulva	*Cpip*	♀
426	FR	Chapaize, Saone-et-Loire	46°33’N, 04°44’E	5 August 2009	*Mmyo*		S. Lutz	*Clec*	♂
428	UA	Selezivka (Žitomyr region)	51°32’N, 28°06’E	16 August 2011	*Paur*	♂	L. Godlevska	*Clec*	♀
	CZ	Znojmo, Karlov	48°48’N, 16°18’E	5 August 2009	*Nlei*	♀a	T. Bartonička	*Cpip*	♀
	CZ	Velké Němčice, Termanec pheasantry	48°59’N, 16°39’E	30 June 2010	*Nnoc*	♀a	T. Bartonička	*Cpip*	6♀♀
	CZ	Nové Mlýny, Křivé lake	48°50’N, 16°43’E	1 June 2010	*Ppyg*	♀G	T. Bartonička	*Cpip*	♀
	CZ	Filena, Záhlinice	49°17’N, 17°28’E	18 June 2006	*Ppyg*	♀a	T. Bartonička	*Cpip*	♂
	CZ	Milovický les, Bulhary preserve	48°49’N, 16°42’E	25 May 2010	*Nnoc*	♂a	T. Bartonička	*Cpip*	♀
	CZ	Grygov, Království forest	49°30’N, 17°17’E	27 May 2011	*Nnoc*	♂a	T. Bartonička	*Cpip*	♀
	CZ	Milovický les, Bulhary preserve	48°49’N, 16°42’E	16 May 2010	*Nnoc*	♂a	T. Bartonička	*Cpip*	♀
	CZ	Velké Němčice, Termanec pheasantry	48°59’N, 16°39’E	31 May 2010	*Nnoc*	♂a	T. Bartonička	*Cpip*	♀
	CZ	Nové Mlýny, Křivé lake	48°50’N, 16°43’E	2 June 2008	*Nnoc*	♂a	T. Bartonička	*Cpip*	♀
	CZ	Nové Mlýny, Křivé lake	48°50’N, 16°43’E	20 June 2009	*Ppyg*	♂a	T. Bartonička	*Cpip*	♀
	CZ	Velké Němčice, Termanec pheasantry	48°59’N, 16°39’E	28 June 2010	*Ppyg*	♂a	T. Bartonička	*Cpip*	♀

feeding but also serves the purpose of dispersal. It is also supported by the prevalence of females in our sample. As the most durable life stage, the adults, especially mated females, represent the most effective agents of dispersal: a single mated female is able to found a new infestation (Usinger 1966, Bartonička 2010). Heise (1988) also reports an unspecified prevalence of females. Of our specimens there are 44 females and 17 males. According to experiments on *Cimex lectularius* (Pfiester et al. 2009) the larvae tend to aggregate while the adults actively disperse when their numbers increase. Females were shown to disperse earlier than males. It is likely that adult *C. pipistrelli* react in a similar way and use bats for intended dispersal.

Bat species transporting bugs: *do the bugs distinguish between them*?

The frequency of cimicids on mist-netted *Nyctalus noctula* was considerably higher than on other bat species. Out of 55 records 41 (75%) were made from this species. Four (7%) were made from other *Nyctalus* species – *N. leisleri* (Kuhl, 1817) and *N. lasiopterus* (Schreber, 1780). Findings on *Pipistrellus pygmaeus* (Leach, 1825) also showed them to not being very rare: six records (11%) come from this bat species. Similarly, the literature (for references see Table 1, Heise 1988 and Rupp et al. 2004) reports over 100 bugs found on mist-netted bats in the West-Palaearctic region. Only four of the published records were made from species other than *N. noctula*; two of these come from *N. leisleri*, a very similar species. Surprisingly, this disproportion has never been discussed.

Fig. 1. In some roosts of *Myotis myotis* the abundace of cimicid bugs is indeed high. Točník, Czech Republic (photo by O. Balvín).

A large number of central European bats have been reported to host cimicids (Balvín 2010). However, the systematic examination of parasite fauna in their roosts is only possible for a few of them, and on some of the others cimicids are rather rare. Thus only *Myotis myotis*, *M. emarginatus* (Geoffroy, 1806), *Pipistrellus* spp., and *Nyctalus noctula* can be confidently assigned as their regular hosts.

The higher frequency of cimicids on mist-netted *N. noctula* is not caused by a prevalence of the species among mist-netted bats. It usually constitutes only a proportion of the bats mist-netted on a particular occasion. Exact data has been recorded by Rupp et al. (2004): Cimicids were found on 15% of 221 individuals of *N. noctula* whereas none were present on 793 individuals of the other 17 bat species. Disregarding occasions when cimicids were not recorded, unfortunately such data is available for only a few of our samples. A total of 163 individuals of *N. noctula* and 221 individuals of other bat species were caught on eight occasions. On 10 *N. noctula* individuals 11 bugs were found. On the other hand, some bat species such as *N. leisleri*, *N. lasiopterus* or *Vespertilio murinus* Linnaeus, 1758 are not easily caught by mist-netting and so miss being evaluated.

Nyctalus leisleri and *N. lasiopterus* are likely carriers of cimicids as well. Though they are rarely caught bat species compared to many others, there are several records of them bearing bugs. In conclusion, it is clear that ectoparasites are sometimes carried between the bat roosts of every host bat species, however, concerning the genus *Cimex* in western Palaearctic, these bugs travel much more often on the body of *Nyctalus* spp., and to a lesser extent on *Pipistrellus* spp. than on *Myotis* spp. Disregarding the possible intentionality of these cimicids to be transferred, it is possible that the behaviour or ecology of their bat hosts could be a reason, at least partially, for this disproportion.

In comparison to *Myotis myotis*, *M. emarginatus* is a much less known bat species but in the behavioural and ecological aspects studied, the two bat species largely resemble each other (e.g. Audet 1990, Zahn et al. 2009). Therefore we may attribute other characteristics known for *M. myotis* to *M. emarginatus* whilst discussing roosting behaviour. Males of *M. myotis* and *M. emarginatus* live mostly solitarily (Zahn & Dippel 1997, Flaquer et al. 2008) and as such they do not constitute an opportune host for cimicids. In southern Europe, females of *M. myotis* and *M. emarginatus* form breeding colonies preferably in caves (Horáček 1984) which are too cold or humid for the bugs (Simov et al. 2006). As far as we are aware, the most southern roost of either of these species infested with cimicids is that in northern Serbia (Protić & Paunović 2006). In the rest of Europe, females gather in large numbers in spacious roosts which are usually the attics of larger buildings (Hanák & Anděra 2006). Females are faithful to their colonies (Horáček 1985). Very little is known about the gathering of females of the two species during the shifts between winter and summer roosts but any temporary shelters are likely to be unfavourable to cimicids as they are inhabited for only one or two short periods during a year. However, maternity colonies of *M. myotis* and *M. emarginatus* are usually heavily infested (Roer 1969, Balvín 2010, Balvín et al. 2012b) (Fig. 1). In the open roosts, the bats have enough space to stretch their wings and get rid of bugs before flying out. This can be one of the possible reasons for the absence of cimicids on most of the mist-netted bats of the two *Myotis* species.

In contrast, throughout their distribution both colonies of females and groups of males (called "bachelor groups") of species of the genera *Pipistrellus* and *Nyctalus* roost in rock crevices (often substituted by crevices in buildings) or tree holes (Barlow & Jones 1999, Davidson-Watts & Jones 2006, Celuch & Kaňuch 2005). In central Europe, these roosts are usually infested with cimicids (Bartonička & Gaisler 2007, Balvín 2010, Balvín et al. 2012b). However, we are not aware of any records of *Cimex* spp. from *Pipistrellus* spp. of southern Europe; these bats are most likely parasitized by *Cacodmus vicinus* (Quetglas et al. 2012). On the other hand, *Nyctalus* spp.

are responsible for all of the records of *C. pipistrelli* known to us from southern Europe (Lanza 1999, Simov et al. 2006, our records).

Bats of the genera *Pipistrellus* and *Nyctalus* are known to switch roosts quite often from spring to autumn (Feyerabend & Simon 2000, Fleming & Eby 2003, Bartonička et al. 2008). *Nyctalus noctula* is known to produce loud calls in order to let other bats of his species know about suitable roosts (Ruczynski et al. 2007, Furmankiewicz et al. 2010). In the same way males attract females during mating season, as these bat species exhibit a resource-defence polygyny mating system (Gerell-Lundberg & Gerell 1994). In *Pipistrellus* spp. it has been suggested that the fissure-like roosts are changed in order to reduce the number of ectoparasites (Bartonička & Gaisler 2007, Bartonička & Růžičková in press). Communities of these bat species maintain a kind of pool of known roosts that are used throughout the year. Adult cimicids, in particular, are able to survive long periods of starvation there (Bartonička & Gaisler 2007). It is possible that fissure-like roosts are often too narrow for grooming in order to remove ectoparasites, especially from the wing membranes where transported cimicids are often located (Heise 1988, Roer 1975, our own experience) (Fig. 2). This way the bats of the genera *Nyctalus* and *Pipistrellus* are more likely to leave their roosts carrying a cimicid than are those of *M. myotis* or *M. emarginatus*. Also, these

Fig. 2. Bug found on the wing of mist-netted *Nyctalus noctula*. Nitra, Slovakia (photo by M. Celuch).

roosts can be ones serving as resting places during night activity for bats of these genera, unlike *M. myotis* and *M. emarginatus* which usually rest perching "outdoors" (e.g. Bartonička & Rusiński 2010). Therefore, as the *Nyctalus* spp. and *Pipistrellus* spp. have multiple opportunities to encounter cimicids during the night, their chance of carrying a cimicid during flight increases compared to other bat species.

As well as the character of the roosts, the body structure of the bat may also influence the proficiency of self-grooming in order to remove cimicids. Also, the characteristics of the skin and fur of these two groups of bats is different and may influence the ability of the bugs to remain attached to the host body or jabbed in their skin (Gaisler & Baruš 1978).

All males and non-reproducing individuals of the bat species mentioned lower their metabolism during the day when resting in roosts (Bartonička & Řehák 2007). As cimicids react to temperature and CO_2 production (Usinger 1966), such resting bats probably do not attract them. When they awaken and become active again in preparation to fly out they then provide a more appealing target for the cimicids. These climb onto the bat to feed and can then be accidentally transported from the roost. Bartonička (2008) supports this idea by the observation of a higher level of selfgrooming in bats occupying roosts infested with cimicids prior to their emergence. The hypothesis also seems to be supported by our data. Lactating females do not use torpor and so are continuously attractive as hosts. The probability of them flying out with a bug is therefore much lower. The status and sex is known for 41 bat individuals carrying a cimicid from our data and literature (Krištofík & Kaňuch 2006, Krištofík et al. 2012, Orlova & Pervušina 2010, Orlova et al. 2011), but only eight of them are possibly lactating females. As in *M. myotis* and *M. emarginatus* the cimicids are likely to be present only in female breeding colonies, this could also be a partial reason for such a low frequency of transmission of bugs by these species.

However, the large difference between the number of records of cimicid transmission by *N. noctula* and *P. pygmaeus* may also not be coincidental. The available information on the behaviour and ecology of these bats is not substantial enough to suggest an explanation for the difference. Possibly the difference in size and maybe the character of the body could be the reason. Cimicids are found on specific parts of the bat body and therefore having less surface area for such parts could mean less probability of keeping attached.

All suggested reasons for the unequal frequency of the transmission of cimicids by different bat species are more or less speculative as they are based on an incomplete knowledge of bat ecology and behaviour. As we may see differences in the frequency among bats with a similar ecology the reason can still lie in the different behaviour of the bugs of each bat species. This could either be developed by local adaptation due to selective pressures over generations or caused by behavioural plasticity. The phenomenon of behaviour plasticity is characterized by the ability of members of the same genotype to adjust their behaviour in response to different conditions (Mery & Burns 2010). However, it has never been observed in ectoparasitic arthropods. Disregarding the primary cause, the different behaviour of cimicids would be consistent with the extent of the migratory behaviour of the bat hosts and thus indeed beneficial. *M. myotis* and *M. emarginatus* females are sedentary and faithful to their roosts. For the cimicids the roosts are a stable food source and flying out on a bat would mostly lead to a return to the same roost or being lost in a hostile place. In contrast, *Pipistrellus* spp. and especially *Nyctalus* spp. switch roosts during season, use multiple roosts during the night, and often travel long distances, at least between winter and summer sites. In *Nyctalus* spp. the distances often exceed 1000 km (Petit & Mayer 2000). Attaching to the body of their host can help the cimicids maintain populations in the system of multiple roosts. It also helps them travel long distances and spread among other bat species which may be encountered in the roosts.

In conclusion, the occurrence of cimicids on bats outside their roosts could be due to the coincidence of the bug feeding at the time of the bat flying out. However, only adult and mostly female bugs are found on bats outside roosts. Therefore, we believe it is more likely caused by dispersal aimed behaviour of the bug. The adult bugs either actively search for a host in order to be brought to another location, or at least keep attached, unlike juveniles, when the bat moves during feeding. However, this theory needs to be further tested.

There are large differences in the roosting ecology among European bat species. Therefore the different dispersal strategies of cimicids on each bat species are likely to be beneficial. Indeed, the frequency of the transmission of bugs by bats differs among different bat species. As the frequencies are congruent with the extent of the migratory behaviour in each particular bat species this suggests a different adaptive behaviour of the cimicids on each of them. However, we cannot say that the different frequency is due to the unequal opportunities of cimicids to fly out with the bat or to the different ecology and behaviour of the bats themselves, or a combination of both.

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