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Distribution and host relations of species of the genus *Cimex* on bats in Europe

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Abstract. The species of the genus *Cimex* (Heteroptera: Cimicidae) are important ectoparasites of European bats. Unlike other ectoparasites, they are attached to the body of their host only when they need to feed, otherwise they stay in refugia in bat roosts. Consequently, they are often overlooked by bat specialists and in many countries they are either unknown or poorly characterized. This study reports results from thorough investigations of bat roosts of diverse bat species in a Northwest-Southeast transect across Europe: Czech and Slovak Republics, Hungary, Serbia and Bulgaria. The distribution of *Cimex lectularius* follows the synanthropic habitats of its principal hosts, *Myotis myotis* and *M. emarginatus*, both Mediterranean elements of the European fauna. The climate in natural roosts (i.e. caves) inhabited by these bats in southern areas appears to restrain the presence of cimicids. In central Europe, *C. pipistrelli* parasitizes, beside *M. myotis*, many crevice-dwelling bat species indigenous to the boreal zone. However, in southern Europe, it appears only in connection with *Nyctalus noctula*. *C. lectularius* was confirmed for five host bat species and newly recorded for *Rhinolophus ferrumequinum*, *C. pipistrelli* was confirmed for seven bat species and newly recorded for *Myotis nattereri*. The first record of *C. emarginatus* outside of its type locality and *Myotis alcathoe* as a new host are reported. The host preferences of the species of the genus *Cimex* are discussed.

Key words: biogeography, faunistics, ectoparasites, ecology, host-parasite relationship

Introduction

Because their social behavior, bats constitute a particularly favourable environment for diverse fauna of ectoparasites (Marshall 1982). Bat aggregations have allowed bugs of the family Cimicidae (Heteroptera) to develop a unique exploitation strategy. No life stage of cimicids is permanently attached to the body of a bat. Both larvae and adults remain hidden in refugia in bat roosts and use the hosts only in order to feed on their blood (Usinger 1966). However, it is also likely that cimicids actively search for host as means of dispersal (Heise 1988, Balvín et al. 2012b).

The impact of cimicids on bats can manifest itself as an increase in self-grooming (Bartonička 2008). Such discomfort makes the colony of "crevice-dwelling" bats (i.e. bat species with a habit to roostin tight crevice spaces) switch roosts (Bartonička & Gaisler 2007, Bartonička & Růžičková 2013). This reduces the abundance of cimicids, but can also promote their spread to other suitable bat roosts. Colonies of philopatric species of bats, which have a habit to roost in large open spaces, i.e. attics in central Europe (reffered as "attic-dwelling" bats elsewhere in this paper) respond by moving within these spaces which are often large enough to escape the reach of cimicid refugia (Bartonička & Růžičková 2012). Furthermore, cimicids are vectors of diverse bat pathogens or can cause secondary infections (Williams et al. 1976, Bowers & Woo 1981, Adelman et al. 2013).

The diversity of Cimicidae comprises 110 known species classified in 24 genera and six subfamilies (Henry 2009). About two thirds of the species are

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associated with bats, which were suggested to be the original host of the family (Horváth 1913). The remaning species are related to birds. Three bat-associated species, including the bed bug *Cimex lectularius* Linnaeus, 1758, have adopted humans as another host.

The European fauna of cimicids is represented by the genera *Cimex* and *Oeciacus*, which were deemed synonymous (Balvín et al. 2013, 2015), and the recently discovered *Cacodmus vicinus* Horváth, 1934 (Quetglas et al. 2012). Species of the former genus *Oeciacus* are parasites in nests of birds of the family Hirundinidae. Since bats may occupy these nests (Loye 1985, Schulz 1995, Ritzi et al. 2001), *Oeciacus* bugs are occasionally found on bats as well (Rotschild 1912, Ritzi et al. 2001). However, there are three strictly bat-associated *Cimex* species in Europe: *Cimex lectularius*, *C. pipistrelli* Jenyns, 1839 and *C. emarginatus* Simov, 2006.

The lineages of the bed bug *C. lectularius* specialized to people and bats are completely isolated and, as a result, morphologically and genetically distinct (Balvín et al. 2012a). The population parasitizing on bats has historically been considered a separate species (Poppius 1912). Recent evidence is consistent with this (Booth et al. 2015). Thanks to human migration, the bed bug became cosmopolitan. However, little is known about the original distribution of the bat-associated population. The bed bug has been reported on several bat species (Table 1) but can be regarded as common only in roosts of *Myotis myotis*. Bed bugs are also found quite often in roosts of *M. emarginatus*. In central Europe, the two species usually roost in spacious attics. In southern Europe, these bats roost in caves that are too humid and cold for cimicids (Simov et al. 2006). The synanthropy of bats probably developed only in the last several centuries (Horáček 1983). Before then, bed bugs might have inhabited caves in the Middle East, as suggested by Povolný & Usinger (1966), who published the only report of a bed bug in the natural habitat of a cave (Afghanistan). The only other records from bats in this region are by Abul-Hab (1979), from mist-netted *Pipistrellus kuhlii* in Iraq and possibly a meadow in Iran (Golestan province, 37°22′1″ N 55°59′3″ E, 27 May 2006, A. Reiter and P. Benda lgt.; assigned as bat-associated bed bug based on morphology by Balvín et al. 2012a). It is possible that the European population of the bed bug found on bats in the present study is of rather recent origin. Furthermore, this bed bug population appears to be discontinuous from the original population inhabiting caves.

The validity of two of the former three European species of the *C. pipistrelli* group was recently dismissed (Balvín et al. 2013). Though the taxonomy has not been completely resolved, only one species is likely to exist in Europe and only one is therefore recognized in this study. Morphological variation in diagnostic characters was connected with association to different bat species. Since the taxonomy of the other seven species of the *C. pipistrelli* group described from Asia is based on similar metric characters, the situation found in European taxa also makes the validity of this taxonomy questionable. Therefore, any conclusions regarding the distribution of taxa from the *C. pipistrelli* group are not currently possible. It is clear, however, that the species group is the dominant cimicid parasite of bats in the Palaearctic region. While the records of *C. lectularius* on the crevice-dwelling bat species like *Nyctalus* and *Pipistrellus* spp. are sporadic, these bats are common hosts for *C. pipistrelli* (Povolný 1957, see Table 1 for other references). *C. pipistrelli* is common in roosts of *Myotis myotis* as well (e.g. Lederer 1950, Usinger 1966). In contrast to *C. lectularius*, because of its association with *Nyctalus* spp., the area of *C. pipistrelli* in Europe stretches as far as the southern peninsulas (Lanza 1999, Simov et al. 2006, Balvín et al. 2012b).

Cimex emarginatus was known only from the type locality, a roost of *M. emarginatus* in a building near Primorsko, Bulgaria (Simov et al. 2006). Recently, this species was confirmed to be distinct from but related to *C. lectularius* based on mtDNA data (unpublished), as Simov et al. (2006) presumed.

This paper reviews the records of bat-associated *Cimex* species from bat roosts in Europe made during collection of material for population genetic studies (Balvín et al. 2012a, Balvín et al. 2013, Booth et al. 2015). The geographic distribution of the two species in Europe is reviewed. Also, their host and habitat preferences are discussed.

Material and Methods

In the Czech Republic, a systematic monitoring of three species of bats (*R. hipposideros*, *M. myotis* and *M. emarginatus*) included in the Natura 2000 system is carried out (Bartonička & Gaisler 2010). Roosts of other bat species are also occasionally visited or searched for. The localities monitored in the Czech Republic are maternity colonies consisting of females bearing their young in the summer shelters. They are mostly located in buildings. The material reported in this study has been mostly collected from such summer roosts by the authors by joining the monitoring teams,

Table 1. Review of records of *Cimex lectularius* and *C. pipistrelli* for European bat species in the literature and our material. Records from *Pipistrellus kuhlii* are from Iraq. The first reference for each bat species known to us is listed. For details on our records from roosts see Supplementary material Table 2. Country codes: BG – Bulgaria, CZ – Czech Republic, FI – Finland, FR – France, GE – Germany, HU – Hungary, CH – Switzerland, RS – Serbia, SK – Slovakia, UK – United Kingdom. The single record for *Rhinolophus ferrumequinum* refer to a case when hosting cimicids was directly proved; however, *Rhinolophus* spp. are often found in colonies mixed with usual hosts of cimicids where they can serve as substitution hosts as well. Bold records refer to newly recorded host-parasite relationships. * - roost shared with *M. myotis*. The names *M. blythii* and *M. oxygnathus* may be synonymous.

Bat species	*Cimex lectularius*		*Cimex pipistrelli*	
	Reference	No. of roosts in our material	Reference	No. of roosts in our material
Eptesicus serotinus	Baagøe 2011	2 (CZ, HU)	Southwood & Leston 1959	
Myotis bechsteinii	Scheffler 2008		Morkel 1999	
Myotis blythii	Tagilcev 1971 (*Cimex* sp.)		Tagilcev 1971 (*Cimex* sp.)	1*(HU)
Myotis brandtii			Heise 1988	1 (CZ)
Myotis dasycneme			van Rooij et al. 1982	
Myotis daubentonii	Wagner 1967		Heise 1988	2 (CZ), 1 (GE)
Myotis emarginatus	Usinger & Beaucournu 1967	3 (CZ), 2 (HU), 4 (RS), 2 (SK)	Usinger 1966	2*(HU, SK)
Myotis nattereri				**1 (CZ), 1 (GE)**
Myotis myotis	Povolný 1957	23 (CZ), 3 (GE), 5 (SK), 3 (FR, CH, HU)	Lederer 1950	41 (CZ), 2 (HU), 9 (SK), 2 (FR, CH),
Myotis mystacinus	Poppius 1912		Kerzhner 1989	
Myotis oxygnathus	Usinger 1966	1*(HU)		
Nyctalus lasiopterus			Balvín et al. 2012b	
Nyctalus leisleri	Bobkova 2001		Nelson & Smiddy 1997	
Nyctalus noctula	Heise 1988		Povolný 1957	3 (CZ), 4 (BG, GE, SK, UK)
Pipistrellus kuhlii	Abul-Hab 1979		Abul-Hab & Shihab 1990	
Pipistrellus nathusii			Heise 1988	
Pipistrellus pipistrellus	Rybin et al. 1989		Jenyns 1839	
Pipistrellus pygmaeus			Bartonička 2007	3 (CZ), 1 (UK)
Pipistrellus sp.		2 (CZ), 1*(SK)		3 (UK)
Plecotus auritus	Balvín et al. 2012b			
Rhinolophus ferrumequinum		**1*(RS)**		
Vespertilio murinus	Dubinij 1947		Horváth 1935	

starting 2005. Some material of cimicids has also been collected by the monitoring specialists during the colony censuses.

The data from Bulgaria were collected 1) during a thorough survey targeted at cimicids, covering about 500 roosts between 1997 and 2008 and 2) during the course of a project entitled "Mapping and identification of conservation status of natural habitats and species" (Phase I in Natura 2000 zones in Bulgaria), covering about 1600 diverse bat roosts since 2011.

In Serbia, a systematic monitoring of mixed maternity roosts of *Myotis emarginatus* and *Rhinolophus ferrumequinum* has been carried out since 2003 in the area of southern Banat, Vojvodina province. Six roosts have been found and shown to communicate with each other based on capture-recapture experiments. In addition to these, about 500 roosts of bats, mainly of species *Myotis capaccinii*, *M. myotis*, *M. oxygnathus*, *Miniopterus schreibersii*, *Nyctalus noctula* and *Pipistrellus pipistrellus*, often mixed with each other

or *Rhinolophus* spp., are known over the entire area of Serbia and examined for the presence of ectoparasites, though not as regularly as those in Vojvodina province or Bulgaria.

Finally, about 10 days of field work in bat roosts in Slovakia and Hungary were carried out. Part of the material was collected by bat specialists in other European countries (see Supplementary material Table 2). If possible, the close surroundings of the bat colonies were examined for the presence of cimicids, paying special attention to the most likely shelters of their refugia: crevices in walls and wood below and around the bat colony, or bottom side of objects located below the colony. In some spacious roosts, the colony was unreachable and only the guano and surrounding floor could be inspected. If unsuccessful, dead cimicids were searched for in the guano or spider webs. The number of female bats was noted. Maximal number of cimicids were collected, or, at least dead individuals and exuviae; however the collection had often to respect the need to keep the presence of bugs from the wardens of the respective buildings.

Results and Discussion

Host relations

The records of *Cimex lectularius* and *C. pipistrelli* in bat roosts in Central Europe, Serbia, Bulgaria and some other European countries are summarized in Table 1 and Supplementary material Table 2. Generally, the number of colonies monitored annually varied among bat species. It was high in non-dwelling bats with high fidelity to shelters, such as *Rhinolophus hipposideros*, *Myotis myotis* and *M. emarginatus*. In species with low philopatry the long-term monitoring is difficult. Even in common species (e.g. *Pipistrellus pipistrellus*, *Nyctalus noctula*) it is difficult to locate summer colonies. If found, the roosts cannot be checked in the following years as they are often destroyed or the bats relocate during large-scale renovations of buildings (especially prefabricated houses). Furthermore, such roosts are often difficult to check for both bats and cimicids because of their crevice character, in contrast to the spacious roosts of philopatric bat species. Therefore, the numbers of records for each bat species are not representative with regard to the incidence of cimicids in their roosts. However, the incidence can be considered high at least in some species like *Nyctalus* spp. and *Pipistrellus* spp., given the number of records on mist-netted individuals (Balvín et al. 2012b) or roosts inhabited by these species (Supplementary material Table 2).

Cimex pipistrelli was confirmed as a parasite of the attic-dwelling bat species *M. emarginatus*, *Myotis myotis* and, possibly, *M. blythii*, as well as the crevice-dwelling bat species *Myotis brandtii*, *M. daubentonii*, *Nyctalus noctula*, *N. leisleri*, *Vespertilio murinus*, *Pipistrellus pygmaeus* and, possibly, *P. pipistrellus*. It was newly recorded for *Myotis nattereri* (Lužnice, Czech Republic, Supplementary material Table 2). The new record for *Nyctalus lasiopterus* was already mentioned by Balvín et al. (2012b).

Cimex lectularius was confirmed to parasitize on the attic-dwelling bat species *Myotis myotis*, *M. emarginatus* and, possibly, *M. oxygnathus*, as well as the crevice-dwelling bat species *Eptesicus serotinus* and *Pipistrellus* sp. (see below).

Among attic-dwelling bat species, both cimicid species were shown to be very common in roosts of *Myotis myotis* in central Europe. Less than 25 % of these synanthropic roosts inspected by the authors were negative. In the Czech Republic, out of about 140 monitored roosts about 80 were inspected for the presence of cimicids, which were found in 64 (~80 %) roosts. In total, *Cimex lectularius* was recorded in 36 roosts of *M. myotis* and *C. pipistrelli* in 46. No cimicids were found in the cave roosts in Serbia and Bulgaria.

Myotis myotis was the only bat species hosting both cimicid species in one roost, though only in few isolated cases. Mixed infestation was found only at the colony in Dubá (Czech Republic) in 2013 and 2014, whereas in 2009 only *C. lectularius* was discovered (Supplementary material Table 2). In 2009, this bat colony was complemented by several hundred bats from a nearby roost in Doksy. In this roost, only *C. lectularius* was found in the year the bats moved to Dubá, so other, unknown bats had to have brought *C. pipistrelli*. A mixed infestation was also revealed found in Zemianske Kostoľany (Slovakia), but among remains of bodies of unknown age. A change of infestation from *C. pipistrelli* to *C. lectularius* over years has likely been recorded in Úštěk and Držovice (Czech Republic). However, samples from these roosts were not numerous and may not reflect the composition of the species. Part of samples from other roosts also contained only a few individuals but comparing the numbers of roosts with consistent and inconsistent record of *Cimex* species it is likely that populations of cimicids in single roosts mostly consisted only of one species. Based on this limited evidence, the mechanisms of coexistence or competition between *C. pipistrelli* and *C. lectularius* can only be speculated on. However, the co-occurrence of the two species is likely caused by the co-occurrence of different bat species in a single roost. Attic-dwelling bats like *M. myotis*, frequent

hosts of *C. lectularius*, often share attics with crevice-dwelling bats like *Pipistrellus* spp. (e.g. Hosťovce) or *Eptesicus* spp. (e.g. Oleksovice; see Supplementary material Table 2 or Czech bat Conservation Society database, unpublished), frequent hosts of *C. pipistrelli*. *Myotis oxygnathus* was confirmed as a host of *C. lectularius* only in a colony mixed with *M. myotis* (Martonyi, Hungary, Supplementary material Table 2). In the same area of the Aggtelek Karst in Hungary, two more roosts inhabited only by *M. oxygnathus* were visited and no trace of cimicids was found. As *M. oxygnathus* is physically and ecologically almost identical to *M. myotis*, the absence of cimicids in the roosts of this species may not be a coincidence, considering the at least 80 % incidence of cimicids in synanthropic *M. myotis* roosts in our record. It is possible that *M. oxygnathus* does not constitute a suitable host for cimicids for an unknown reason.

In roosts of *M. emarginatus*, only *C. lectularius* was confirmed. It was found in 11 synanthropic roosts, often shared with *Rhinolophus* spp. A similar number of roosts with similar microclimates was negative. There is a single published record of *C. pipistrelli* from *M. emarginatus* (Usinger 1966), while the records of *C. lectularius* are at least three (Usinger & Beaucournu 1967, Protić & Paunović 2006). *C. pipistrelli* was found only in two roosts of *M. emarginatus* shared with *M. myotis*. It is possible that *M. emarginatus* is the only host that *C. lectularius* does not share with *C. pipistrelli*, at least in Central Europe and Serbia.

Further south, however, *M. emarginatus* has been shown to host *C. emarginatus* (Simov et al. 2006). The colony from which the type material originated flew away in 2005. Since then, only a single record (female) of *C. emarginatus* is available from mist-netted *Myotis* cf. *alcathoe* (Bulgaria, Monastery Sveti Archangel, Malashevska planina Mts., Blagoevgrad district, 41°51′23.04″ N, 22°59′31.92″ E, 10 September 2011, B. Petrov, I. Alexandrova lgt.). If the determination of the bat species is correct, it is also the first record of a cimicid for this newly described species. In 2006, *C. emarginatus* was unsuccessfully attempted to be confirmed by investigating a large unfinished building of a hotel near the type locality in Primorsko, which was inhabited by multiple colonies of *M. emarginatus* and many other bat species (*Myotis blythii*, *Myotis* sp., *Miniopterus schreibersii*, *Rhinolophus* spp., see Benda et al. 2003). Only two specimens of *C. pipistrelli* were collected in this study (Supplementary material Table 2).

The presence of *C. lectularius* in roosts of *Pipistrellus* sp. was shown indirectly. The bugs attacked people in a gamekeeper's house near Hnanice, South Moravia, and a hunting hide nearby. In both buildings, colonies of *Pipistrellus* sp. were recorded (*P. pipistrellus* or *P. pygmaeus*; not distinguished at that time). Although these bugs were unusually small, similar to *C. pipistrelli* from *Pipistrellus* spp., in other morphological characters they clearly corresponded to *C. lectularius* from other bat species (Balvín et al. 2012a). The third record of *C. lectularius* from *Pipistrellus* sp. was made from a roost shared with *M. myotis* (Hosťovce, Slovakia).

Roosts inhabited only by *Rhinolophus* spp. were always free of cimicids, which is consistent with the literature. Unlike vespertilionid bats, *Rhinolophus* spp., at least in the synanthropic roosts in Central Europe, rarely form tight clusters (Gaisler 1966) and readily move through the roosting space. This likely makes them an unsuitable host for cimicids. Until recently, *Plecotus* spp. was similarly considered an unsuitable host for cimicids, regarding the entire lack of published records for such common bats. Unlike *Nyctalus* or *Pipistrellus* spp., most of the maternity colonies of *Plecotus* spp. are comprised of only a few individuals (Anděra & Horáček 2005), which were believed to be incapable of hosting a population of cimicids, similar to the diffusive colonies of *Rhinolophus* spp.

Out of the 140 summer roosts that are annually monitored in the Czech Republic, at least 23 are inhabited by species that commonly host cimicids together with *Plecotus* or *Rhinolophus* spp. (Bartonička & Gaisler 2010). *Rhinolophus* spp. are also listed as hosts of cimicids in records from colonies mixed with, for example, *Myotis emarginatus* (Usinger 1966, Usinger & Beaucournu 1967, Protić & Paunović 2006). A recent record of *C. lectularius* has been made from *Plecotus auritus* (Balvín et al. 2012b). Furthermore, the first record of *Cimex* (*C. lectularius*) from bats from Serbia was made from *Rhinolophus ferrumequinum* caught by harp trap. More recently, *C. lectularius* was found on three more individuals of *R. ferrumequinum* caught using the same technique, as well as on five specimens of *M. emarginatus*. These bats came from a mixed colony of the two species. One of the visits of the colony was made in August 2013, when only a few *M. emarginatus* individuals remained among about a thousand *R. ferrumequinum* bats. However, the bugs were numerous and recently fed. It is therefore clear that *Plecotus* and *Rhinolophus* spp. are able to serve at least as occasional or temporary, though likely less suitable, hosts of cimicids.

Moreover, the preference for a specific host was not detected in host-specificity experiments. *C. pipistrelli* repeatedly sucked on the bat species in whose roosts they have never been observed (Zedníková 2010). In conclusion, the bugs of the genus *Cimex* appear to be common ectoparasites of 20 bat species in Europe (Table 1). The difference between the ranges of host species of *C. pipistrelli* and *C. lectularius* may suggest different host preferences. These preferences can result from different ecologies of the respective bat species (tree or building dwellings versus large attics), as *C. lectularius* is found mostly on attic-dwelling bat species. However, the historical distribution of some of the host bat species, especially *Myotis myotis*, may have played a more important part.

Geographic distribution of cimicids and their hosts

While *Cimex lectularius* as a parasite on man is cosmopolitan, the distribution of the bat-related lineage has never been reviewed. To our knowledge, the records come from the following countries: Afghanistan (Usinger 1966), the Czech Republic (Povolný 1957), Finland (Poppius 1912), France (Usinger & Beaucournu 1967), Germany (e.g. Eichler 1937), Serbia (Protić & Paunović 2006, misidentified as *C. pipistrelli*) and Slovakia (Usinger 1966). Our records extend the known distribution to Hungary, Switzerland (Table 1) and Ukraine (Table 2 in Balvín et al. 2012b, record from a mist-netted bat).

The distribution of *Cimex pipistrelli* has been recently reviewed by Péricart (1996). More recent records of *C. pipistrelli* are by Krištofík & Kaňuch (2006, Slovakia) and Simov et al. (2006, Bulgaria, Greece). The species was newly recorded from Lebanon, Ukraine and Spain; however, all these findings come from mist-netted bats and were listed already by Balvín et al. (2012b).

As cimicids are parasites of bats in their summer roosts, the geographic distribution of cimicids follows the breeding areas of their host species. Records from overwintering bats are singular (Simov et al. 2006). The host range recorded for *C. pipistrelli* and *C. lectularius* (Table 1), comprising many bat species with diverse ecologies, may suggest that their distribution evenly covers all Europe. However, this is not true based on comprehensive data available from five countries covering a Northwest-Southeast transect across Europe: the Czech and Slovak Republics, Hungary, Serbia and Bulgaria. Although the incidence of cimicids in roosts of crevice-dwelling bat species in central Europe cannot be exactly determined, considering the numerous records in our material or the literature, cimicids can be regarded as more or less frequent in their roosts. The incidence of cimicids in roosts of attic-dwelling bats in Central Europe appears to be high.

This situation is in contrast with the frequency of records from Bulgaria. Records from 1997-2006, coming from the comprehensive survey of about 500 roosts in caves, buildings, bat-boxes and tree holes, as well as from examination of about 20000 captured bats were summarized by Simov et al. (2006). They comprise the finding of the newly described *C. emarginatus* in a roost of *M. emarginatus* and only two records of *C. pipistrelli* from *Nyctalus noctula*. Since 2011, an even more extensive survey as part of Natura 2000 has covered about 1600 bat roosts. Furthermore, an additional ca. 10000 mist-netted bats were examined for ectoparasites during the period 2007-2013 in the Tabachka Bat Research Station. During these surveys, no cimicids were found. In addition to these surveys, 1) the second record of *C. emarginatus* was made; 2) *C. pipistrelli* was found in Primorsko, as mentioned above; 3) *C. pipistrelli* was found in 2004 (though only at a photograph) and in 2013 in a bat-box inhabited by *Nyctalus noctula* at Sedemte Prestola Monastery (Western Balkan Mts., see Supplementary material Table 2); and 4) unidentifiable *Cimex* specimens were found in 2006 in guano under a roost likely inhabited by *Nyctalus noctula* in the entrance of Devetashka cave (Lovech Province, see Supplementary material Table 2).

Numerous roosts of *Myotis emarginatus* were examined in southern Vojvodina, a northern province of Serbia, documenting the likely reason for the absence of *C. lectularius* in bat roosts in the southern Balkans. If the non-dwelling bat species *M. myotis* and *M. emarginatus* can be regarded as the principal hosts for *C. lectularius*, as suggested by the limited records from other bats, the absence of *C. lectularius* on bats in the Balkans can be explained by the characteristics of roosts, as suggested by Simov et al. (2006). The temperature in deep caves, where *Myotis* spp. typically roost, is usually below 15 °C, while the humidity often reaches 80-90 % (e.g. Paksuz et al. 2007). The combination of low temperature and high humidity has been shown to be unfavourable or even lethal for *C. lectularius*, and its development is arrested below 13-15 °C (Kemper 1936, Omori 1941). In central Europe, these bat species are synanthropic, inhabiting warm and dry attics. In more southern areas, they mostly occupy their natural habitats of large caves, which are often too humid and cold for cimicids. In Vojvodina province, northern Serbia, *C. lectularius* seems to be common in roosts of *M. emarginatus* in

buildings, whereas in the roosts in caves in central and south Serbia, cimicids have not been recorded.

However, the reason for such low frequency of records of *C. pipistrelli* in Bulgaria and Serbia is less clear. Only about one third of the bat roosts examined during the Natura 2000 mapping in Bulgaria were in humid and cold caves, which are often inhabited by *M. myotis* and *M. emarginatus*. The rest inhabited shallow, dry caves or their entrances (e.g. the entrance of Devetashka cave, Bulgaria, where remains of bugs were found), tree holes, bat-boxes and buildings which should be suitable for cimicids.

As an explanation for the low frequency of records of both *Cimex* species in southern Europe, it is possible that stable colonies of attic-dwelling bats like *M. myotis* provide long-term local reservoirs for infestations in roosts of crevice-dwelling bats. Colonies of such bat species as *Pipistrellus* spp. or *Nyctalus* spp. often split and change roosts during the breeding season, a phenomenon that has been described as the fission-fusion behavioural model (Kummer 1971). This behaviour efficiently reduces the numbers of bugs in the roosts and may be occurring, at least partially, for this purpose (Bartonička & Růžičková 2012). Infestations of a local population of a bat species can eventually be eliminated through this behaviour. This is supported by genetic data on both *C. lectularius* (Balvín et al. 2012a, Booth et al. 2015) and *C. pipistrelli* (Balvín et al. 2013, Wawrocka in litt.), which show no host-associated structure and suggest frequent switching between bat species within regions. In southern Europe, stable infestations in roosts of attic-dwelling bats are absent and therefore cannot be the source of re-infestation of crevice-dwelling bats.

However, this is only partly true for *Nyctalus* species, at least *N. noctula*. Almost all records of *C. pipistrelli* from southern Europe [Bulgaria, Greece (Simov et al. 2006) and Italy (Lanza 1999)] and Lebanon (Balvín et al. 2012b) are from *N. noctula*. Only the record from Spain (Balvín et al. 2012b) was from *N. lasiopterus*. The southern limit of the breeding area of *N. noctula* is 48° N (Kaňuch & Celuch 2004). In summer, only males and non-reproductive females are found south of this limit. As suggested by Simov et al. (2006), it is possible that all the records of *C. pipistrelli* from southern Europe are only temporary transmissions by *N. noctula*. However, at least in the bat-boxes in Cherven and Sedemte Prestola Monastery (Bulgaria), *C. pipistrelli* was found in two subsequent years (Simov et al. 2006, Supplementary material Table 2). It is therefore possible that stable populations may occur here. *N. noctula* transmits cimicids much more often (Balvín et al. 2012b) and is much more migratory than other bat species. Therefore, if the hypothesis of local reservoirs of cimicids in *M. myotis* roosts is valid, in situation when the reservoirs are missing, the local populations in *N. noctula* roosts are not likely to die off like in other crevice-dwelling bat species.

In conclusion, the distribution of *Cimex lectularius* and *C. pipistrelli* is not consistent across the areas of distribution of their host bat species (i.e. different host relations are found in different areas). The distribution of cimicids is presumably shaped by the ecology of bat species. However, it is possible that some bat species provide reservoirs of cimicids, and changes in their ecology across their area of distribution may affect populations of cimicids on other bat species.

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Supplementary online materials

Table 2. List of records of cimicids in bat roosts. IC – identification code of samples in the collection of Ondřej Balvín. Unlabeled collections are deposited in the collection of Tomáš Bartonička; CC – country code (BG – Bulgaria, CZ – Czech Republic, FI – Finland, FR – France, GE – Germany, HU – Hungary, CH – Switzerland, RS – Serbia, SK – Slovakia, UK – United Kingdom); HS – host species: more species listed mean mixed colonies (UBS – unknown bat species, *Eser – Eptesicus serotinus*, *Mbra – Myotis brandti*, *Mdau – M. daubentonii*, *Mema – M. emarginatus*, *Mmyo – M. myotis*, *Mbly – M. blythii*, *Moxy – M. oxygnathus*, *Mnat – M. naterreri*, *Nnoc – Nyctalus noctula*, *Pip* sp. – *Pipistrellus* sp. (*P. pipistrellus* or *P. pygmaeus*), *Ppyg – Pipistrellus pygmaeus*, *Reur – Rhinolophus euryale*, *Rfer – R. ferrumequinum*; NF – number of female bats at the collony; BS – cimicid species (*Clec – Cimex lectularius*, *Cpip – C. pipistrelli*). (Excel file; URL: http://www.ivb.cz/folia/download/balvin_supplementary_table_2.xls).