

Bed bugs: The move to humans as hosts

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Abstract

Cimicid insects, bed bugs and their allies, include about 100 species of blood-feeding ectoparasites. Among them, a few have become widespread and abundant pests of humans. Cimicids vary in their degree of specialization to hosts. Whereas most species specialize on insectivorous birds or bats, the common bed bug can feed on a range of distantly related host species, such as bats, humans, and chickens. We suggest that association with humans and generalism in bed bugs led to fundamentally different living conditions that fostered rapid growth and expansion of their populations. We propose that the evolutionary and ecological success of common bed bugs reflected exploitation of large homeothermic hosts (humans) that sheltered in buildings. This was a departure from congeners whose hosts are much smaller and often heterothermic. We argue that interesting insights into the biology of pest species may be obtained using an integrated view of their ecology and evolution.

Key words: bed bug, Cimicidae, evolutionary biology, parasite–host interactions, public health

The common bed bug (*Cimex lectularius* Linnaeus, 1758) is a widespread and locally abundant pest of humans. It is one of about 100 species of cimicid insects, most of which are small, flightless, obligate blood feeders (Usinger 1966; Reinhardt and Siva-Jothy 2007). Males and females eat only blood and a blood meal is required for egg production, mating, growth, and development to adulthood. Most cimicids consume the blood of bats (Molossidae and Vespertilionidae) or birds (Apodidae—swifts; Hirundinidae—swallows). Some populations of common bed bugs, however, have adapted to living with and on humans, and perhaps chickens (Reinhardt and Siva-Jothy 2007). About once a week, captive adult cimicids feed for 10–20 min. When not feeding, cimicids hide in cracks and crevices (Usinger 1966; Reinhardt and Siva-Jothy 2007). Although they spend most of their time off of their hosts' bodies, cimicids are often considered ectoparasites because they remain within the host's roost, nest, or dwelling. According to other definitions, however, they could be classified as micropredatory blood-suckers (Balashov 2006).

Cimicids exhibit variation in the range of host taxa used by any species (e.g., Usinger 1966; Reinhardt and Siva-Jothy 2007). Two subfamilies (Primicimicinae and Latrocimicinae) use New World bats as hosts, whereas two others (Cacodminae and Afrocimicinae) use Old World bats. The hosts of Haemosiphoninae are a variety of birds in the New World. *Cimex lectularius* and *Cimex hemipterus* occur mainly on humans, but can survive on chickens (Benoit 2011; Criado et al. 2011). Furthermore, one lineage of *C. lectularius* occurs on several species of Old World bats.

Among parasites, weak generalists use several closely related species of hosts (Mazé-Guilmo et al. 2016). These may be more efficient feeders and have higher fecundity when feeding on preferred hosts (Reinhardt and Siva-Jothy 2007). Strong generalists are species using several phylogenetically distinct hosts (Mazé-Guilmo et al. 2016). Only a few cimicids, such as the common bed bug and possibly the

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tropical bed bug *C. hemipterus*, appear to be strong generalists. Most other cimicids are weak generalists. Molecular data provide evidence for adaptation by cimicids to different hosts. There has been a significant divergence among and within cimicid species at genes coding for salivary proteins, which are important for blood feeding. Divergence has been recorded among different cimicid species associating with different hosts across the world (Talbot et al. 2017). The same is true among populations of a single species associating with different bat species in North America (Talbot et al. 2018). Flexibility in choice of hosts may benefit strong generalists when conditions change. The purpose of this paper is to speculate about key ecological changes that some cimicids would have encountered as they began, and then continued, to include humans as preferred hosts. This meant a transition from weak to strong generalism, which resulted in population growth and emergence of a worldwide human pest.

The first record of a cimicid-like insect comes from Cretaceous amber from Myanmar (Grimaldi et al. 2002). Bats appeared somewhat later (Fenton and Simmons 2014). Like others, we propose that bats were early hosts for cimicids (Usinger 1966; Balvín et al. 2012; Booth et al. 2015). The importance of cimicids to the life cycles of trypanosomes associated with bats (Bower and Woo 1981) suggests a long association between bats and these insects. A stable transition of some cimicids to human hosts possibly occurred in the Pleistocene epoch. In Eurasia, although the common bed bug occurs on a range of insectivorous bat species, populations of one lineage associate mostly with humans (Balvín et al. 2012, 2015; Booth et al. 2015). This lineage appears to have diverged from the rest of the group about 245 000 years ago. By the late Pleistocene and early Holocene, the association between cimicids and humans appears to have become widespread. Reinhardt and Siva-Jothy (2007) reported evidence of at least 4000 years of association between humans and cimicids. Recent discoveries in western North America suggest that at least three cimicid species and humans were in contact in shelter caves since about 11 000 years ago (Adams and Jenkins 2017).

Despite their small individual body size, communal roosting makes groups of bats a relatively large and stable food supply for cimicids. In summer, vespertilionid and molossid hosts typically roost in dark crevices and hollows (e.g., Willis and Brigham 2007). Depending upon the species, these bats weigh about 5–30 g and often roost in groups. In a roost, bats themselves may be as important to other bats as the exact nature of the roost. This reflects the clear thermoregulatory benefit to clustering with others (Brown 1999; Willis et al. 2005; Pretzlaff et al. 2010). Clusters of day-roosting bats in summer are usually conspecifics, and regular roost-switching is taken to reflect a fission–fusion social organization (Willis and Brigham 2004). Nursery colonies consist of pregnant and lactating females with their dependent young. These groups represent a ready supply of blood for cimicids. Movements of individuals and fission–fusion social organization means that cimicids living in any bat roost are mainly exposed to one species, but may feed on several individuals over the summer. Many species of bats show different levels of roost fidelity, perhaps making these mammals predictable food sources (Lewis 1995). However, high roost-switching frequency in many species is hypothesized to be a strategy to reduce parasitism (Willis and Brigham 2004; Bartonička and Růžicková 2013). Therefore, host fidelity in most cimicid species is probably more a function of bat behavior than choices made by cimicids.

Although offset to some extent by communal roosting behavior, the size of individual bats and aspects of their thermoregulation may, nonetheless, be limiting factors for blood-feeding ectoparasites. The body mass of unfed adult female common bed bugs is 5 mg, on average, but they eat, on average, 7.6 mg in any blood meal (Usinger 1966). In mammals, blood constitutes about 10% of body mass, so a 10 g adult bat holds approximately 50 000 times less blood than a human. Humans are also more consistently homeothermic than vespertilionid or molossid bats. Although a bat's body temperature is elevated when flying and foraging, its metabolic rate, and consequently body temperature, are reduced

after returning to its roost (Stawski et al. 2014). For individuals that enter torpor, declines in body temperature can be rapid, within 30 min of returning to the roost (Audet and Fenton 1988). Based on efforts to collect blood from bats, biologists have learned that it is difficult to obtain samples from torpid individuals (Martin and Stehn 1977). If body temperature affects blood flow, and possibly, as a consequence, cimicid blood feeding behavior (DeVries et al. 2016), cimicids feeding on bats likely have relatively little time to efficiently consume blood. The behavior of cimicids and their bat hosts suggests that effective feeding must occur as soon as possible after bats return to the roost. Thus, heterothermy may reduce the resource value of bats as hosts for cimicids compared with consistently homeothermic vertebrates such as birds or humans. Overall, the combination of small size and heterothermy could mean that for cimicids, bats represent a more limiting resource.

By occupying cracks, crevices and hollows in human dwellings, bats would have brought their cimicid parasites into close contact with humans (Usinger 1966). The proximity of roosting bats and their cimicids to people likely created opportunities for cimicids to adapt to new hosts. There are contemporary records of cimicid individuals from species commonly associated with bats, such as *C. adjunctus*, *C. pipistrelli*, and *C. pilosellus*, occasionally feeding on humans visiting or residing near a bat roost (Goddard et al. 2012). Unlike many insects, female cimicids cannot store seminal fluid but instead may use it for nutrition (Hinton 1964). For this reason, female cimicids may be able to survive in the absence of the host for a limited time. Nonetheless, in the event of bats not returning to a roost for an extended duration (Bartonička and Růžicková 2013), humans would constitute a convenient alternative food source. Mechanisms underlying reproductive isolation, which could subsequently lead to speciation, have been explored in bat- and human-associated *C. lectularius* lineages in Europe (Wawrocka et al. 2015; DeVries et al. 2017).

For a blood-feeding ectoparasite, transition to a relatively large, consistently homeothermic host could dramatically increase resource availability and carrying capacity (Morand et al. 2006). Phylogeographic data for European *C. lectularius* suggests 20% higher effective population sizes in lineages associated with humans compared with the ancestral lineage that is mainly associated with bats (Balvin et al. 2012). In contrast, *C. adjunctus*, a North American species typically associated exclusively with bats, shows an overall decrease of effective population size across the continent over the last 300 000 years (Talbot et al. 2016). Overall, phylogeographic analyses suggest higher effective population size and potentially greater population stability over the long term for cimicid lineages associated with humans compared with bats. Thus, humans are large, dependable sources of blood, and constitute a stable food source for cimicids. Furthermore, human dwellings offer many crevice retreats for cimicids and a stable environment.

In conclusion, we argue that key differences between bat and human hosts, particularly in body size and thermoregulation, allowed the ecological release of cimicid populations that moved to humans as hosts. These differences contributed in large part to the evolutionary and ecological success of at least one lineage of Cimicidae that has emerged as the cosmopolitan common bed bug. We suggest that this example illustrates the interesting insights into the biology of pest species that may be obtained using an integrated view of their ecology and evolution.

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Author contributions

BT, NK, and BF conceived and designed the study. BT, NK, and BF drafted or revised the manuscript.

Competing interests

BF is currently serving as a Subject Editor for FACETS, but was not involved in review or editorial decisions regarding this manuscript.

Data availability statement

All relevant data are within the paper.

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