Biology of the Bed Bugs (Cimicidae)

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Key Words

ectoparasite, hematophagy, passive dispersal, reproductive behavior, sexual conflict, traumatic insemination

Abstract

The cimicids, or bed bugs, belong to a highly specialized hematophagous taxon that parasitizes primarily humans, birds, and bats. Their best-known member is the bed bug, *Cimex lectularius*. This group demonstrates some bizarre but evolutionarily important biology. All members of the family Cimicidae show traumatic insemination and a suite of female adaptations to this male trait. Cimicids therefore constitute an ideal model system for examining the extreme causes and consequences of sexual selection. Our dual goal in re-examining the extensive literature on this group is to identify issues relevant to pest control, such as dispersal ecology and the recent global spread, and to understand the selective forces that have shaped the unique aspects of this insect's biology.

INTRODUCTION

The common bed bug, *Cimex lectularius*, is one of the most widely recognized insects in the world. Its close association with humans has been documented for more than 4 millennia (136) and is further corroborated by the extensive linguistic variation in common names (125, 185). Despite this long (and painful) association, we know remarkably little about several aspects of the biology of this economically important insect and its close relatives. Usinger's (185) monograph forms the core of our understanding of this taxon, although there are other more recent reviews (163). Because cimicids cause discomfort rather than transmit disease, their decline in the developed world (29) was followed by a decline in academic interest. However, this interest was recently rekindled by new ideas in sexual selection. The taxon played a key role in developing the idea that females could exercise mate choice after copulation (so-called cryptic female choice) (59) and that different optima in the mating rate of both sexes could drive sexual conflict (6, 137), a form of selection that can produce antagonistic male sexual traits. Because bed bugs show such antagonistic male traits (traumatic insemination) (32, 33) they became an attractive model organism with which to examine sexual conflict.

It is also apparent that global bed bug infestations are increasing (see Recent Spread, below). Their ability to spread discomfort makes a re-examination of aspects of the reproduction and ecology of these insects, in the context of control, timely.

This review builds on the foundation of bed bug biology provided by Usinger (185). We do so in a conceptual framework that encompasses modern evolutionary and ecological thinking about host-parasite interactions, sexual selection, reproductive isolation, physiology, and ecology, including the host perspective. Throughout this review we refer to bed bugs, cimicids, and Cimicidae synonymously.

Traumatic insemination: the act of inseminating through the body wall, into the body cavity (rather than into the female's genital tract); involves physical breaching of the epidermis

Refugium: an enclosed space (e.g., a crack in a wall) in which bed bugs conceal themselves between blood meals

Mesospermalege: the hemocyte-containing bed bug organ into which sperm are introduced

Paragenital system: the secondary genital system of female cimicids

BASIC BED BUG BIOLOGY

Two major adaptations are central to cimicid biology: obligate hematophagy and traumatic insemination (185). Both sexes feed only on blood, and eclosion into the subsequent instar requires a blood meal. Moreover, egg production in adult females (and presumably sperm production in males) requires regular blood meals (see Reference 185 for a review on egg production). Feeding behavior in *C. lectularius* coincides with periods of minimal host activity, when bed bugs leave their refugia to feed. An adult *C. lectularius* fully engorges in 10 to 20 min, after which it returns to its refugium (185). Under ad libitum conditions imaginal *C. lectularius* feeds once per week (185). The time between feedings is spent concealed inside the refugium. Few quantitative data exist on the preferred sites for refugia, refugium faithfulness, or the site of mating activity in natural populations.

In addition to driving ontogeny and fecundity, feeding is an essential prerequisite for mating: *C. lectularius* males direct their sexual interest at recently fed females (45, 119, 168, 177) (for information on *Ornithocoris toledoi*, see Reference 170). Such females receive approximately five traumatic inseminations per feeding (not necessarily from the same male) (177), during which the male pierces the female's abdominal wall. In all species except *Primicimex cavernis*, the sperm are injected into the mesospermalege (185), a component of the female's paragenital system, through which sperm migrate (32, 33, 185). Female cimicids also possess the normal female reproductive tract that functions during oviposition. Males never use the genital tract for insemination.

Female bed bugs therefore have a paragenital tract that functions in mating and through which sperm migrate to reach eggs, and a genital tract that functions during oviposition. Readers seeking details about bed bug biology are referred to Usinger (185).

REPRODUCTIVE BIOLOGY

The reproductive biology of the Cimicidae in general and mating of *C. lectularius* in particular have been examined in some detail (32, 33, 51, 97, 126, 144, 145, 149, 157, 158, 169, 173, 177). The facts that cimicid reproductive biology evolved in the context of selection by sexual conflict and that the resultant anatomical and physiological traits are well documented and easy to study mean that this system lends itself to studies of sexually antagonistic coevolution.

Mate Recognition and Preference

How males encounter and recognize recently fed females in the dark is unclear. Almost all studies reported here focus on *C. lectularius*. Movement of any bed bug–sized object in the vicinity produces an approach response in males (154, 163). If the disturbance is a recently fed adult, the detecting male mounts the bug's dorsum, regardless of gender, without any apparent courtship (185). However, males can differentiate the sexes to some extent because they mount females more often than males, perhaps via chemical cues (116; but see 154 for a different view). Once on the dorsum the mounting male immediately begins probing the underside of the other bug's abdomen with his intromittent organ. He probes in the neighborhood of the female's ectospermalege (the site of penetration) and so receives tactile, behavioral, and morphological signals of the sex of the mounted bug (50). Intrasexual insemination is uncommon in nature and has been found only in one species (32). Under restrictive laboratory conditions, intrasexual inseminations in *C. lectularius* and *C. hemipterus* (144) occurred with increased sexual isolation and were apparently fatal for the receiver (144). Given that protracted sexual isolation is unlikely, the biological relevance of these results is unclear. The observed high incidence of rapid death (144) may be due to trauma to the unprotected gut.

Recent evidence shows that males monitor and assess their partner during intromission: Matings with recently mated females result in a 75% reduction in ejaculate volume (169). Despite this reduction, the male still achieves a paternity of 68% (177). Why the first male to mate introduces more sperm despite receiving lower paternity (177) is unknown—perhaps first males rely on as yet unidentified patterns of long-term sperm precedence that favor either first males or larger ejaculates.

Mating Frequency and Its Evolutionary Consequences

Cimicid polyandry (e.g., 120, 177) in a system with traumatic insemination has several important and, in this group, unique evolutionary consequences for females. Its early explanations were made by group selectionists proposing that males provided nutritional benefits to females via sperm (3, 46, 75). These hypotheses are unlikely from theoretical viewpoints and because female cimicids mate after a blood meal (i.e., when they are least likely to need additional nutrients). However, the possibility that females may utilize nutrients/micronutrients in ejaculates may be supported by the observation that sperm are phagocytosed by hemocytes in the female's paragenital system and hemolymph (3, 32, 97, 173). Morrow & Arnqvist (126) found that while mechanical copulatory damage reduced female life span by 50%, the overall effect of mating was only a 30% life span reduction. The recovery of 20% of the longevity costs in the treatment with ejaculates suggests some nutritive gain is shunted into female survival. Whether sperm phagocytosis after multiple matings by females functions to exercise cryptic choice (59) or, alternatively, is directed to remove dead or defunct sperm is unclear.

Multiple traumatic inseminations are costly to females. They directly affect female fitness by causing death (119), as well as reducing life span in *C. hemipterus* (197). Males impose a mating rate on females that is 20 to 25 times higher than is required to maintain

Ectospermalege: the cuticular groove that guides the male's intromittent organ into the mesospermalege

Spermalege: a unique bed bug organ positioned under the area of the female's abdominal exoskeleton that receives sperm

Seminal conceptacles: the mesodermally derived sperm storage organ of female cimicids

fecundity (177), resulting in ~25% to 30% reduction in life span (177). This fitness loss does not appear to be compensated by an increase in offspring quality (177), a core prediction in the original arguments marshaled in support of cryptic female choice theory (59).

Reproductive Physiology

Several studies have addressed aspects of the reproductive physiology of bed bugs. Although we detail these studies below, we believe this route has not been sufficiently exploited for its potential use in pest control.

The female spermalege. The spermalege was predicted to be a counteradaptation to the trauma associated with insemination (32, 177). Experimental tests (126, 149) revealed that the spermalege (*a*) reduced wounding costs in a short-lived (126) but not in a normal (149) population of *C. lectularius* and (*b*) reduced the effects of pathogens introduced during traumatic insemination only in the population with normal longevity (149). Recently mated females were occasionally found dead with ruptured guts (92), a condition likely caused by intromission extending through the mesospermalege.

Sperm storage. *C.lectularius* females stop laying fertile eggs approximately 35 to 50 days after sexual isolation (46, 50, 95, 119, 177, 185) because they are depleted of sperm (95, 119) or because the sperm became nonfunctional (119). The female swallow bug, *Oeciacus vicarius*, hibernates after mating in the autumn and starts laying fertile eggs the next spring when its hosts arrive (64, 110), suggesting a long period of efficient sperm storage. Other cimicids that utilize migratory hosts may have a similar capacity for prolonged sperm storage. The site of major concentration of sperm within the female paragenital system is the paired seminal conceptacles (32), which have evolved independently of the normal insect sperm storage organs (the bursa copulatrix

and spermatheca), which are ectodermal in origin (173).

Sperm morphology, physiology, and movement through the female body. The male ejaculatory pump is connected to the vasa deferentia (the male sperm reservoir) (50) and regulates the transfer of sperm during insemination. Cragg (46) reported limited female fertility after mating with young males, probably resulting from sperm limitation in such males. Males transfer about one fifth of the contents of the vasa deferentia when mating with a virgin female (95) but do not fertilize all virgin females offered to them (86). These observations coupled with that by Cragg (46) suggest males can sometimes be sperm limited and so need to be prudent with their mating efforts.

Cimex spermatozoa length ranges from 400 μm to 800 μm (3, 45). Sperm are ejaculated in bundles (47) directly into the mesospermalege (173), where they become activated by male accessory gland fluid (so-called mesadenal fluid) (51, 144). Mesadenal fluid initiates sperm motility (144) and sperm aggregation (51). Sperm leave the mesospermalege via the so-called conductor lobe after ~4 h (32, 173). Tracheoles in or near the conductor lobe may facilitate sperm movement by providing oxygen (144, 173). The sperm of *C. lectularius* utilize glycolytic (i.e., external) substrates to maintain motility, whereas those of *C. hemipterus* additionally maintain motility by oxidative phosphorylation (i.e., without external substrates) (144, 158). Once a sperm cell is activated in the mesospermalege, it remains motile as it passes through the hemolymph, moving along an oxygen gradient (144) toward the seminal conceptacles (173). Sperm enter the seminal conceptacles, where they reaggregate (50). Female hematophagy results in sperm moving toward the ovaries via hemolymph-filled canals running inside the oviduct walls (the spermodes) (32, 50, 173). Sperm eventually arrive in the ovaries, where they either fertilize mature oocytes or die.

Reproductive immunity. In bed bugs, reproduction and immune function are interrelated (32). The repeated breach of the abdominal wall during mating is likely to introduce microbes into the female and necessitates wound healing. The wound occurs in the exocuticle of the mesospermalege but not the epidermis (173). It is repaired by the so-called scarring substance (32, 173), a granular matrix that develops in the epidermis and migrates to the wound. The mesospermalege reduces the effects of infection associated with traumatic insemination (149). Nine species of bacteria and fungi were identified from the male intromittent organ and in the bed bugs' refugia. These are candidate organisms for sexual transmission (150).

The female paragenital system is replete with hemocytes (32); these cells are a major component of an insect's immune defense, and morphological studies of these immune cells have revealed at least two morphotypes (97, 171) in *C. hemipterus* and *C. lectularius*. Sperm that fail to travel to the periphery of the mesospermalege are phagocytosed by hemocytes (173) or attacked with lysozyme (97). Sperm that leave the mesospermalege (50, 173) are also accompanied by hemocytes during this transit (3, 30, 32, 173), a phenomenon that occurs in intrasexual inseminations as well (158). The function of these hemocytes is not clear.

Oviposition. Egg production stops rapidly if females do not feed, presumably because the protein for egg production is lacking or because sperm migration to the ovaries is not solicited (50). Laying senescence starts between day 30 and 200 of adult age depending on species (83, 162, 185, 200) and temperature (83).

FEEDING BIOLOGY

Hematophagy probably evolved only once in the Cimicidae, because all species are obligate hematophages. Whether it evolved from sapsucking or nest-associated fur- and feather-feeding is unclear (104), but it is central to this taxon's biology: All life-history stages and both sexes exclusively require vertebrate blood for survival, growth, and reproduction (185). We know surprisingly little about how cimicids detect or distinguish suitable from unsuitable hosts.

Host Choice

Compared with other hematophagous insects (104, 114), cimicids have a relatively narrow choice of hosts. Many species parasitize vespertilionid and molossid bats (162, 205) or swifts and swallows (185). The cimicid subfamilies Primicimicinae and Latrocimicinae are restricted to parasitizing New World bats, the Cacodminae and Afrocimicinae to Old World bats, and the Haematosiphoninae are associated with several orders of birds in the New World. For example, *Primicimex cavernis* appears to accept only one host (183a). *C. lectularius* and *C. hemipterus* are closely associated with humans but survive well on bird, bat, and rabbit hosts in the laboratory (185). Wild *C. lectularius* has also been found on several different bird (71, 114, 185) and bat hosts (124, 156, 196).

Cimicid hosts share several ecological features. All hosts occur in temporally and spatially predictable, gregarious assemblages in enclosed spaces such as caves and buildings and all have a relatively high body temperature. Bats, swifts, swallows, and humans often coexist, a feature that probably facilitates host switching (185). Usinger (185) suggested that three species [*C. lectularius*, *C. hemipterus*, and *Leptocimex boueti* (88, 185)] made the transition from bats as the primary host to humans. Another hypothesis emphasizes the human relationship with domestic birds (198). The transition from bat to bird hosts is believed to have evolved four times (185). What triggered these host switches is unknown, but starvation caused by the absence of the main host can result in switching to an alternative, human host (72, 93, 128, 135, 162, 172, 175, 199, 200). If temporal switching results in

increased or recovered fitness, selection will favor parasitism of this new host. For example, *C. lectularius* produces more eggs and the resultant nymphs develop faster when reared on mice (a host they rarely encounter naturally) than on natural hosts (85, 86). *C. hemipterus* performs best on humans compared with rabbits, rats, chickens, and bulbuls (197).

However, any switch to a new host requires overlap in the host detection cues, a stylet morphology that can pierce the epidermis of both hosts, a pump structure that can cope with both hosts' blood, and a digestive system that is compatible with both types of blood. These traits are also likely to be important in cimicids that routinely utilize different hosts. Chicken erythrocytes are 11.2 μm in diameter (5) and human erythrocytes are 6 to 8 μm in diameter. The diameter of the adult *C. lectularius* food canal is 8 to 12 μm (69, 179) making feeding on human blood easier. However, *C. hemipterus* has a hinge and joint system that may control the diameter of the food canal (166). Such flexibility may enable *C. hemipterus* (and by extension *C. lectularius*) access to a large range of hosts. Simple physical constraints may also explain the differences in feeding times observed on different hosts: *O. vicarius* takes 10 to 30 min to engorge on swallow chicks but only 8 min on mice (110).

The bat parasite *Stricticimex antennatus* prefers bats to rabbits and humans (135), and *Ornithocoris toledoi* prefers chicken to turkey, duck, and pigeon (170). One population of *C. lectularius* preferred the smell of humans to that of dogs and guinea pigs (2), while another showed a preference for rabbits (185). Which cues determine these differences are unclear, but other hematophagous insects use heat, CO_2 in the breath, blood group, sex, age, a habit of cigarette smoking, physical health, and even hormone levels as cues (104).

Another aspect of bed bug feeding behavior that has received little attention is how the host's response to the bug affects subsequent feeding ability. For example, a localized immune response to flea bites in rabbits dramatically increased the mortality of fleas that fed on blood from the inflamed site (104). When *C. lectularius* bites human hosts, it tends to concentrate on the arms, legs, and back (9, 12, 79), as well as on the face around the eyes (40). These sites are exposed during sleep and so are unlikely to represent immunologically safe sites (93). However, given that bed bugs may be restricted to using the same exposed site on the same human host, bed bugs may have been selected to avoid generating host immune responses that are detrimental to them.

When biting bats, cimicids concentrate on hairless sites such as the wings, forearms, uropatagium, feet, and penis (74, 135, 183a, 196). Birds are bitten primarily on the featherless base of the legs and around the eyes (141). Preferred biting sites thus lack hair and feathers and have a thin epidermis and plentiful peripheral blood supply, features that reduce feeding time. The amount of time spent in contact with the host is under strong negative selection because this probably constitutes the highest mortality risk for the insect.

Host Location

Host location is of paramount importance to cimicids: Nymphs of *C. lectularius* die within few days of emerging from the egg if they do not feed (185), and egg production ceases soon after adult females are prevented from feeding (185). Host location in blood-sucking insects has three phases: (*a*) appetitive searching, (*b*) orientation toward the host (i.e., activation by host stimuli), and (*c*) host contact (104). Random appetitive searching is important for *C. lectularius* (93). Other studies suggest *C. lectularius* detects human hosts from as far away as 1.5 m (116) through the use of heat cues, host kairomone(s), and/or CO_2. Temperature sensors are present on the antennae (1, 116, 135, 153, 167) and are capable of resolving differences of 1°C–2°C (167). Kairomones such as dried human sweat, sebaceous gland material, and dried ear secretions are important just prior to host contact when they elicit proboscis extension (2, 135, 153, 167). However, some host compounds

may act as allomones. The major component of sweat, butyric acid, repelled bugs (2, 153), but in biologically unrealistic concentrations. Sweat, xylol (2, 153), naphthalene, kerosene, xylol, ethanol, and ammonia (2) also repelled bugs when presented on filter paper but not necessarily when applied to human skin (116), suggesting that bugs monitor a suite of host traits during orientation. Despite this variety of detection methods, human hosts can remain undetected in rooms for several weeks (91, 116).

Once a bed bug is engorged, previously attractive cues become neutral or repellent (2). A switch occurs from positive thermotaxis in hungry bugs to negative thermotaxis in engorged *C. lectularius* (1) and *S. antennatus* (135). Because of this and other such switches bugs leave the risky host environment as soon as feeding is complete.

Feeding Frequency, Meal Size, and Quality

Cimicid feeding frequency depends on digestion rate, environmental temperature, and host availability. Individuals in laboratory populations of *C. lectularius* fed approximately every 7 days (168, 185). *C. lectularius* that naturally infested rat cages also showed a weekly feeding frequency (120) and *O. toledoi* fed every 8 days (170). However, field-collected *C. hemipterus* fed every day after collection for several days in hot climates (70). Field surveys of other cimicid species revealed that 15% to 29% of randomly collected individuals were fully engorged (120, 135, 202), suggesting feeding cycles between 3 and 7 days. Such similarity between field and laboratory data supports the notion that cimicids may often not be food limited in the field.

Blood meals represent between 130% (86, 197) and 200% of the unfed adult body weight. Adults take larger blood meals than nymphs do (for meal sizes see Reference 114), and larger adults take larger blood meals (10, 86, 119). A single complete blood meal precedes eclosion into the next instar, and there

is a minimum meal size to achieve eclosion in *C. lectularius* (179), *Hesperocimex sonorensis* (159), and *S. antennatus* (135). Different host species or individuals may generate meals of different sizes and quality because of variation in protein content (see Reference 104 for general discussion) or blood micronutrients such as calcium or vitamin B (53, 54, 104).

Blood Digestion: The Role of the Microbes and Mycetomes

All cimicids harbor microbial symbionts in paired structures called mycetomes (26, 139, 185). In other hematophagous insects the mycetomes harbor symbionts vital for the biosynthesis of key micronutrients from the nutrient-limited blood diet.

Mycetomes are present in both sexes (185), increase in size as the insect reaches adulthood, but decrease with adult age (26, 36). Senescent females cease laying eggs (82, 83, 86) and no longer have mycetomes (36). Mycetomes seem larger in males than in females (36), for reasons that are not apparent. The functional significance of the mycetomes in cimicids has not been examined experimentally, but *C. lectularius* females exposed to 36°C for 2 weeks simultaneously suffered a 90% reduction in fecundity and showed a range of microbe abnormalities in their mycetomes (34). Three symbiont morphotypes in *C. lectularius* have been identified (26, 34–36, 109): a *Rickettsia*-like pleiomorphic spheroblast; a *Rickettsia*-like rod-shaped symbiont; and so-called filae structures, termed primary, secondary, and guest symbionts. The first two structures are inherited maternally (26). Despite their role in digestion, the mycetomes of bed bugs are associated directly with the gonads (rather than the gut), particularly in male *C. lectularius* (50). Buchner's (26) statement, "strangely, they are slightly fused with the *vasa deferentia* of the testes of the male," suggests he felt the association had implications for sexual transmission.

The primary and secondary symbionts are largely mycetome organized and form

Mycetome: the organ containing symbiotic microorganisms, usually *Rickettsia*, that aid in the digestion of vertebrate blood

a relatively homogeneous mixture therein. However, Buchner (26) reported microbes morphologically similar to those from the mycetomes in the gut, ovaries, Malpighian tubules, free-circulating hemocytes, and mesospermalege (26, 35). It is unknown whether microbes inside and outside the mycetome are different taxa (26, 174).

Guest symbionts are motile (36) and are found in the ovaries, mycetomes, and the Malpighian tubules (35, 36). Louis et al. (109) maintain that the rod-shaped symbionts occur in a nonmotile form in the mycetomes but in a motile form in the hemolymph. Molecular evidence (81) has not clarified this issue, because entire ovaries rather than the mycetomes alone were screened for microorganisms. The 98%–99% *Wolbachia* sequence similarity between microbes harvested from *C. lectularius* and *O. vicarius* extracts (147) suggests the two bed bug species share a common ancestor, but there was also a 97.7% sequence similarity with a leafhopper symbiont (81) and a 97%–99% similarity to a termite symbiont (147). The evolutionary history of these associations requires robust empirical dissection.

The Effects of Bed Bugs on Their Hosts

Bed bugs can affect their hosts in many ways. Some effects of bed bug feeding on hosts include (*a*) elicitation of an immune response that causes discomfort (and, in human hosts, psychological distress), (*b*) secondary infection and pathogen transmission, (*c*) physiological changes in the host, (*d*) alteration of the host's reproductive success, and (*f*) economic costs (in the case of human hosts). These effects may lead to behavioral, morphological, physiological, and social avoidance strategies in hosts such as grooming, avoiding infested sites (16, 18, 111), and choosing microhabitats that are unfavorable for the parasite but also increase natal dispersal (17), as well as using pest control.

Host immune response, stress, and discomfort. The host's initial erythemal reactions to bed bug bites are caused probably by vasodilatory substances in the saliva (104, 152, 188). The subsequent allergic response (73) is caused probably by other xenogenic constituents of bed bug saliva. The strength of the reaction varies from no response to death (73, 160–162, 182, 204). Few people are insensitive to bed bug bites (185); the frequently cited value of 20% insensitivity in humans is based on one study (91) that did not consider the effect of previous exposure on the onset of the allergic reaction. One human host became desensitized after 2500 bites (68), but others showed no desensitization after 100,000 bites (93). People insensitive to bed bug bites do not become sensitive after repeated exposure (68, 73, 93). Allergic responses to repeated bed bug bites have been studied only in guinea pigs, which show a decrease in latency to response (185). The immunological nature and timing of the human response to bed bug bites is a major discomfort to humans (73, 93, 125, 127, 160, 161, 181, 182) especially when infestations are large.

Secondary infections and pathogen transmission. Feeding wounds caused by bed bugs may allow other infections to enter a host, yet such secondary infections are scarcely documented (180; see Reference 101 for a possible example in bats). Bed bugs are capable of carrying the infectious particles of typhus, kala-azar, anthrax, plague, relapsing fever, tularemia, Q fever, hepatitis B virus, and HIV (28, 162, 185). Silverman et al. (165) provide a good overview of the association between *C. lectularius* and HIV and hepatitis B virus. Despite the fact that both viruses can persist within the bed bug's gut for several weeks, no viral replication, and therefore no infectivity, has been found. Sensitive molecular techniques (11) suggest there is little danger of *C. lectularius* vectoring these viruses.

Swallow bug (*O. vicarius*) mortality was not affected by viruses (25) but it vectors several arboviruses (20, 25 and references therein).

Virus transmission rate is linked to swallow bug population size (25).

Cimicids also harbor trypanosomes (14, 185) including *Trypanosoma cruzi* (37, 87, 176, 185), the causative agent of Chagas disease. Although cimicids are capable of transmitting trypanosomes to bats (14, 62, 185 and references therein), the transmission of trypanosomes from bed bugs to bats was low, and the trypanosomes do not replicate in the host (14, 62).

Physiological effects on the hosts. Naturally, recently fed bed bugs also contain more iron than do starved bugs (192). Yet contrary to common claims, no evidence exists that bed bug bites lead to an anemic iron deficiency in the vertebrate host. In the only patient thus investigated (Usinger himself) anemia was caused by insufficient blood regeneration rather than iron deficiency, because the prevention of bites, rather than supplemental iron, led to recovery (185).

In response to bed bug infestation swallow chicks showed increased total blood protein, including gamma globulins (52), and increased hemoglobin, hematocrit, and erythrocyte concentrations (38). Cliff swallows living in colonies artificially cleared of bed bugs had 20% smaller spleens than those in colonies with bed bug infestations (20). Whether splenomegaly in infested colonies was caused by increased lymphocyte proliferation is unclear, since similar studies have reported increased (39), decreased (38), or unaltered (122) numbers of peripheral leukocytes in response to cimicid infestations.

Fitness effects on the hosts. The best studies of the fitness effects of bed bug feeding are on the swallow bug/cliff swallow system, and readers are referred to References 18–25 for details.

Adult house martins nesting in infested nests suffered a significant 4% decrease in body mass during the breeding season [compare with a 0.6% decrease in birds from bug-free nests (39)]. It is unclear whether this difference is the result of blood loss, compensatory foraging activity of adults in infested nests, or energetic demands of bite-induced immunity. Bug-parasitized swallow chicks had slower feather growth than did nonparasitized chicks (38), and the tail streamers (a correlate of foraging success in cliff swallows) of juveniles from bug-free nests were more symmetrical than were those in control nests (an effect that disappeared in adults) (19).

Adult vertebrates, even humans (160), can occasionally be killed by the severity of cimicid bites. An adult mouse and sparrow died after being fed upon by 180 and ~35 hungry bugs, respectively (68). The long-term survival rate of adult cliff swallows cleared of swallow bugs was 14% greater than the rate for untreated cliff swallows from the same colony (24). Although *Oeciacus hirundinis* did not affect host clutch size (18), bed bug feeding had negative consequences for chick survival: No nestling survived beyond its first year if it was parasitized by five or more bed bugs while in the nest (18, 38). Chicks were even observed to jump out of heavily infested nests (18) with fatal consequences. Eradicating bugs from nests increased cliff swallow chick survival by 50% to 100% (18, 22) and led to higher body mass (an important predictor of survival) in nestlings (18). The effect of cimicids can persist even in nestlings that survive bug exposure in the nest. Such chicks suffered a mortality 50% higher than that for nonparasitized chicks before their first breeding season (18). Reduced body mass and growth rates in parasitized chicks have also been reported from other swallow studies (52, 121, 122), but unfortunately these studies lacked controls, had insufficient sample size, or were not randomized with regard to clutch size.

Avoiding host behavioral responses. Although poorly documented, hosts can defend themselves behaviorally against cimicids, primarily by choosing noninfested sites (16) or grooming. Older swallow nestlings, which preen themselves, have lower bug numbers

(18), and birds with damaged beaks harbored higher numbers of ectoparasites than did birds without damaged beaks (114). Bed bugs may avoid being removed from their hosts during grooming by (*a*) reducing feeding time [by using anticoagulants and vasodilatants (104)] and the pain associated with it, (*b*) maintaining superficial contact with the host, (*c*) feeding when the host is inactive (i.e., at night) (64, 86, 120, 128, 185, 196), and (*d*) feeding at sites the host cannot reach while grooming.

Economic impact on human hosts. Cimicid infestations result in multimillion dollar (49) damage in the hospitality industry, poultry industry, and private and communal households. Costs arise from payment for pest control, damage to social reputation (12, 49), replacement of infested infrastructure (80), and claims for monetary reparation (113, 164). Complex consequences in poultry farms include loss of productivity via the allergic reactions by workers, reduced egg value due to bug fecal spots, lower egg production from affected chickens, and increased feed consumption (7, 170).

ECOLOGY

Population and Dispersal Ecology

Population and dispersal ecology is probably the area in which the least progress has been made since Usinger (185) or Johnson (86). This applies particularly to the paucity of field studies (86, 110, 120, 135, 148, 183a). Yet, a better understanding of refugia use, aggregation behavior, and chemistry as well as pathogens should provide important tools for pest control.

Aggregation and refugium structure. Bed bugs aggregate in refugia (18, 135, 185). Such refugia contain a broad mixture of bed bugs of different age classes, feeding stages, and mating status (86, 110). Adults form approximately one third of populations (86, 120, 135) but can be present in higher proportions (63),

especially after winter (*C. lectularius*) (61, 86). The relatedness of individuals in refugia is completely unknown despite its importance for understanding mating behavior, dispersal, and colonization. Sex ratios in cross-sections of natural populations showed no consistent biases (86, 110, 114, 115, 135, 148, 177, 199), suggesting there is no local mate competition and females do not/cannot use refugia to avoid males and therefore traumatic insemination.

Aggregations appear to be maintained by short-range (a few centimeters) aggregation substance(s) emitted by adults (86, 105). Moreover, aggregations can be stimulated by the mechanical detection of adjacent individuals via antennal mechanoreceptors (107). The tendency to aggregate decreases as starvation increases, but this effect may be restricted to females (116) owing to the dramatic effect of starvation on their fitness. Aggregation behaviors have not yet been examined for their pest management potential.

Predators and parasites. Several reviews have considered the predators and parasites of cimicids (93, 176, 185). Predators include spiders, pseudoscorpions, solifugids, mites, pyralid moth larvae, assassin bugs, ants, and rodents (93, 135, 185). Spiders (93, 128, 148) may be their primary natural predators, and the fungus *Aspergillus flavus* and *Serratia* spp. bacteria are pathogens that are effective at eradicating laboratory colonies (42, 148).

Alarm pheromones. Like many Heteroptera (4), cimicids emit substances from a so-called scent gland (106) in response to injury, high CO_2 concentration (135), ant attacks, or when sand is trickled onto their body (107), causing adjacent bed bugs to disperse. This alarm pheromone, detected by sensilla in the antenna and readily apparent to humans, consists of two major components that elicit an evasion response in a dose-dependent manner (107). The alarm pheromone of *C. lectularius* is specific to a certain degree: It did not cause *S. antennatus* to disperse (135).

C. lectularius alarm pheromone also has defensive properties. Bed bugs hand-fed to bats were spat out as soon as they emitted alarm pheromone (106), perhaps explaining why cimicids are rarely found in the stomachs of bats (135).

Infestation rates. Infestation rates of *C. lectularius* in human populations in temperate climates have been documented to occur in approximately 1% (29, 80, 112, 117, 191) up to 100% (123) of dwellings at a given locality. There was a marked reduction in infestation rates between the 1930s and the 1980s (29, 44, 67, 77, 96, 117, 191). In tropical areas *C. hemipterus* were found to infest from 1%–20% (131) and up to 90% (181) of houses or rooms.

C. lectularius and *C. pipistrelli* were found in 8% and 12%, respectively, of maternity roosts of the bat *Myotis myotis* (124), and 92% and 56% of sympatric house martin and barn swallow nests, respectively, were infested with *O. hirundinis* (199).

Larger colonies of hosts tend to support higher densities of cimicids in humans (117) and swallows (18). However, contrary to popular belief (29), the number of people in a house (130) and the level of sanitation (80, 99, 129) are not good indicators of the presence of bed bugs. The turnover of residents is probably a more important indicator (12, 13). Backpackers, immigrants, guest workers, and homeless people have been specifically identified as sources of infestation (9, 57, 58, 67, 80, 108, 131). These groups share three features that may predispose them to transmitting cimicids: (*a*) frequent translocation and (*b*) brief occupancy of (*c*) high-density accommodation (e.g., dormitories) (67, 80). Infestation rates suggest that larger cities, which disproportionately attract backpackers, immigrants, guest workers, and homeless people, are also disproportionately highly infested. A better understanding of the transmission dynamics of bed bugs that feed on humans may be gained by examining the cliff swallow–cimicid system. In cliff swallows, the larger per capita host load of bugs in larger colonies

is caused by the attractiveness of large host populations to swallow transients, i.e., birds more likely to travel between large colonies and carry bugs with them (18, 23).

Mixed infestations of *C. lectularius* and *C. hemipterus* are relatively common (57, 63, 131–133). Whereas Gbakima et al. (63) report almost equal numbers of both species, Newberry et al. (131–133) show that usually less than 1% of dwellings were infested by both species (131). This mutual exclusion is caused most likely by the decreased survival and fertility of *C. lectularius* females when these two similar species interbreed (133, 134, 194, 195). Co-occurrence of bed bug species also occurs in bat roosts (98, 124, 202).

Cimicid population sizes. The size of natural populations is poorly documented, ranging from a few individuals per bat roost or bird nest (141, 185) to several hundred per nest (66, 103) and many thousand per cave (114, 135). In cliff swallow colonies, swallow bug populations ranged from 30 to 141,000 bugs (110, 143). One mark-recapture study of *C. lectularius* carried out in a rat colony estimated ~4000 adult bed bugs in one small room (120). Cimicid populations in human dwellings range from 4 to 221 cimicids per house (131) to 5000 bed bugs per bed (102, 108). Cimicid population size increases with population age (18, 86), although recently founded colonies can sometimes be very large (18). Different but sympatric swallow host species harbored different cimicid population sizes (199). Average bed bug/host ratios in natural populations range from near 1:1 in large bat colonies (114) to 1:200+ in smaller bat and bird colonies (15, 18, 135).

Recent spread. The few recent systematic studies (**Figure 1**) suggest a dramatic spread of *C. lectularius* that possibly arose between the 1970s and the 1980s (67, 191) in the developed world (12, 13, 27, 41, 43, 57, 58, 80, 138, 151). The recent first records of *C. hemipterus* in the United Kingdom (27) and Australia (57) suggest this spread may be a global pattern (58),
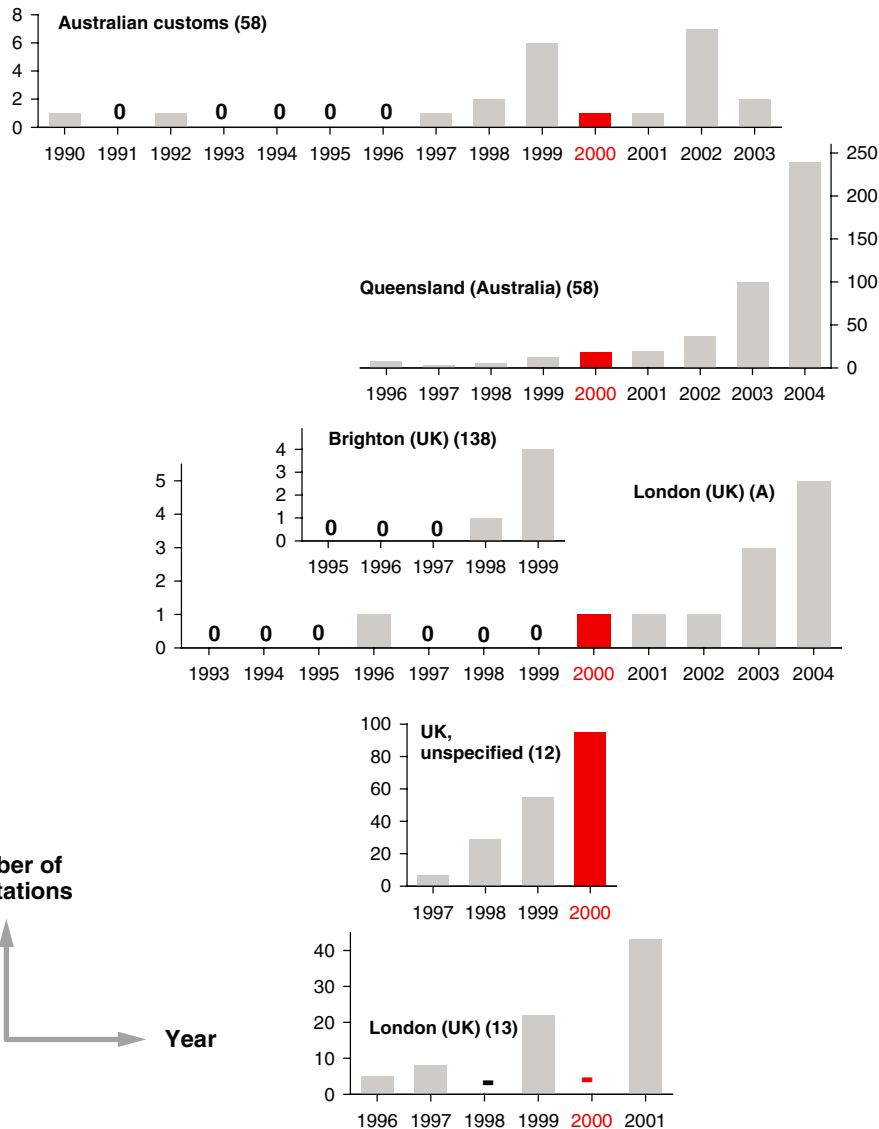
Figure 1

Post-1990 sources that provide data on a temporal change in infestation rates in bed bugs. References are given in parentheses (Reference A: C. Boase, personal communication). Data in the top panel refer to introductions of *C. lectularius* and *C. hemipterus* via aircraft into Australia.

driven probably by the availability of cheap air tickets and the ability of cimicids to disperse locally (12). This latter aspect of cimicid biology is enhanced likely by recent building techniques as well as control methods (12, 13).

Active dispersal. Bed bugs can remain motionless in a refugium for 35 days at room temperature before they disperse (86). First instars walk readily and female adults are slightly more active walkers than males are (86, 120).

Swallow bugs walk up to 3 m and perhaps more within host colonies: One bug was found 65 m from the release point three days after marking, but this finding could not be unequivocally ascribed to walking (18). Although walking is initiated most likely by hunger, it is not necessarily related to feeding (86). Because walking is the most likely mode of dispersal between rooms in infested buildings, its costs (118) and causes warrant further attention.

Passive dispersal. Passive dispersal is the most important way for wingless cimicids to reach new hosts. Bed bugs can be transported by humans in clothing, luggage, and furniture (7, 12, 43, 44, 58, 94, 108, 138). They have been detected while people were traveling by foot, car, train, ship, and airplane (94, 108, 201).

New sites have been rapidly colonized by human-associated bed bugs (80) as well as bat- and swallow-associated bugs when they are transported in the fur or feathers of their hosts (18, 74, 65, 98, 114, 155, 185). In birds and bats the proportion of flying hosts carrying cimicids is bimodally distributed: either below 5% (18, 55, 56) or approximately 50% (56, 148a). Usually fewer than two to four bugs are found per host (18, 55, 124, 148a, 156), and there is a record of two individuals of two different species co-occurring on a flying bat (98).

Swallow bugs cluster at the entrance of unoccupied nests, a behavior that may facilitate transport to other nests by adults (18). Dispersing bed bugs do not appear to be a random sample of bed bugs from original refugia, suggesting that some bed bugs actively enter the passive dispersal stage. More than 85% of dispersers are adults (23, 74, 148a), most of which are females (74, 110). Furthermore, dispersing bed bugs were not incidentally displaced while feeding and had accumulated a large amount of fat (148a). Another feature of dispersing bed bugs that suggests dispersal is actively sought is that the attachment sites differ between dispersing and feeding individuals (18, 148a). Brown & Brown (18) found that 0.11% of 40,827 adult cliff swallows carried adult swallow bugs on their feet rather than in their feathers. The numbers of swallow bugs thus dispersing varied between 1 and 6, with an exceptional 13. Remarkably, they were concentrated on transient individuals (18).

On occasion, new sites are colonized by the massive transport of bed bugs on their hosts (18). For example, four weeks after a group of cliff swallows departed from their colony and occupied a new one, 13,388 swallow bugs were counted in 115 nests (18). The largest number of cimicid bugs ever recorded on a host was 132 on a single swallow (56).

Between-colony movement is poorly documented for *C. lectularius* (58, 80). The largest known distance over which swallow bugs were moved was 42 km (21). The further the distance, the fewer individuals were transported (21). The number of swallow bugs introduced into swallow colonies also varied with swallow colony size (21, 23), between years, and within season (23), resulting in a 60-fold difference of bed bug immigration over a host population range of 1500 nests (21). In some colonies the number of immigrant bed bugs varied more strongly between nests than within nests (23). Such interesting repeatability across nests was stronger in larger colonies and not explained by nest size or distance to the nearest nest (23).

FUTURE DIRECTIONS

Perhaps the single most important aspect of bed bug ecology is the dramatic worldwide increase in *C. lectularius* infestations, particularly in hotels. Although these increases are facilitated by cheap air transport, they are probably exacerbated by the disappearance of folk-knowledge of these insects in the developed world. Most people under age 50 in the developed world have no ability to recognize (e.g., by smell) bed bugs and take first measures to control infestations of these insects. Given the speed with which they are spreading, and their resistance to pest control (127), a better understanding of their natural ecology is urgently needed.

OUTLOOK

Many aspects of the biology of this unusual taxon warrant detailed empirical scrutiny. However, we feel two issues have considerable current importance. First, there is a need to apply molecular techniques to clarify the origin of the association between bed bugs and humans, as the bugs' presence in ancient Egypt (136), their records in the classical
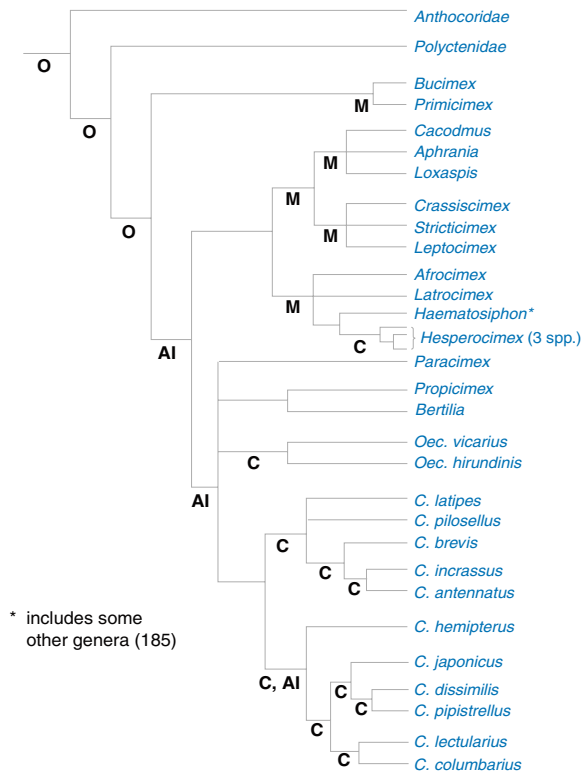
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M — Bucimex / Primicimex

M — Cacodmus / Aphrania / Loxaspis

M

M — Crassicimex / Stricticimex / Leptocimex

M — Afrocimex / Latrocimex / Haematosiphon*

C — Hesperocimex (3 spp.)

Anthocoridae
Polyctenidae
Bucimex
Primicimex
Cacodmus
Aphrania
Loxaspis
Crassicimex
Stricticimex
Leptocimex
Afrocimex
Latrocimex
Haematosiphon*
Hesperocimex (3 spp.)
Paracimex
Propicimex
Bertilia
Oec. vicarius
Oec. hirundinis
C. latipes
C. pilosellus
C. brevis
C. incrassus
C. antennatus
C. hemipterus
C. japonicus
C. dissimilis
C. pipistrellus
C. lectularius
C. columbarius

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* includes some
other genera (185)

Figure 2

Hypothetical relationships among the Cimicidae based on morphological differences (M) (185), the absence of mycetome in *Primicimex* (26, 31), reproductive isolation as revealed in cross-matings (C) (72, 134, 183), and artificial insemination (AI) (185). An important parameter to characterize related families is the number of ovarioles (O) (185).

literature (185), and occurrence in a supposedly ancestral habitat (186) do not demonstrate their origin(s).

Second, the phylogeny of cimicids is currently based on the structure of the female paragenital system, host relations, bristle shape (32, 33, 76, 185), and chromosome pattern (184). While recent experimental evidence has revealed strong selection for a spermalege-like structure (126, 149, 150), the current phylogeny is useless for reconstructing the evolutionary trajectory of this unique trait that ranges from absent in *Primicimex* (30) to highly complex in *Crassicimex* and *Leptocimex* (185). Despite Usinger's (185, p. 276) statement, "It is the lack of the spermalege that provides the best evidence that *Primicimex* is primitive," the issue is not so simple: Females in a sister group of the Cimicidae, the family Anthocoridae, possess a spermalege (33), raising the possibility that the lack of a spermalege in *Primicimex* is derived. Similarly, the Nabinae, a subfamily of the family Nabidae, may also have lost the spermalege (33). We have constructed a working hypothesis for a phylogeny by using Usinger's (185) morphological data and the supposedly ancestral absence of mycetome in *Primicimex* (26, 31) and combining them with the degree of pre- and post-mating reproductive isolation demonstrated in cross-matings (72, 134, 183) and artificial insemination (185) (**Figure 2**).

SUMMARY POINTS

1. We examine aspects of reproductive biology that result in high levels of traumatic insemination.

2. We examine the nature of sperm production, insemination, and migration through the female's paragenital system in the context of the reproductive interests of both sexes.

3. We examine the nature of cimicid feeding preferences, behavior, and effects on the host. We identify the important aspects of feeding biology that are linked to cimicid mating and survival (i.e., fitness).

4. We draw together evidence of local and global cimicid dispersal patterns and their effects on humans and examine their population and dispersal ecology to better understand factors that underpin the recent global spread of bed bugs. These data suggest bed bug infestations are likely to become a major economic and health issue in the near future.

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