RESISTANCE TO DEHYDRATION BETWEEN BOUTS OF BLOOD FEEDING IN THE BED BUG, CIMEX LECTULARIUS, IS ENHANCED BY WATER CONSERVATION, AGGREGATION, AND QUIESCENCE

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Abstract. To determine how the bed bug, *Cimex lectularius*, survives in a dry environment for many months without feeding, water-balance characteristics were compared for all stages from first-instar nymphs to adults. This species is characterized by a low net transpiration rate averaging < 0.2%/h, high tolerance for dehydration (30–40% loss in body water), and an impermeable cuticle as indicated by a high critical transition temperature (CTT) in the 35–40°C range, implying that this insect is adapted for desiccation-hardiness. The capacity of adults to survive for 2 weeks at 0.00a_v (a_v = % RH/100) with no access to food or water exemplifies this trait. In contrast to more mature stages, first-instar nymphs contain more water, lose water at a faster rate, experience abrupt water loss at a lower temperature, and survive less time in dry air, suggesting that this stage is the most sensitive to water stress. This insect relies on blood to replenish water stores; none of the stages examined have the capacity to absorb water vapor (critical equilibrium activity, CEA ≥ 0.99a_v), and they drank only sparingly when offered free water. As the bed bugs progress through their development, they gradually reduce their water requirements while increasing their desiccation resistance. Surviving water stress is considerably enhanced behaviorally by quiescence, characterized by prolonged periods of inactivity, and by the formation of clusters that generate a water-conserving group effect.

INTRODUCTION

The common bed bug, *Cimex lectularius*, has a remarkable ability to survive 4 months to 2 years without feeding, a feature that presumably accounts for their incredible capacity to persist for long periods in human bedding and other locations. Recently, there has been a resurgence of bed bugs in human dwellings, including hotels. The prolonged absence of a suitable host is problematic for these obligate blood feeders due to a lack of fluid uptake to counter desiccation. How do bed bugs cope with this challenge? Besides cannibalism, no other attributes have been described that would account for their impressive survival capacity between bouts of blood feeding. Despite the current bed bug epidemic, few studies, with the exception of earlier works by Johnson and those summarized in Usinger, have focused on the physiology of bed bugs, especially their mechanisms for enduring prolonged periods of fasting. Epidemiologically, *C. lectularius* is a nuisance pest to humans, causing loss of sleep due to annoying bites. The bed bug does not appear to be a disease vector, but it has been associated with iron deficiency, secondary bacterial infection from bite sores, and allergic hypersensitivity. This species is broadly distributed, occurring throughout much of the temperate zone, and is most successful in cosmopolitan areas with high human density. All five nymphal stages and adults are mobile and require a blood meal to molt, and the adult requires an additional blood meal to reproduce. Bed bugs remain hidden during the day, and because of their small size, lack of wings, and flat body shape, they are able to crawl into tight crevices. After feeding forays, the bugs return to these sites, resulting in the formation of dense aggregations (mixed stages), known as “brood centers,” where eggs, fecal material, and exuviae also accumulate. When in these clusters, the bugs enter a quiescent state while the blood meal is digested; they venture out again only for host seeking when their metabolic reserves have been depleted.

Previous research, discussed in a review by Johnson, on the water requirements of *C. lectularius* indicates that this bug is particularly tolerant of drying, but factors influencing their unique dehydration resistance and how these factors may contribute to the recent proliferation of bed bugs have not been determined. In this study, we construct a water-balance profile for *C. lectularius* with the goal of examining habitat preference and suitability, features that are critical for survival and for determining the bug’s potential to spread into new regions. We examine the entire life cycle (except eggs), using bugs of similar age to illustrate developmental shifts in water requirements and to pinpoint the stages that are most and least vulnerable to water stress. We assess percentage body water content, dehydration tolerance limit, net transpiration rate (integumental plus respiratory water loss), critical transition temperature (CTT, denoting the temperature threshold of an abrupt lethal water loss), and free water drinking ability. The benefit of clustering for water conservation was evaluated by measuring net transpiration rates of individual bugs and of different-sized groups. Rivnay and Johnson showed prolonged survival of various bed bug stages at conditions of water deficiency that are similar to those regularly encountered in human dwellings (30–50% RH and 22–24°C based on comfort standards) thus suggesting that these bugs may have the capacity to absorb water vapor from the air. An additional goal of our study was to determine the bed bug’s critical equilibrium activity (CEA), to test if the bugs can use atmospheric moisture as a primary source of water.

MATERIALS AND METHODS

Bed bugs and test conditions. *C. lectularius* was acquired from The Ohio State University Insectary. The colony was established in 2002 from individuals collected in Columbus, OH. Bugs were stored at 85% RH, 15 h:9 h light/dark until
they were used for these experiments. Temperature was 25 ± 1°C for the colony and also for basic observations; this temperature allows us to compare our results with previous studies on insect water balance. Each of the five nymphal stages and male and female adults were used in the experiments. All individuals were used 1 week after molting or after hatching in the case of the first instar. An aspirator and felt-tipped soft forceps were used for transferring the bugs and for handling the bed bugs during mass measurements.

Test relative humidities (% RH) were generated with the use of saturated salt solutions (33% RH with MgCl2, 75% with NaCl, 85% with KCl, 93% with KNO3, 98% with K2SO4) as described by Winston and Bates,16 distilled water (100% RH) or calcium sulfate (CaSO4, 0% RH; 1.5 × 10−2 % RH)14 that was placed in the base of sealed glass desiccators (5,000 cc). A hygrometer (SD ± 0.5% RH; Thomas Scientific, Philadelphia, PA) was used to verify each experimental relative humidity. To relate the water present within the bugs to that in the surrounding atmosphere, relative humidities were expressed as water vapor activities (a; a = % RH/100; thus, 0.00a, 0.33a, 0.85a, 0.93a, 0.98a, and 1.00a) and the activity of the body water (aw) of the bug = 0.99aw based upon mole fraction.17 Bed bugs were housed individually within 1-cc mesh-covered chambers that were placed on perforated porcelain plates to prevent contact with the solution used to generate the water-vapor activities.

Bugs were weighed individually using an electrobalance (CAHN; SD ± 0.2 µg precision and ± 6 µg accuracy at 1 mg; Ventron Co., Cerritos, CA) without enclosures and without the use of anesthesia. Briefly, a bug was removed from its enclosure and permitted to crawl onto the weighing pan of the balance, the mass was determined, and the bug was picked up with an aspirator and returned to the 1-cc mesh enclosure and test conditions. This was accomplished in < 1 minute. Before being used in experiments, the bugs were held at 0.33a, until a 4–6% loss in body weight occurred, thus minimizing the effect of excretion, digestion, and reproduction on mass changes18,19 and standardizing the bugs with regard to water flux so that mass changes only reflected internal fluctuations of the bug’s water content.20 At the end of each experiment, bugs were placed at 90 °C and 0.00a, and monitored until mass became constant, then held for an additional 3 days of drying; this mass was then recorded as the dry mass.

**Water-balance characteristics.** Wharton’s methods18,19 and equations, with modifications by Yoder and Spielman,21 Kahl and Aldousti,22 and Benoit and others,20 were used to determine the various water balance characteristics. Dry mass (d) was subtracted from initial (fresh) mass (f) to determine the amount of water that is available for exchange, which is defined as the water mass (m). Water mass was expressed as a percentage of the initial mass to determine the percentage body water content. Bugs were placed at 0.33a, and 30°C, weighed every hour, and tested for their ability to right themselves and crawl five body lengths. The mass measurement that corresponded to the point where they were unable to achieve this behavioral task was defined (after subtracting corresponding dry mass) as the critical mass, mcr, and was used as an estimate of dehydration tolerance based on the percentage change in mass lost from initial to critical mass (mcr).

To determine net transpiration rate (= integumental plus respiratory water loss), bugs were weighed, placed at 0.00a, and reweighed at various intervals, for a total of five readings of mass; weighing intervals varied between instars depending on the extent of their desiccation. Net transpiration rate was determined at 0.00a, because the amount of water mass lost declines exponentially such that water loss rate can be derived from the slope of a line described by the equation: 

\[ m = m_0 \exp(-k_t) \]

where \( m_0 \) is the water mass at any time \( t \), \( m_0 \) is the initial water mass, and \( -k_t \) is the rate of transpiration expressed as %/h. Rates were established for isolated individuals and also for individuals in groups of different sizes. Individuals were marked on the dorsum with a spot of paint (Pactra, Van Nuys, CA) and allowed to cluster naturally. The paint-marked bugs were removed for mass determinations and then returned to the group; paint had no effect on mass changes (data not shown). Critical transition temperature (CTT), the temperature threshold of a rapid water loss, was based on change in activation energy (\( E_a \)) determined by analyzing water-loss rates over a broad temperature range (4–60°C) as described by the Arrhenius equation: 

\[ k = A \exp[-E_a/(RT)] \]

where \( k \) is the net transpiration rate, \( A \) is steric (frequency) factor, \( T \) is absolute temperature, \( R \) is gas constant, with \( E_a \) based on the slope, which is equal to \(-E_a/R\).

Avenues of water gain were also investigated. Drinking free water was analyzed by offering bugs 5- to 20-µL droplets of 0.5% Evans blue-stained water in a 100 × 15 mm petri dish (0.75% RH, 25°C). Ten bugs were placed in each dish, examined for 20 minutes (40× microscopy), and then every 2 hours thereafter. After 24 hours of observation, bugs were dissected in 0.1% NaCl under the microscope (100×) and examined for the presence of blue coloration in their digestive tract and liberation of dye when the gut was opened. Water vapor absorption was examined by long-term daily monitoring of water mass (m) of individual bugs held at different water-vapor activities. The capacity to maintain a steady water mass in subsaturated air (< 0.99aw) of the bug’s body water, thus balancing water loss with water gain from the air (water gain = water loss), was taken as evidence of the bug’s ability to use atmospheric water vapor as a primary source of water. Survivorship was assessed based on 40× microscopic observations of dead bugs; bugs were considered dead if they were immobile, unable to right and crawl, and failed to respond to prodding or bright light.

**Sample sizes and statistics.** Each experiment was replicated 3 times with 10 bed bugs per replicate, for a total of 30 individuals for each water-balance characteristic determination. Data, reported as the mean ± SE, were compared with analysis of variance (ANOVA), and arcsin transformation was used in the case of percentages.23 A test for the equality of slopes of several regressions was used to compare characteristics derived from regression lines. Survivorship times were compared using \( t \) statistics.

**RESULTS**

**Water content.** Initial mass, dry mass, and water mass increased with each successive stage (Table 1). Percentage body water content was highest for first-instar nymphs (71%) and lowest (67%) for female adults (ANOVA; \( P < 0.05 \)). No significant difference in percentage body water content was observed between sexes (ANOVA; \( P > 0.05 \)). In all cases, within a particular stage, the water mass was a positive correlate of dry mass, with \( R \geq 0.93, 0.89, 0.94, 0.93, 0.95 \) for first- through
Comparison of water balance characteristics for different stages of *Cimex lectularius*.

<table>
<thead>
<tr>
<th>Characteristics</th>
<th>Nymphs</th>
<th>Adults</th>
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<tbody>
<tr>
<td></td>
<td>1st</td>
<td>2nd</td>
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<tr>
<td>Initial mass, f (mg)</td>
<td>0.124 ± 0.023</td>
<td>0.255 ± 0.016</td>
</tr>
<tr>
<td>Dry mass, d (mg)</td>
<td>0.379 ± 0.009</td>
<td>0.077 ± 0.011</td>
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<tr>
<td>Water mass, m (mg)</td>
<td>0.087 ± 0.010</td>
<td>0.178 ± 0.021</td>
</tr>
<tr>
<td>Water content (%)</td>
<td>70.9 ± 2.1</td>
<td>69.8 ± 1.7</td>
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* f, fresh (initial mass); d, dry mass; m, water mass; %, percentage body water content; m<sub>c</sub>, critical water mass where they were unable to right and crawl; NTR, net transpiration rate; DT, dehydration tolerance as percentage lost to m<sub>c</sub>; CTT, critical transition temperature; survivorship is based on 50% of the bugs; drinking confirmed by presence of blue tracer in water droplet upon dissection; and CEA (critical equilibrium activity), the range of water vapor activities (a<sub>v</sub> = % RH/100) where water vapor absorption occurs. Data shown are means ± SE, n = 30.

Net transpiration rate. First-instar nymphs lost water (net transpiration rate) at a rate of 0.402 ± 0.011%/h (Table 1). The corresponding rate of water loss for individuals (paint marked) in a group of 20 (0.247 ± 0.010%/h) was approximately half that of isolated individuals (Table 1; Figure 1; ANOVA; P < 0.05). Net transpiration rates of first-instar nymphs in groups of 5 (0.360 ± 0.014%/h) and 10 (0.311 ± 0.017%/h) were between these extremes (ANOVA; P < 0.05). In all cases, the paint-marked individuals were returned to the group after mass determination, and they remained in the group. It is also important to note that members of the groups did not disband when disturbed by removing or reintroducing the paint-marked individuals and individuals were in direct contact with neighboring bugs. Periodically, the location of the bed bugs was recorded and movement was noted; these observations suggested that individuals likely spend nearly equal time in the middle and at the edges of the group. Net transpiration rates of other stages are presented in Table 1 and follow a similar exponential pattern of water loss (R > 0.99; ANOVA; P < 0.001), reflecting proportionate loss at 0.00<sub>a</sub>, on a semilogarithmic plot as illustrated by first-instar nymphs in Figure 1. Net transpiration rate increased with each successive stage during development (Table 1; ANOVA; P < 0.05). Net transpiration rate also correlated with dry mass (y = −0.38x, R = 0.94; ANOVA; P < 0.001; Figure 2), indicating that water loss varies according to body size. Net transpiration rate was 4× higher for first-instar nymphs than adult females, a stage that is nearly 50× larger (Table 1). We conclude that water is lost most rapidly when the surface area is greatest relative to volume and that a strong, positive relationship exists between aggregation size and suppression of water loss.

Critical transition temperature. Net transpiration rate of first-instar nymphs increased with increasing temperature and exhibited a Boltzmann temperature function (R > 0.95; ANOVA; P < 0.001; Figure 3). A distinct critical transition temperature (CTT) was detected in these first-instar nymphs as evidenced by a steep slope of the regression line indicative of a new temperature range (biphasic, two-component curve) and a change in activation energy (E<sub>a</sub>). The change in slope was due to higher proportionate amounts of water loss in the higher temperature range. The CTT of first-instar nymphs was 34.5°C, as determined by identifying the point of intersection of the two regression lines plotting the E<sub>a</sub> changes. Other stages responded similarly to temperature and yielded nearly identical net transpiration rate–temperature relation-
ships as shown for first-instar nymphs in Figure 3; the results indicate Boltzmann dependence on temperature ($R > 0.95$; ANOVA; $P < 0.001$), different proportionate water mass losses in low and high temperature ranges leading to a change in slope, and evidence for a CTT. The CTT increased through development from 34.5°C for first-instar nymphs to 39°C for female adults (Table 1; ANOVA; $P < 0.05$). Compared with adults, earlier stages are more at risk of abrupt, rapid desiccation at high temperature.

**Dehydration tolerance.** When examined under the microscope (40×), bed bugs remained immobile and failed to respond to prodding for 15–20 seconds, then slowly uncurled their legs, righted, and began to crawl. Once having lost about ½ of their water content, they failed to right themselves and crawl 10 body lengths, as indicated by critical mass ($m_c$) values (Table 1). No significant differences were observed among the various stages when critical mass was expressed as a percentage of the amount of body water that was lost, averaging 35% (Table 1; ANOVA; $P > 0.05$). Throughout their life cycle, bed bugs tolerated similar levels of dehydration stress.

**Survivorship.** Female adults were capable of surviving a remarkable 16 days (50% of adults) at 0.00a, with no food or water, demonstrating their ability to withstand prolonged periods of starvation and desiccation. Females survived approximately 2 days longer than males ($t$ statistics; $P < 0.05$). These survivorship estimates for adults agree well with our calculated dehydration tolerance limits and net transpiration rates (Table 1). Similarly, the time required to reach critical mass (dehydration tolerance limit) calculated from net transpiration rates for each of the immatures closely matched length of survival in dry air (Table 1; $t$ statistics; $P < 0.05$). Thus, the relationship between net transpiration rate, dehydration tolerance, and length of survival in dry air are consistent for all stages throughout the life cycle. Once they reached their critical mass, the bugs were unable to be rescued by placing them at 1.00a, or by offering them droplets of free water (each $N = 10/stage$), thus indicating that they had sustained an irreversible level of dehydration. None of the bugs in this condition survived. Our results show that adults are more resistant to desiccation than immatures.

**Free water drinking.** When bed bugs were placed into a petri dish containing droplets of Evans blue-stained water, they crawled about quite actively as though engaged in a searching type of behavior, characterized by tapping the bottom of the dish with the antennae as they moved about the arena. Within 1–2 minutes, most of the movement stopped and the bed bugs were observed to be clustered around the edges of the dish. Little movement was observed within these aggregations or to adjacent clusters. In all cases, water droplets were encountered passively, and none of the bugs displayed deliberate movements away or toward the droplets of water. They did not appear to be attracted or repelled by the droplets. On occasion, upon encountering a droplet of water, the bug paused, inserted its proboscis into the droplet and drank; this lasted for approximately 1 minute (Table 1). This set of behavioral observations included each of the various stages examined. Blue dye could be seen filling the gut diverticula when the bug was observed under the microscope (40×), and blue coloration was liberated from the gut upon dissection (100×), a confirmation that the bugs consumed the colored liquid. Attempts to encourage the bugs to drink by dehydrating them by losses of 20–25% of their body mass (0.00a, and 30°C) prior to exposing them to the water droplets were futile. Instead, these dehydrated bed bugs formed clusters and only a few were observed to imbibe the water and the water droplets were still encountered passively; that is, no deliberate movements were made to the droplets. Although bed bugs have the ability to drink water, they appear to do so rather sparingly.

**Water vapor absorption.** First-instar nymphs failed to maintain their water mass over a period of several days when exposed to subsaturated air (Figure 4). This was due to the activity gradient created between the activity of the body wa-
ter (0.99αv,18) with that of surrounding air, thus 0.99αv > 0.98αv, 0.93αv, 0.85αv, and 0.75αv, and this resulted in water loss by simple diffusion. Less net water loss was measured as the air became more humid (R > 0.97; ANOVA; P < 0.001), which demonstrated an effect of greater passive adsorption onto the surface of the cuticle as water vapor activity approached saturation. Water gain occurred and the uptake was maintained in saturated air of 1.00αv because the activity gradient was reversed, 1.00αv > 0.99αv (body water), and this drove water inward into the bug’s body and contributed to water mass. Because net water loss occurred at 0.98αv and net water gain at 1.00αv, water balance was achieved (gain = loss) at 0.99αv, which is equivalent to the 0.99αw body water activity estimated by Wharton.18 Accordingly, the critical equilibrium activity (CEA) of first-instar nymphs was ≥ 0.99αv. Other stages displayed a similar pattern of water loss in subsaturated air and gain at saturation consistent with properties of diffusion as illustrated by Figure 4 for the first-instar nymph. For all stages, CEA ≈ 0.99αv (Table 1). Thus, bed bugs cannot use water vapor as a significant source of water.

**DISCUSSION**

Outstanding water balance features of *C. lectularius* include a low net transpiration rate (< 0.2%/h) that is similar to rates observed in desert-adapted arthropods, an ability to tolerate loss of ½ of their body water (most arthropods only tolerate 20–30% loss), and a high (> 35°C) critical transition temperature consistent with arthropods that have water impermeable cuticles.5,18,24 This set of water-balance characteristics is typical for arthropods that are differentially adapted for life in a dry habitat according to Hadley.15 Thus, *C. lectularius* is xerophilic with regard to water balance. As such, *C. lectularius* is modified for water conservation and to resist desiccation, wherein their ability to retain water (low water loss rate) is more important than their ability to gain water. Other water-balance characteristics of *C. lectularius*, such as the ~ 69% body water content, free water drinking, and lack of ability for water vapor absorption are similar to features observed in most arthropods.15 In fact, as adults, the characteristics of *C. lectularius* resemble those of another blood-feeding hemipteran, *Rhodnius prolixus* (69% water content, 50% dehydration tolerance, low water loss, xeric ecologic classification).15,25,26 Notably, emphasis on water retention and desiccation-resistance properties by *C. lectularius* enables this species to function effectively in a dry environment and dually protects the bugs against desiccation between blood meals or in the absence of a host.

The fact that *C. lectularius* failed to absorb water vapor is not unusual, as most arthropods lack this ability.15,17 Arthropods that achieve this feat maintain body water levels at otherwise dehydrating conditions by absorbing water against the atmospheric gradient using a mechanism frequently involving a salt-driven process.27,28 Because water vapor absorption does not occur in *C. lectularius*, the long-term survivability in the absence of food and in relatively dry air, reported by Rivnay15 and Johnson,29 must be the consequence of water conservation properties rather than the ability to use water vapor from the air. For all stages, the CEA ≈ 0.99αv, indicating that water gain can only occur from air that is completely water-saturated at 1.00αv, a water vapor activity that corresponds to water as a liquid. This necessarily implies that water must be imbibed in fluid form.19 In the presence of free water, however, stages of *C. lectularius* were not attracted to droplets of water and only drank on occasion, displaying no real interest in the water even when they were dehydrated. Such inconsistent drinking patterns were similarly observed in certain ticks22 and are typical of arthropods that feed on blood.15 Indeed, blood feeding is responsible for the majority of the contributions to the internal body water content of *C. lectularius*,11 as well as *R. prolixus*,29 a species that shares many water-balance characteristics with *C. lectularius*. Although free water represents a viable water resource, the most likely primary source of water for *C. lectularius* is their blood diet.

Other noteworthy features related to water balance in *C. lectularius* are primarily behavioral regulators of water loss due to the capacity to enter long-term quiescence and the ability to form clusters. The quiescence is characterized by a complete lack of activity, including retraction of the legs that give the bugs a dead appearance. This quiescence can only be broken by persistent prodding and provoking. Clearly, this shut-down makes a major contribution to conservation of the body water content by helping to reduce respiratory water loss,15 an ability that is similar to that seen in the spider beetle, *Mezum affine*, a species that can survive without water for many months.20 Suppression of net transpiration rate is common in arthropods that aggregate, including mites,30 beetles,31 and cockroaches.32 A well-known additional benefit of aggregation is to increase access to mates,31 and this is consistent with the designation of the bed bug cluster as a “brood center.”30 Although our experiments on the group effect were restricted to first-instar nymphs, it is likely that all stages experience and benefit from this effect. Our preliminary results using flowing dry air suggest that the mechanism of the group effect operates by generating a humidified boundary layer, as noted in beetles.33 Linkage between quiescence and enhanced water conservation is similar to that observed during overwintering diapause.34 This feature raises the yet untested possibility that quiescent stages of *C. lectularius* may also be cold tolerant.

Developmentally, the stage of *C. lectularius* that is most
sensitive to desiccation stress is the first-instar nymph. This stage has the highest percentage body water content, indicating that it requires more body water to function. The first-instar nymph is also the smallest in body size, thus making it more vulnerable to rapid water loss rate due to its surface area to volume properties. Greater cuticular permeability to water is implied by a lower CTT, suggesting that the cuticular structure of the first instar is more easily disrupted. The high water requirement must be met by increased feeding activity or a greater reliance on clustering. Stage differences in water requirements are unlikely to be indicators of a different habitat preference because all instars are found clumped together within the same microhabitat. Through development, percentage body water content declines concurrently with an increase in dry mass (= fat); thus, the bugs require less water and accumulate greater fat reserves as they become older. In addition, as the bed bugs proceed through development, they increase in body mass (size), allowing for greater water retention, and the CTT increases by 5°C, implying that the integument becomes progressively more water-tight. Thus, there is a gradual shift through development from a high to a low water requirement, and this is reflected by differences in survival enabling adults to live the longest in a desiccating environment.

From this study it is clear that the water balance strategy of *C. lectularius* emphasizes water retention. These effective water-conserving traits are supplemented behaviorally by a quiescence marked by periods of inactivity and a group effect that enhances protection against desiccation stress. Effective water conservation thus enables the bed bugs to persist for long periods without rehydration. It would appear that the human comfort standards of 0.30–0.50°C and 22–24°C create an ideal habitat for *C. lectularius*. As long as a host is available on occasion for blood feeding, the species is well adapted to survive the water balance challenges encountered in most human dwellings.

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