Adult German Cockroach (Orthoptera: Blattellidae) Feeding and Drinking Behavior as a Function of Density and Harborage-to-resource Distance

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ABSTRACT  There was an effect of harborage-to-resource distance but no main effect of density on the frequency of feeding and drinking activity of adult Blattella germanica, videotaped continuously for 96 h. Feeding and drinking diel periodicity was more pronounced when the resource was placed further from the harborage with activity peaking ca. 2 h into scotophase and declining at the onset of photophase. Nongravid females and males fed and drank more often than gravid females, with a high percentage of females carrying oothecae never feeding or drinking during the recording period.

THE DIEL ACTIVITY and exploratory behavior of the German cockroach, Blattella germanica (L.), have been investigated using a variety of methods. Wilson et al. (1981) studied B. germanica circadian rhythms by confining individuals in a microcalorimeter, such that heat released during periods of activity resulted in measurable electrical responses (thermograms). Hocking (1958) developed an instrument that recorded weight shifts of individual cockroaches as they moved from a harborage to a food or water source. Sommer (1975) used radiotracer techniques to monitor the circadian activity of a single cockroach at a time. He found that activity was highest in males, followed by nongravid females, gravid females, older nymphs, and younger nymphs. These methods are useful for examining circadian rhythms of isolated cockroaches and defining the environmental conditions that control these rhythms, without direct observation. However, the movement and feeding behavior of many interacting individuals cannot be obtained. Photocell methods by Fuchs (1983) and others have been used to record the movement of large numbers of insects. Using this method, one individual may cross a light beam numerous times in a single period and may give the false impression that many insects are active. The exploratory behavior of groups of German cockroaches under conditions such as varying density and food deprivation was reported by Ballard et al. (1984). They used modified Ebeling choice boxes (Ebeling et al. 1966) with sticky traps inside to monitor cockroach movement. This method revealed general movement patterns of B. germanica without identifying individual variation.

This paper analyzes feeding and drinking behavior of adult B. germanica under conditions of varying density and harborage-to-resource distance. The activity of individually marked cockroaches was videotaped continuously for 96 h to obtain complete feeding and drinking behavior profiles. The implications of resource visitation in cockroach control are discussed briefly.

Materials and Methods

The configuration of the experimental unit that was videotaped appears in Fig. 1. Clear plastic containers (40 by 28 by 17 cm) were used to house cockroaches, food, water, and harborage. Food and water were placed at two different distances from the harborage. Single containers were used where the food, water, and harborage were placed in close proximity (ca. 40 cm). Greater separation between food and harborage was obtained by joining two containers with a clear plastic tube (2.5 cm by 2.5 cm diam). A thin plastic baffle (5 by 3 cm) was placed in the resource container perpendicular to and against the passage between the two containers. This increased the insect’s chance of locating the passage after visiting the resource, thereby making it less likely that cockroaches would seek harborage in the resource container. An inverted cardboard box (20 by 14 by 9 cm) provided harborage for the cockroaches. A film of petroleum jelly was placed along the inside rim of each container to prevent insect escape. Several pieces of pet food (Purina Cat Chow) were glued to a piece of cardboard to restrict the cockroaches to a specific feeding site. A narrow-mouth water bottle (50 ml) with a paper wick was placed next to the food. The food and water were placed in the corners of each arena (single or tandem container) so that resource sites for all four arenas were in the viewing field. Therefore, data for all four conditions (high density/distal resource, low density/distal resource, high density/proximal resource, and low density/proximal resource) could be recorded concurrently.

Adult B. germanica (mixed age) were obtained
from a colony maintained at American Cyanamid for >30 years and free from insecticide exposure. They were tagged dorsally with individually numbered paper disks (0.8 cm diam), which were fastened with double-sided tape. Forty-five labeled adults (15 males, and 15 gravid females and 15 nongravid females at undetermined points in their reproductive cycles) were placed in each arena. Also, an additional 100 unmarked nymphs and 50 unmarked adults were added to the two high density arenas. Cockroaches were initially confined to the harborage side of the distal resource arenas for 24 h, followed by 4–7 days of acclimation in the entire arena before filming. The same acclimation period was allowed for cockroaches in the proximal resource arenas. Videorecordings of the four resource locations were made with a high resolution camera (RCA TC 1005) and monitor (RCA TC 1115) connected to a VHS recorder (RCA). A 25-W red light was on throughout the 96-h taping period and a 60-W white light was connected to a timer for a 12:12 (L:D) photoperiod with lights on at 0600 hours. Temperature and humidity throughout the experiment were 26 ± 2°C and 50–70% RH. The reproductive condition (gravid [with ootheca] or nongravid) of all labeled females was recorded 2 days after the filming was completed. Mortality counts of all labeled individuals were recorded each week for 4 weeks following the experiment.

Behavior of individual cockroaches was characterized in terms of frequency and average duration of feeding and drinking “events” (where events are defined by use of a resource for at least 5 s), and of the frequency of feeding or drinking “activity periods” (2-h blocks of time in which at least one feeding or drinking event occurred).

Each cockroach for which at least one feeding or drinking event was recorded was considered to contribute an independent observation on the above frequency and duration responses. The effects of the three factors, density, distance, and sex (reproductive condition), and all interactions among these, were examined in three-way analyses of variance (ANOVA) conducted separately for each response. Responses were transformed where appropriate to improve conformity with the standard ANOVA assumption.

Means and tests of hypotheses were adjusted for imbalance where appropriate. Multiple-comparisons were considered in the Fisher’s least significant difference (LSD) test (Milliken and Johnson 1984). A significance level of 0.05 was adopted for inference.

Results

Feeding and drinking profiles of individual cockroaches at two different resource locations are presented in Fig. 2. Each line represents a single cockroach and each block indicates that one or more feeding (lower block) or drinking (upper block) activity periods occurred within a given 2-h period. There was no main effect of density on the frequency of feeding ($P < 0.32$) or drinking ($P < 0.49$) activity periods. Therefore, only one density (high) is displayed. The distance between resource and harborage had a significant effect on food and water utilization. Of the cockroaches which fed or drank during the 96-h observation period those in
the proximal harborage-to-resource arenas averaged 7.4 feeding activity periods (Fig. 2A) versus 3.4 feeding activity periods for individuals in the distal resource arenas (Fig. 2B) \((F_{(1,106)} = 31.9, P < 0.0001)\). Similarly, drinking occurred more often in the proximal arenas, mean = 3.8 activity periods, versus the distal arena, mean = 2.2 activity periods \((F_{(1,113)} = 11.4, P < 0.001)\). An analysis of activity periods blocked in 30- or 60-min segments revealed nonsignificant density effects, while the independent variables harborage-to-resource distance and sex (reproductive condition) had a significant \((P < 0.001)\) effect on feeding and drinking.

During the experiment many females produced oothecae while others dropped their oothecae. Nongravid females were much more active feeders (mean = 10.8 periods) than gravid females (mean = 3.2 periods; \(F_{(2,106)} = 36.4, P < 0.0001\)). Nongravid females also drank more often than gravid females (mean = 4.5 versus 2.1 activity periods, respectively; \(F_{(2,113)} = 11.1, P < 0.0001\)). Therefore, when a female changed from nongravid to gravid during the experiment but no feeding or drinking occurred, the ootheca probably formed toward the beginning of the test. Nonfeeding or nondrinking females that dropped their oothecae probably did so toward the end of the experiment.

To describe the relationship between photoperiod and resource utilization, a tally of feeding and drinking blocks from Fig. 2 is presented in Fig. 3. Despite large fluctuations, cockroach activity was greatest at the onset of the scotophase, and least at the beginning of the photophase. The cyclical nature of \(B.\) germanica feeding and drinking was more pronounced when food and water were placed farther away from the harborage (Fig. 3B). Inspection of all arenas every 6 h revealed no cockroach aggregations outside of the harborage. Therefore, a return to the harborage probably occurred between resource visits spaced several hours apart. It is unlikely that cockroaches that fed or drank every few minutes returned to the harborage between events.

When events were considered singly instead of in blocks of 30, 60, or 120 min the absence of a density effect on feeding \((P < 0.54)\) and drinking \((P < 0.81)\) frequency was still apparent. There was also no main effect of cockroach density on the average duration of each feeding \((P < 0.99)\) or drinking \((P < 0.28)\) event. Furthermore, analysis of single events versus blocks of events revealed,
in contrast to the results described above, no effect of harborage-to-resource distance on feeding frequency ($P < 0.07$) or duration ($P < 0.22$), and drinking frequency ($P < 0.37$) or duration ($P < 0.38$). Cockroaches were often observed feeding or drinking for several seconds, leaving the resource, then returning within 5–30 s. This behavior was sometimes repeated 10- to 20-fold in a 15-min period. It also occurred independent of the harborage-to-resource distance. Once located, the resource was utilized intermittently. Since many events occurred once the resource was located, the effect of harborage-to-resource distance was not detected.

No significant interaction between density and gender was observed for feeding frequency ($P < 0.08$). However, this interaction was significant ($F_{(2,110)} = 3.9, P < 0.02$) for drinking frequency, with males drinking more often at the low (4.4 events) versus high (3.3 events) density. Drinking by females was unaffected by density. Both drinking frequency ($F_{(2,110)} = 15.2, P < 0.0002$) and duration ($F_{(2,110)} = 5.7, P < 0.02$) were affected by the interaction of density and harborage-to-resource distance. However, feeding was unaffected. Conditions of high cockroach density coupled with distal resource placement, and low density with proximal placement, had drinking frequency and duration values that were higher than high density/proximal resource placement and low density/distal resource placement.

Feeding frequency ($F_{(2,110)} = 28.58, P < 0.0001$) and duration ($F_{(2,110)} = 6.08, P < 0.002$) differed according to sex and reproductive condition (Table 1). Males and nongravid females fed and drank more often than gravid females. Also, the average duration of each feeding event was lowest for gravid females while the duration of each drinking event was lowest for males.

Ninety-seven percent of males and 78% of females fed in the 96-h period with the food near the harborage (data from combined density arenas), 87 and 56% in the first day for males and females, respectively (Fig. 4A). In arenas with the harborage and food spaced far apart, 75% of the males fed within the 96-h observation period, with 47% feeding within the first 24 h (Fig. 4B). Only 40% of the total female population fed within 96 h, with 14% in the first 24 h. Most of these non-feeding females were gravid (Fig. 2B). Despite the relative lack of feeding and drinking in the distal arenas, cockroach mortality was low (<10%) through 4 weeks.

When visiting the resource 6 or more h after a feeding or drinking event, cockroaches drank before eating ($P < 0.05$; $t$ paired-comparison test). A period of 1 h between first and second events was considered part of the same resource visit, and only the first feeding/drinking (drinking/feeding) sequence for each insect was used in the analysis. Abstention periods of 3, 6, 12, 24, 36, and 48 h resulted in drinking followed by feeding in 59, 66, 66, 79, 74, and 75% of the resource visits, respectively.

**Table 1. Frequency and duration of adult *B. germanica* feeding and drinking events during 96-h observation period**

<table>
<thead>
<tr>
<th>Sex/reproductive condition</th>
<th>Avg no. resource visits per insect</th>
<th>Avg duration (min) at resource per insect</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Food</td>
<td>Water</td>
</tr>
<tr>
<td>Non-gravid ♀</td>
<td>10.76a</td>
<td>4.59a</td>
</tr>
<tr>
<td>Gravid ♀</td>
<td>3.60b</td>
<td>2.02b</td>
</tr>
</tbody>
</table>

Column means followed by the same letter are not significantly different ($P = 0.05$; Fisher's LSD test).
Discussion

A detailed account was provided of individual adult *B. germanica* feeding and drinking activity by using continuous videotaping. It is important to note that the analyses of both activity periods and the frequency and duration of single feeding and drinking events were based on those insects which utilized the resource at least once during the 96-h period. These responses would be lower if the total population was considered. Photocell methods can at best provide estimates based on the total population, with a further loss of resolution when the sexes and reproductive classes are not segregated.

Although the resource was visited throughout any given day, feeding and drinking peaks coincided with locomotor activity peaks observed by Hocking (1958) and Dreisig and Nielsen (1971) for *B. germanica* and by Rollo (1984) for *Periplaneta americana* (L.). Fuchs (1983) observed activity peaks 3 h before scotophase and 1 h before photophase, in addition to a peak just after the onset of scotophase. However, the first two peaks occurred only in the harborage. This study revealed a more discernible rhythm when food and water were placed far from the harborage (Fig. 3B) suggesting that short-range foraging by some individuals always occurs, while long-range foraging is more likely to take place at specific times.

Although there was no overall effect of density on feeding or drinking events, more drinking by male *B. germanica*, which was attributed to the presence of aggregation pheromone in the harborage. However, in the present study, more frequent and prolonged drinking activity occurred at high rather than low density when the resource was placed far from the harborage, suggesting that more foraging occurs under crowded conditions. Less frequent drinking and shorter drinking periods were observed at high versus low density when the resource was near the harborage, which may be in response to increased competition at the water source, causing drinking to be interrupted when the cockroach density was high. It is uncertain whether the absence of nymphs at the low density affected the density/sex and density/distance interactions.

Far fewer cockroaches reached the resource at the greater distance than when it was placed in the same container as the harborage. This difference in feeding and drinking probably had more to do with the inability to locate the conduit between the cages rather than the actual harborage-to-resource distance, since cockroaches were frequently observed moving about the harborage container but bypassing the resource access port. These laboratory-reared cockroaches may be less effective foragers than a field strain. Akers and Robinson (1983) demonstrated that field collected *B. germanica* moved more than two different laboratory-reared strains. The configurations used in the present study are not unlike those that would be found in the field, whereby cockroaches may or may not have to forage great distances with many obstacles separating harborage and resource. It is apparent that when using insecticidal baits,
placement closest to cockroach harborage will produce the most satisfactory control.

The longevity of nonfeeding or nondrinking insects did not differ from that of insects that fed and drank during the experiment. An extended monitoring period may have revealed additional resource visits especially from gravid females, which, according to Durbin and Cochran (1985), survive water deprivation for ca. 5 days, and even longer periods without food.

The effect of sex and reproductive status on food and water utilization was considerable. More males than females reached the food or water, particularly at the large harborage-to-resource distance. This is consistent with the results of Sommer (1975) and Ballard et al. (1984), who demonstrated that male *B. germanica* were more active and explored more than females. A. G. Appel (personal communication) found that males had a 2-fold greater rate of cuticular water loss than females, which may indicate that males must search for water more actively.

Nongravid females fed and drank slightly longer and more frequently than males. Gravid females fed and drank much less often. Cochran (1985) measured food and water consumption of female German cockroaches through several reproductive cycles, and found that feeding and drinking peaks occurred during the egg maturation period, which ended abruptly at the appearance of an egg capsule. He calculated an average feeding and drinking interval of 1.1-1.3 days for nongravid females and a 6- to 8-day feeding interval and 3-day drinking interval for oothecae-carrying females. These studies were conducted in a manner such that little foraging was necessary for locating the food and water. In the present study, nongravid females fed and drank 1-1.5 days in arenas with a short harborage-to-resource distance. However, the interval was considerably protracted when food and water were far from the harborage. Although feeding and drinking by gravid females was also a function of harborage distance, most of these individuals did not feed or drink within the 96-h observation period. However, within this period gravid females tended to eat and drink with equal frequency. Since females bearing oothecae infrequently forage for food and water, they are less likely to contact insecticidal residues or baits and appear to be the main source of a population resurgence following insecticide treatment.

Willis and Lewis (1957) and Durbin and Cochran (1985) reported that *B. germanica*, especially females, could withstand lack of food longer than water deprivation. The greater immediate need for water may explain why most cockroaches in the present study visited the water before feeding, particularly when the refractory period exceeded 12 h. Since the results obtained were significantly different from that expected for random foraging (1:1, food: water), directed movement (hydrotaxis) to water may have occurred. Hygroreceptors have been identified in *P. americana* by Yokohari (1978), but have not been investigated in *B. germanica*. Once satiated with water, random foraging may bring the cockroach to the food source (<2 cm away).

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