FOUR: Diets and Foraging

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FOUR | # Diets and Foraging

Timid roach, why be so shy?
We are brothers, thou and I.
In the midnight, like yourself,
I explore the pantry shelf!

— C. Morley, "Nursery Rhymes for the Tender-Hearted"

Cockroaches are typically described as omnivores, scavengers, or "classic generalists" (Dow, 1986), insects that feed on most anything they encounter. Indeed, the success of pest cockroaches in human habitations may be based largely on their ability to feed on soap, glue, wire insulation, and other materials that they certainly did not encounter during their evolution and do not encounter while living in more natural habitats. Our knowledge of cockroach diets stems largely from studies of these domestic pests, and it is assumed that their dietary habits are the norm (Bell, 1990). Some non-pest species (e.g., certain cave cockroaches) do appear omnivorous, but the term is not an adequate descriptor for the majority of Blattaria. Outside the man-made environment, the cockroach diet typically contains more refractory material than is generally appreciated (Mullins and Cochran, 1987). They can be selective eaters, and in some cases, specialized. There are several reasons for this rather biased image of cockroach diets. Some species will eat almost anything in urban or laboratory settings, but are highly selective in the wild. Few feeding observations or gut analyses from cockroaches in natural habitats have been conducted; in existing studies the picture is far from complete. We may have an indication of the menu at a particular point in time; however, we do not know if the food item in question is a small or large component of the diet. Further, the menu may vary with availability of certain foods, and with the age, sex, and reproductive or developmental status of the consumer.

FORAGING BEHAVIOR

With some exceptions, three feeding syndromes characterize the cockroaches that can be observed from ground level in tropical rainforest. First, nymphs of most species become active at nightfall, and begin to forage in the leaf litter on the forest floor. They can be seen skeletonizing wet, dead leaves, leaving harder veins and similar tissue. Leaf chips or dead leaf mush dominate the gut contents, but nematodes, fungi, insect larvae, and

61

oligochaetes are also found. This feeding strategy was confirmed in the laboratory, where cockroach nymphs were observed ingesting the entire "sandwich": the leaf and everything on it (WJB, pers. obs.). Second, adults emerge from tree holes, leaf litter, and other harborages, and begin a vertical migration up into the canopy; the heights reached are species specific and probably relate to nutritional preferences (Schal and Bell, 1986). When the adults have reached the "correct" height, they move onto leaves and begin feeding on materials that have fallen or grow on the leaves. Third, a subset of species, mostly blattellids, shelter in curled dead leaves at a height of 1.5 to 2 m; palm fronds are commonly chosen as harborage. At night the cockroaches flit about leaves in the canopy, scraping algae and other microvegetation from the phylloplane. These species do not feed at a preferred height. Other foraging strategies include feeding on bark and epiphylls of rotting logs (*Capucina*) and feeding in rotting wood (nymphs of *Megaloblatta*). Some species have never been observed feeding, such as the green cockroach *Panchlora nivea,* but their guts contain a sweet-smelling substance that may be nectar from the upper canopy (WJB, pers. obs.)

Locating Food

Individually marked cockroaches in the rainforest generally home in on food via exploration and olfactory cues, sometimes arriving at fruit falls from quite long distances (Schal and Bell, 1986). Once near the food item, the cockroach's antennae and palps are used to inspect the resource; the information gathered is then used as basis to decide whether ingestion should proceed (WJB, unpubl. data). In domestic species (*Blattella germanica*), food closest to the harborage is exploited first (Rivault and Cloarec, 1991); this is probably also the case for cockroaches in natural habitats.

Individuals of *Diploptera punctata* in Hawaii are attracted to moist, dead leaves (WJB and L.R. Kipp, unpubl. obs.). Experiments were conducted on a large (2 m tall) croton bush in the late afternoon, during the inactive period of the cockroach. The insects previously had been seen foraging in the bush at 9:00 the same morning. Dead, wet leaves were placed on a branch about 1.2 m from the ground, and within 5 min individuals appeared near the bait leaves, apparently lured from their harborages at the base of the plant by the leaf odor. When "activated" by the odor they scurried about, waving their antennae. When a branch route took them near, but not to the dead leaf, they would get to the end of the branch, antennate rapidly, then turn and run down the branch to seek another route. Sometimes an individual made several attempts, over various routes, before locating the wet leaf.

They were never observed flying to the bait. In Hawaii, *D. punctata* foraged from early evening (6:00 p.m.) to mid-morning (10:00 a.m.), with two peaks in activity at 8:00 a.m. and 10:00 p.m. Nonetheless, the cockroaches could be activated to return to the above-ground portions of the plant at any time by hanging new decaying leaves within the canopy. Members of this population survived and reproduced for 6 mon in WJB's laboratory in Kansas on a diet consisting solely of dead oak and hackberry leaves.

Relocating Food

Urban cockroaches (*B. germanica*) search individually and independently for food. Items are not transported back to shelter, but eaten where they are found (Durier and Rivault, 2001a). In at least two cockroach groups the place where food is acquired differs from where it is utilized. Obtaining food and using it are thus separated in time and space, and the obtainer and the user are not necessarily the same individual (Zunino, 1991). Both groups that employ this "grocery store" strategy live in excavated underground chambers. The Australian soil-burrowing cockroaches forage during the night and the early morning hours of the wet season. After a rain and above a certain threshold temperature, they emerge, transport a quantity of dead leaves down into the burrow, and then do not emerge again until the next rain. Females grasp a food item in their mandibles and drag it backward down into the burrow. If they are approached when they are on the surface they will drop whatever they are carrying and "get a fair scuffle up" running back to their burrow (D. Rugg, pers. comm. to CAN). Gathered leaves are eaten by both the forager and any young offspring in the nest. Nymphs begin provisioning their own burrow when they are about half-grown. The food cache accumulated during the rains must sustain burrow inhabitants throughout the dry season (Rugg and Rose, 1991, pers. comm. to CAN). Other cockroaches known to transport and store food live in the tunnels of small vertebrates. *Arenivaga apacha* in the burrows of kangaroo rats in Arizona can be found nesting amid *Yucca, Ephedra, Atriplex,* and grass seeds that they have filched from the supply gathered and stored by the host rodent. "Our suspicion that the cockroaches gather and hoard provisions was confirmed when we saw the cockroaches carry dried dog food and sesame seeds that were sprinkled over the top of the aquaria soil into small caches underground" (Cohen and Cohen, 1976).

There are records of other cockroach species transporting food, but in these cases it occurs only in competitive situations. Rivault and Cloarec (1990) discovered that *B. germanica* began to "steal" food items from a dish as the items became small enough to carry and as food be-

came scarce. Adults and larger nymphs stole more food than younger nymphs, and more stealing occurred when two or more individuals were present at a food source than when a lone individual was feeding. Similarly, when LMR fed crowded laboratory cultures with rice, he observed young nymphs position individual pieces of it between their front legs and mouthparts and run off on their hind legs (identity of species is lost to memory). Annandale (1910) documented *Periplaneta americana* using the mandibles to seize, hold, and transport termite alates in Calcutta.

Competition at food sources can trigger intraspecific aggression in *B. germanica.* The insects vary their tactics with age, and tailor them to the developmental stage of the opponent. Most agonistic interactions are between individuals of the same developmental stage. Young nymphs are primarily biters, but begin kicking more often as they develop; a good boot becomes more effective with the increased body weight characteristic of older stages (Rivault and Cloarec, 1992c). Young nymphs are generally tolerated by older stages and often reach food by crawling beneath larger conspecifics (Rivault and Cloarec, 1992a, 1992b). The relative amount of food required by large and small nymphs lowers the cost of benevolence for older insects.

Food relocation and aggression are both proximate mechanisms for obtaining and securing food from competitors. In burrow dwellers, relocation also allows them to feed at leisure in a location relatively safe from predators. Resource competition also may influence life history strategies, resulting in the distribution of competitors within a guild either in time (Fig. 3.5) or in space.

Learning

In many species, the location of the night harborage is spatially separated from other resources such as food and water. In the laboratory and in urban settings, individuals of *B. germanica* learn the position of their shelter and of stable food sources in relation to visual landmarks; however, olfactory information, which provides more reliable information about the presence of food, can override the visual cues. The insects learned to associate a certain type of food with a specific site, and were "disturbed" (exhibited complex paths) when the association between food type and food position was modified (Durier and Rivault, 2001b). Young nymphs of this species tend to explore smaller areas, cover shorter distances, and remain longer at depleted food sources than older cockroaches, eventually learning that "there is no point in waiting near a depleted patch, as it will not be renewed immediately" (Cloarec and Rivault, 1991). *Periplaneta americana* is differentially attracted to various dietary nutrients, and

learned to associate certain odors with a proteinaceous food source, particularly when they were protein deprived. No such association between odor and carbohydrate could be established (Gadd and Raubenheimer, 2000). Watanabe et al. (2003) demonstrated that *P. americana* can be classically conditioned to form olfactory memories. The species also begins including novel foods in its diet after nutrient imbalances (Geissler and Rollo, 1987). It is probable that similar associations occur in nature; cockroach species known to have a wide dietary repertoire may both acquire knowledge of food-associated odors and benefit from past experience.

FEEDING VARIATION AND FOOD MIXING

Urban pest cockroaches (*Supella longipalpa*), like many omnivores (Singer and Bernays, 2003), balance their diet by selecting among available foods rather than by trying to obtain all nutrients from one food type (Cohen et al., 1987). *Periplaneta fuliginosa* is described as a "cafeteria-style eater" that will sample several types of food before concentrating on one (Appel and Smith, 2002). Other species known to have a varied diet in natural habitats, like *Parcoblatta* (Table 4.1), may do the same thing. Laboratory studies indicate that cockroaches are capable of selecting their diet relative to nutrient demand at every point in the lifecycle. Within a species, foraging behavior and dietary preferences vary with sex and ontogeny, and undergo dramatic changes correlated with reproductive and developmental cycles. In the field, it is possible that these predilections are also influenced by the seasonal availability of specific foods. Just after a local mast fruiting, for example, their diet may be higher in sugars and yeasts, and lower in fiber. When fruit is not available or their needs change, they may rely on less nutritious, higher-fiber foods such as litter or bark, or seek items that provide specific nutrients.

Age

As in most young animals (Scriber and Slansky, 1981; White, 1985) the dietary requirements of young cockroach nymphs differ from those of older nymphs and adults. Cochran elegantly demonstrated this in his studies of *Parcoblatta* spp., cockroaches that void urates to the exterior in discrete pellets if dietary nitrogen levels exceed a certain "break even" point with respect to nitrogen demands. In nymphs less than 1 mon old, a diet of 4% nitrogen results in only minimal urate excretion. On the same diet, nymphs 1–2 mon old void urates at a rate of 8–13% of excreta by weight and large nymphs reach an equilibrium at less than 1.5% nitrogen in the diet (Cochran, 1979a; Cochran and Mullins, 1982). In nu-

merous species, this high requirement for nitrogen is reflected in the behavior of neonates, whose first meals are largely derived from animal or microbial sources. In many species the first meal consists of the embryonic membranes and the oothecal case. The female parent may provide bodily secretions originating from glands in or on the body, or from either end of the digestive system (Chapter 8). The few studies of coprophagy to date indicate that this behavior is most prevalent in early instars, suggesting that microbial protein is a crucial dietary component (Chapter 5). The need for animal or microbial protein may help explain why it is difficult to rear many cockroaches in the laboratory. While adults may thrive, "nymphs are more difficult to rear, starving to death in the midst of a variety of food stuffs" (Mackerras, 1970).

As they develop, juveniles may adopt the same diet as adults (e.g., wood, guano in caves) or feed on different materials, such as the rainforest species in which nymphs feed on litter but adults have a more varied menu. Studies in laboratory and urban settings indicate ontogenetic changes in foraging behavior, as well as variation in feeding behavior and food choice within a stadium. Immediately after hatch nymphs of *B. germanica* are able to find food and return to shelter, but they improve their foraging performance as they age (Cloarec and Rivault, 1991). *Periplaneta americana* nymphs take large meals during the first three days post-molt, then feed very little until the next (Richter and Barwolf, 1994). Juveniles of *Su. longipalpa* change their dietary preferences within a stadium. Protein consumption remains relatively low and constant, whereas carbohydrate consumption is highest during the first week, then declines gradually until the end of each instar (Cohen et al., 1987) (Fig. 4.1A). When given a wide range of protein:carbohydrate choices, *Rhyparobia maderae* nymphs consistently selected a ratio of approximately 25:75, suggesting that they have the ability to balance their diet (Cohen, 2001). Subadults of *B. germanica* are impressively capable of compensating dietary imbalances by choosing foods that redress deficiencies (Raubenheimer and Jones, 2006).

Sexual Differences

Current evidence suggests that male foraging behavior and food choice differs from that of females; generally, male cockroaches feed less and on fewer food types. In the Costa Rican rainforest male cockroaches always have less food in their guts than do females after the usual nightly foraging period (WJB, unpubl. data). This is particularly true for seven species of blattellids, in which 50–100% of males had empty guts. In more than 30 male *Latiblattella* sp. examined, none had any food in the gut. In contrast, males of four species of blaberids often had medium to full guts, although females had still fuller guts. This difference may be due to the active mate searching required of blattellid males as compared to blaberids. Male cockroaches tend to have narrower diets than females (Table 4.2), which may relate to the nutrients required for oogenesis. A similar pattern was obvious in *D. punctata* in Hawaii; 44% of females had guts filled to capacity, whereas male guts were never full. Nymphal guts were variable (19% full, 81% not full). It appeared that first instars had not fed at all, suggesting that they were relying on fat body reserves developed *in utero* while being fed by their viviparous mother. Older nymphs had fed to repletion. In all stages, the gut content was homogeneous material resembling dead leaf mush (WJB, unpubl. data). The amount of food consumed by male *P. americana* varies greatly on a daily basis, with the insects fasting on approximately one-third of days (Rollo, 1984b). Male German cockroaches did not exhibit cyclical feeding patterns, but the degree of sexual activity appears influential.

Table 4.1. Diet of four species of *Parcoblatta,* based on 45 nocturnal observations of feeding adults (Gorton, 1980). Note that two species were not observed ingesting animal food sources.

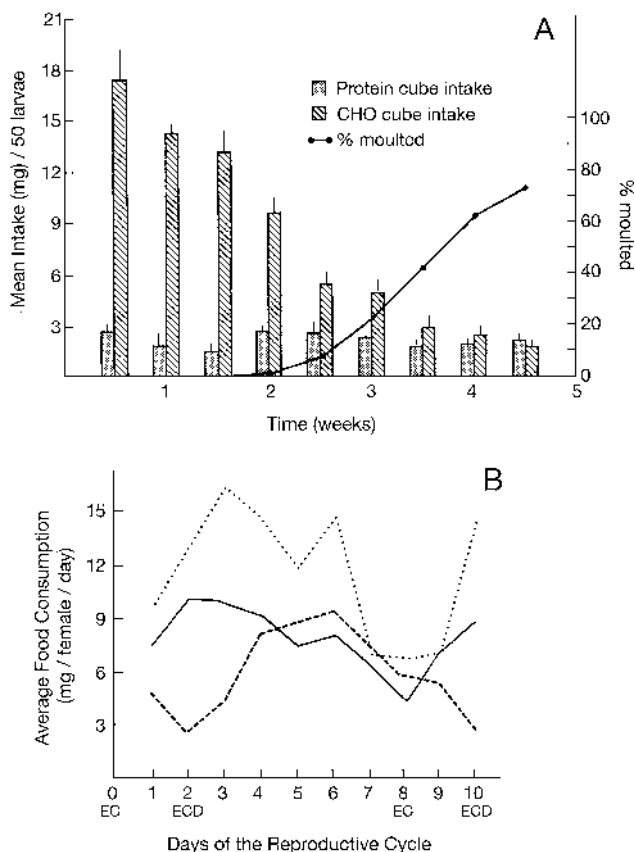|	*Parc. pennsylvanica*	*Parc. uhleriana*	*Parc. lata*	*Parc. virginica*
Mushrooms	+	+		+
Cambium			+	
Flower petals			+	
Moss		+		
Sap	+		+	
Cercropid spittle	+			
Live insect	+			
Bird feces		+		
Mammalian feces	+			
Mammalian cartilage		+		

Fig. 4.1 Dietary self-selection in cockroaches. (A) Mean intake of protein and carbohydrate (CHO) cubes and cumulative percent molting in *Supella longipalpa* first instars over the course of the stadium. From Cohen et al. (1987), courtesy of Randy W. Cohen. (B) Food consumption by adult female *Parcoblatta fulvescens* over the course of the reproductive cycle when given a dietary choice. Dashed line, 5% protein-cellulose diet; dotted line, 5% protein-dextrose diet; solid line, 42% protein diet. EC, egg case formation; ECD, egg case deposition. From Lembke and Cochran (1990), courtesy of Donald G. Cochran. Both graphs reprinted with permission of Elsevier Press.

The food intake of *B. germanica* males mated twice per week was greater than that of males allowed to mate only once (Hamilton and Schal, 1988).

In many oviparous females, food intake and meal type is correlated with the ovarian cycle. Food intake falls to a low level a few days prior to ovulation and remains low until the ootheca is deposited in *P. americana* (Bell, 1969), *Parcoblatta fulvescens, Parc. pennsylvanica* (Cochran, 1986b), *Su. longipalpa* (Hamilton et al., 1990), and *B. germanica* (Cochran, 1983b; Cloarec and Rivault, 1991; Lee and Wu, 1994). Water intake is also cyclical (Fig. 4.2) (Cochran, 1983b, 1986b). In the ovoviviparous *R. maderae,* food intake declines at the time of ovulation and remains at a relatively low level until partition; neural input from mechanoreceptors in the wall of the brood sac directly inhibits feeding (Engelmann and Rau, 1965). In

pregnant females of *D. punctata,* gut fullness varies relative to embryo length, with a trend toward full guts when embryos are small (2–5 mm) and empty guts when embryos are large (6–8 mm) (WJB, unpubl. data).

Females in at least two blattellid species select among various food types according to their vitellogenic requirements. In choice experiments with *Xestoblatta hamata,* Schal (1983) found that high-nitrogen foods were consumed mainly on nights 3 and 4 of the ovarian cycle. Females of *Parc. fulvescens* given one high-protein and two low-protein diets fed so that they remained in nitrogen balance; relative proportions of the different nutrients varied over the reproductive cycle (Fig. 4.1B). Females with access to only high-protein diets excreted urates, an indication that ingested protein levels exceeded their needs. Ovarian cycles of the self-selecting individuals were similar in length to those of the females fed a high-protein diet (Cochran, 1986b; Lembke and Cochran, 1990).

STARVATION

Willis and Lewis (1957) determined the mean survival times of 11 species of cockroaches deprived of food, water, or both (Table 4.3). When deprived of food and water, the insects can live from 5 days (male *Blattella vaga*) to 42 days (female *P. americana*). When given dry food

Table 4.2. Gut contents of cockroaches collected between 20:00 and 4:00 at La Selva Research Station, Costa Rica, between January and May 1992 (WJB and J. Aracena, unpub. data).

| Cockroach species	n	Material in foregut
Blaberidae		
Capucina rufa		
Male	5	Epiphylls
Female	2	Epiphylls, bark scraps
Nymph	6	Epiphylls, bark scraps
Epilampra rothi		
Male	64	Dead leaf chips
Female	20	Algae, green plant, dead leaf, trichomes
Nymph	80	Dead leaf chips, insect parts
Blattellidae		
Xestoblatta hamata		
Male	16	Dead leaf, bird dung
Female	11	*Inga* bark chips, algae, dead leaf chips, fruit, leaf debris
Nymph	25	Finely ground dead leaf, insect parts
Cariblatta imitans		
Male	16	Algae
Female	10	Algae
Nymph	4	Algae
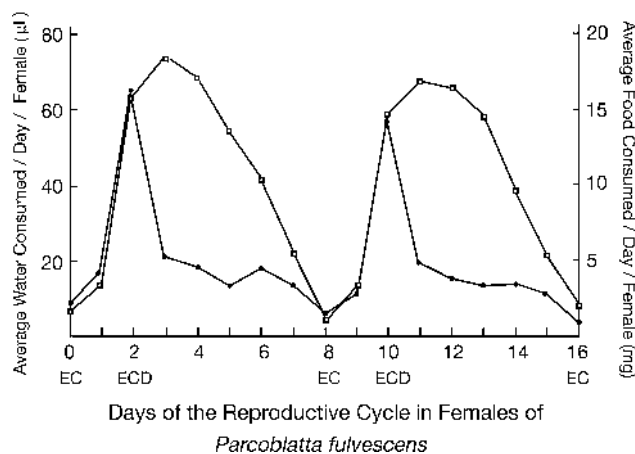
Fig. 4.2 Feeding and drinking cycles in relation to the reproductive cycle of the wood cockroach *Parcoblatta fulvescens*. Filled circles, water consumption; open squares, food consumption; EC, egg case formation; ECD, egg case deposition. From Cochran (1986b), courtesy of Donald G. Cochran, with permission from Elsevier Press.

but no water, they lived for about the same period of time as those deprived of both. If they are provided with water, most lived longer. Some species can live for 2 to 3 mon on water alone, and others significantly longer. Virgin females of *Eublaberus posticus* live an average of 360 days on water alone, whereas starved but mated females can live an average of 8 mon and are even able to produce 1 or 2 litters, yielding about 26 young. One female mated at emergence was starved for 252 days, during which time she produced 2 litters totaling 50 nymphs. She was then given food on day 252 (and thereafter), mated again 4 days later, and lived an additional 525 days, producing 5 more oothecae from which 24, 18, 5, 1, and 0 nymphs hatched. Although this female had been starved for the first 8 mon of adult life, after food was made available she managed to give birth to a total of 98 offspring, which is about normal for this species (Roth, 1968c).

There is a significant difference in starvation resistance between males and females in cockroach species exhibiting sexual dimorphism in body size. In Table 4.3, males and females are of similar size only in *Neostylopyga rhombifolia, Eurycotis floridana,* and *Nauphoeta cinerea;* in these cases, survival of males and females is similar. In the remaining species males are significantly smaller than females and are more vulnerable to starvation. A larger body size is correlated with bigger fat bodies and their accumulations of carbohydrates, lipids, and uric acid; these reserves can be rapidly mobilized on demand (Mullins and Cochran, 1975b; Downer, 1982). The nutrients and water housed in developing oocytes are additional resources available to starving females. The strategy for a food-deprived female of *P. americana* seems to involve re-

sorption of yolk-filled eggs, storage of their yolk proteins, and then rapid incorporation of protein into eggs when feeding re-ensues (Roth and Stay, 1962b; Bell, 1971; Bell and Bohm, 1975).

A variety of digestive attributes help cockroaches buffer food shortages. The large crop allows an individual to consume a substantial quantity of food at one time. This bolus then acts as a reservoir during periods of fasting. When fully distended with food, the crop is a pear-shaped organ about 1.5 cm in length and 0.5 cm at its widest part (in *Periplaneta australasiae*). It extends back to the fourth or fifth abdominal segment, crowding the other organs and distending the intersegmental membranes. A meal may be retained in the crop for several days (Abbott, 1926; Cornwell, 1968). Solid food is also retained in the hindgut of starving *P. americana* for as long as 100 hr, although the normal transit time is about 20 hr (Bignell, 1981); this delay likely allows microbial biota to more thoroughly degrade some of the substrates present, particularly fiber. The functional significance of intestinal symbionts increases in times of food deficiency and helps to maintain a broad nutritional versatility (Zurek, 1997). A starving cockroach is thus indebted to its microbial partners on two counts: first, for eking out all possible nutrients in the hindgut, and second, for mobilizing uric acid stored in the fat body (Chapter 5). When food is again made available, starved *P. americana* binge. After starving for 13 days the amount of food consumed rose to five times the normal level, then leveled off after approximately 20 days. Greater consumption was accomplished by larger and longer meals, not by increasing the number of foraging trips (Rollo, 1984a).

PLANT-BASED FOOD

There is little evidence that any cockroach species is able to subsist solely on the mature green leaves of vascular plants. There are reports of occasional herbivory, such as that of Crowell (1946), who noted that the small, round leaves of the aquatic plant *Jussiaca* are included in the diet of *Epilampra maya*. Often, cockroaches that appear to be feeding on green leaves are actually eating either a small, dead portion at the leaf edge or around a hole, or other material on the leaf (WJB, unpubl. obs.). To test the extent to which tropical cockroaches include fresh vegetation in their diets, WJB set up a series of two-choice tests in laboratory cages at La Selva Biological Station in Costa Rica. Ten species of cockroaches were tested*: Capucina* sp., *Cariblatta imitans, Epilampra involucris, Ep. rothi, Ep. unistilata, Latiblattella* sp., *Imblattella impar, Nahublatella* sp., *Nesomylacris* sp., and *X. hamata.* The insects were offered a choice of green leaves versus dead leaves of the same plant species; only leaves eaten readily by local Or-

Table 4.3. Longevity of cockroaches on starvation diets. Tests were performed at 36–40% relative humidity, except for tests with *R. maderae,* which were run at 70%. Note that controls (+ food, + water) are not adult lifespans; controls were terminated when all the experimental insects of the species died. Modified from Willis and Lewis (1957).

| Species | Sex | Mean length of survival (days) | | | |
		+ food + water	+ food − water	− food + water	− food − water
Blattidae					
Blatta orientalis	Female	64	16.8	32.1	14.2
	Male	40	11.5	20.0	11.9
Neostylopyga rhombifolia	Female	108	25.4	26.7	22.1
	Male	128	24.6	29.3	21.9
Periplaneta americana	Female	190	40.1	89.6	41.7
	Male	97	27.3	43.7	28.1
Eurycotis floridana	Female	86	26.6	43.0	26.7
	Male	70	21.8	29.7	21.1
Blattellidae					
Blattella germanica	Female	85	11.9	41.9	12.8
	Male	54	8.8	9.6	8.2
Blattella vaga	Female	95	7.9	32.4	8.5
	Male	69	5.4	16.8	4.8
Supella longipalpa	Female	80	12.8	14.3	14.5
	Male	74	11.5	10.1	9.0
Blaberidae					
Diploptera punctata	Female	102	18.7	42.9	18.7
	Male	119	14.5	28.9	15.8
Rhyparobia maderae	Female	181	160.0	54.3	51.3
	Male	150	84.0	56.0	35.1
Nauphoeta cinerea	Female	98	24.3	61.1	27.0
	Male	94	22.8	46.1	27.3
Pycnoscelus surinamensis	Female	139	18.8	73.2	24.3
	Male	74	9.9	39.8	10.6

thoptera were used. The feeding behavior of the cockroaches was observed throughout the night, and their guts dissected the next day. Without exception, no cockroach ate fresh vegetation. Individuals that nibbled the greenery appeared repelled and on occasion could be observed jumping away from the leaf. When offered a choice of paper versus green leaves, the cockroaches ate the paper. When only green leaf was offered, they refused to feed.

Nonetheless, there are numerous records of cockroaches as plant pests (Roth and Willis, 1960). In 1789, Captain William Bligh had to wash down his ships with boiling water so that cockroaches would not destroy the breadfruit trees he was transporting from Tahiti to the West Indies (Roth, 1979a). One of the more frequently reported plant pests is *Pycnoscelus surinamensis,* which destroyed the roots of 300,000 tobacco plants in Sumatra. In greenhouses, it is known to girdle rose bushes, eat the bark and stems of poinsettias, and damage orchids, cucumbers, and lilies. It was responsible for the destruction of 30,000–35,000 rose plants in one Philadelphia greenhouse, and regularly hollows the hearts of palms and ferns in the southern United States (Roth, 1979a). Apparently, it managed to sneak into Biosphere 2 and took a strong liking to every kind of living plant. Tomatoes, sweet potato leaves, flowers and fruit of squash plants, rice seedlings, ripe papayas and figs, and green sorghum seeds were each included on the bill of fare (Alling et al., 1993). While the culprit cockroach was never identified, both *Pyc. surinamensis* and *P. australasiae* were found in the beehives brought in to pollinate crops (Susan C. Jones, pers. comm. to CAN).

The most commonly reported type of plant damage by cockroaches is to seedlings, new leaves, and growing root

and shoot tips. These are likely preferred because their actively growing tissues have physically tender, thin-walled cells, lower levels of secondary compounds, and higher levels of nitrogen than mature leaves (Chown and Nicolson, 2004). Examples include *P. americana* destroying 30% of the freshly planted seeds of the quinine-producing plant *Cinchona pubescens* in Puerto Rico (Roth, 1979a), and *Shelfordina* (= *Imblattella*) *orchidae* damaging developing roots and shoots of orchids in Australian greenhouses (Rentz, 1987). *Calolampra elegans* and *Cal. solida* (Blaberidae) are pests requiring control measures in a variety of Australian crops, including sunflower, soybean, sorghum, cotton, navy beans, wheat, and maize. The cockroaches live in litter and the upper layers of soil, and emerge at night to chew the stems of seedlings at or near ground level (Robertson and Simpson, 1989; Murray and Wicks, 1990; Roach and Rentz, 1998). Cockroach herbivory in tropical forests is probably more common than generally realized; damage to newly flushed leaves in the canopy of Puerto Rican rainforest has been correlated with the abundance of cockroaches (Dial and Roughgarden, 1995).

Overt herbivores are not limited to feeding on green leaves of vascular plants; the category includes organisms that feed on other plant parts as well (Hunt, 2003). Many cockroach species, then, are at least partly herbivorous, because they include pollen, nectar, sap, gum, roots, bark, twigs, flowers, and fruit in their diet. Among those known to feed on pollen are *Sh. orchidae* (Lepschi, 1989), *Paratropes bilunata* (Perry, 1978), *Latiblattella lucifrons* (Helfer, 1953), and *Ellipsidion* sp. (Rentz, 1996). *Balta bicolor* is commonly found on the leaves and spent flower heads of *Gahnia* sp. in eucalypt woodlands (Rentz, 1996) and both males and females are attracted to pollen placed on a tree branch (Fig. 4.3). In a survey of insects captured by the pitcher plant *Sarracenia flava* in North Carolina, CAN (unpubl. data) collected males of four species of *Parcoblatta* (*Parc. fulvescens*, *Parc. uhleriana*, *Parc. virginica*, and *Parc. lata*), and both sexes of *Cariblatta lutea*. Since all these are winged as adults, while females of the *Parcoblatta* species are brachypterous, the cockroaches may be seeking nectar as an easily harvested source of energy to fuel flight. This suggestion is strengthened by the observation that volant *Blattella asahinai* adults, but not nymphs, feed on aphid honeydew (Brenner et al., 1988). *Trichoblatta sericea* in India feeds on the gum exuded from the bark of *Acacia* trees, and less commonly on gum from other trees (*Azadirachta, Moringa, Enterolobium*) (Reuben, 1988). Since individuals lived twice as long and had four times the reproductive output when fed a diet of powdered gum arabic when compared to a diet of biscuit crumbs or wheat flour, gum may be providing essential nutrients. The digestive physiology of this species would

be of interest, as most gums are carbohydrate polymers that require microbial degradation if they are to be assimilated (Adrian, 1976). A number of cockroaches are noted as feeding "on flowers" (e.g., *Opisthoplatia orientalis*—Zhu and Tanaka, 2004a; *Ectobius pallidus*—Payne, 1973), but it is unclear as to whether the individuals were actually feeding on flower petals, or standing on the flower ingesting pollen or nectar. *Arenivaga apacha* (Cohen and Cohen, 1976) and possibly other cockroaches that dwell in vertebrate burrows feed on the stored seeds of their host, while sand-swimming species of *Arenivaga* include the roots of desert shrubs in their diet (Hawke and Farley, 1973). Many species feed on ripe fruit, an energy-rich, seasonally available food source. *Diploptera punctata,* for example, feeds on mangoes, papayas, and oranges, as well as on the outer covering of *Acacia* pods (Bridwell and Swezey, 1915) and the bark of *Cypress,* Japanese cedar, citrus, and *Prosopis* spp. (Roth, 1979a).

Leaf Foraging

In tropical rainforests leaf surfaces are "night habitat" for many crepuscular and nocturnal cockroaches. It is the only time and place that the majority of cockroaches that live in rainforests of Queensland, Australia (D. Rentz, pers. comm. to CAN), and Costa Rica (WJB, pers. obs.) can be seen. The insects emerge from harborage on the forest floor, move up the plants, then out onto foliage, or they move onto leaves from the innumerable hiding places in the different strata of the forest canopy. Adhesive footpads (arolia and euplantae) help the cockroaches negotiate sleek planes of vegetation, but it is only young leaves that commonly have smooth, simple surfaces. As leaves age they become elaborate, textured habitats rich in potential food sources (Walter and O'Dowd, 1995) (Fig. 4.4). In general, leaves provide two menu categories for cockroaches (WJB, unpubl. obs.). First, leaves act as *serv-*
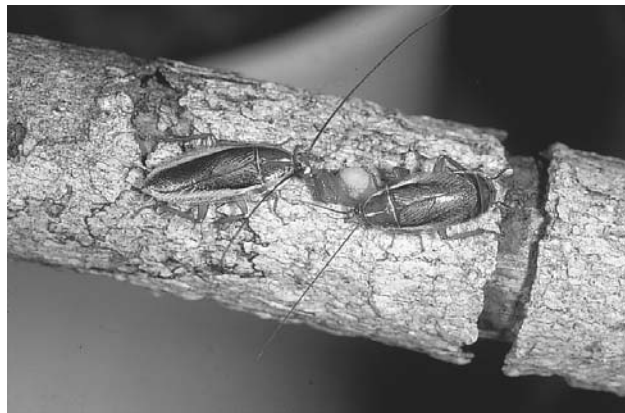

Fig. 4.3 *Balta bicolor* feeding on pollen applied to a branch; male (*left*), female (*right*). Photo courtesy of David Rentz.
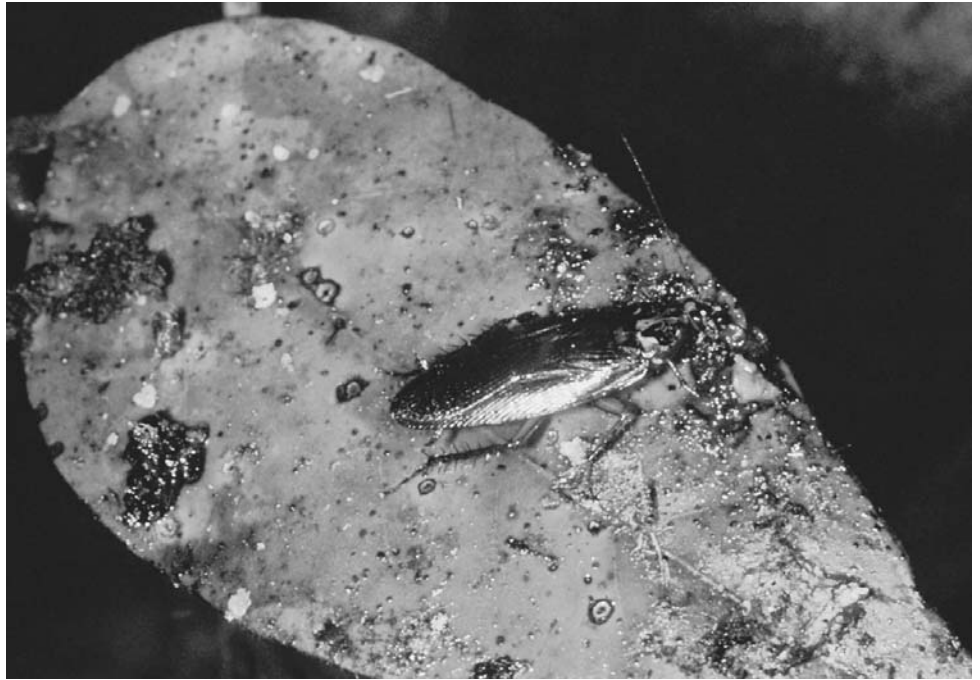
Fig. 4.4 *Beybienkoa* sp., night foraging on leaf surface material, Kuranda, Queensland. Photo courtesy of David Rentz.

ing trays for the intercepted rain of particulate organic matter that falls perpetually or seasonally from higher levels of the forest. This includes bird and other vertebrate feces, pollen, spores, leaves, twigs, petioles, sloughed tree bark, flower parts, and pieces of ripe fruit originating from the plant and from sloppy vertebrate eaters. Also offered on these leaf trays are dead leaf material around herbivore feeding damage, and the excreta, honeydew, silk webbing, eggshells, exuvia, and corpses of other arthropods. Live mites, aphids, and other small vulnerable arthropods on leaves are potential prey items. The second menu category on leaves in tropical forests is the salad course: leaves are *gardens* that support a wide range of nonvascular plants (epiphylls) and microbes. These include lichens, bryophytes, algae, liverworts, mosses, fungi, and bacteria.

Cockroaches in Costa Rican rainforest have been observed feeding on the majority of items listed above (WJB and J. Aracena, unpubl. obs.). Dissections of the cockroaches and inspection of their gut contents, however, indicate that ingestion of the different food types can be rather specific. Those cockroaches for which fairly large sample sizes are available are listed in Table 4.2. *Capucina rufa* and *Cap. patula* forage on dead logs, feeding on epiphylls, fungi, and bark scraps. *Epilampra involucris* females perch near the ground, where they feed on ground litter and the materials that fall onto it. Males of this species, which perch on leaves at heights of up to 50 cm, eat algae, bryophytes, lichens, pollen, spores, fruit, and

flakes of shed bark. A subset of small, mobile species fly about in the canopy and scrape epiphylls from leaf surfaces at night. *Imblattella* and *Cariblatta* feed primarily on leaf trichomes, blue-green algae, liverworts, and spores. Only algae were found in the guts of male, female and juvenile *Car. imitans.* Trichomes, which normally interfere with foraging by small herbivores and carnivores (Price, 2002), are ingested by several cockroach species (WJB, unpubl. obs.). The many tropical cockroaches that fulfill their nutritional requirements by feeding on the broad variety of materials offered on leaf laminae may, like ants (Davidson et al., 2003), be categorized as leaf foragers. Those that specialize on the epiphylls and other plant products (trichomes, pollen, honeydew) found in this habitat may be described as cryptic herbivores (Hunt, 2003).

Detritus

Many cockroaches feed on detritus (Roth and Willis, 1960; Mullins and Cochran, 1987), a broad term applied to nonliving matter that originates from a living organism (Polis, 1991). A unique feature of detritivores is that there is no co-evolutionary relationship between the consumer and the ingested substrate. This is in stark contrast with the relationship between herbivores and higher plants, and in predator-prey systems. A consequence of this lack of co-evolutionary interaction is that detritivores are less specialized than predators and herbivores,

and they defy classification into straightforward food chains (Anderson, 1983; Price, 2002; Scheu and Setälä, 2002). The food of detritivores is nutritionally very different from feeding on living plants or animals because it has been colonized and altered by microbes. Litter is a "resource unit" comprised of recently living material, degraded litter, dissolved organic matter, complex consortia of fungi, bacteria, nematodes, and protozoa, and the metabolic products of these (Nalepa et al., 2001a; Scheu and Setälä, 2002). The notion that detritivores may ingest a large amount of living microbial material, and may develop co-evolutionary relationships with these organisms, is not typically considered (Chapter 5).

Dead plant material in varying states of decay is known to be the primary food source for cockroach taxa in a variety of habitats. This is particularly true for species living at or near ground level in tropical forests, which have an unlimited supply of decaying litter within easy reach. Plant detritus is constantly accumulating on the forest floor, either seasonally or constantly. In the rainforest canopy, detritivores have access to suspended litter and the dead material that typically edges herbivore damage on live leaves (Fig. 3.3). Many cockroaches feed on leaf litter (Table 4.4), which in general is of higher resource quality and decomposes more quickly than twigs and other woody materials (Anderson and Swift, 1983); however, decayed wood may serve as a food source more commonly than is generally appreciated (Table 3.2). In rainforests, practically all wood is rotten to some extent, and the division between decayed wood, rotted plant litter, and soil organic matter is difficult to assess (Collins, 1989). Many cockroach detritivores live within their food source—"a situation reminiscent of paradise" (Scheu and Setälä, 2002).

Physically tough substrates like leaf litter and wood are macerated by a combination of mandibular action and

Fig. 4.5 Proventriculus of *Blattella germanica,* transverse section. From Deleporte et al. (1988), courtesy of Daniel Lebrun. Scale bar = 100 μm. When the "teeth" are closed the inward pointed denticles almost occlude the lumen. Hairs on the pulvilli may help filter the coarse food from the fine (Cornwell, 1968).

passage through the proventriculus, a strongly muscled and often toothed armature that lies just behind the crop (Fig. 4.5). It might be expected that the morphology of this organ is functionally related to diet, but that does not appear to be the case. The various folds, denticles, and pulvilli on the structure are, in fact, useful characters in phylogenetic studies of cockroaches (McKittrick, 1964; Klass, 1998b). The proventriculus of the wood-feeding taxa *Cryptocercus* (Cryptocercidae) and *Panesthia* (Blaberidae), for example, are completely different; that of *Cryptocercus* resembles that of some termites, and *Panesthia* has the flaccid, wide proventriculus of a blaberid. *Macropanesthia rhinoceros,* which feeds on dead, dry leaves, lacks a proventriculus (Day, 1950). This species, as well as *Geoscapheus dilatatus, Panesthia cribrata,* and *Cal. elegans* are known to ingest sand, probably to aid in the mechanical fragmentation of their food (Zhang et al., 1993; Harley Rose, pers. comm. to CAN).

ANIMAL-BASED FOOD

Like a large number of herbivores and detritivores (e.g., Hoffman and Payne, 1969), many cockroaches incorporate animal tissue into their diet when the opportunity arises. *Parcoblatta uhleriana* has been observed feeding on mammalian cartilage (Gorton, 1980), but most records of cockroaches feeding on living and dead vertebrates come from species that dwell in caves (discussed below) and from pest cockroaches. The latter can eat a great deal of flesh, particularly of human corpses. They also nibble on the calluses, wounds, fingernails and toenails, eyelashes, eyebrows, earwax, dandruff, eye crust, and the nasal mucus of sleeping individuals, particularly

Table 4.4. Examples of cockroaches subsisting largely on leaf litter.

Habitat	Cockroach taxon	Reference
Rainforest	*Epilampra irmleri* 6 species (Malaysia) 20 species of nymphs (Costa Rica)	Irmler and Furch (1979) Saito (1976) WJB (pers. obs.)
Dry forest, scrub	Geoscapheini *Thorax porcellana*	Rugg and Rose (1991) Reuben (1988)
Desert	*Arenivaga investigata* *Heterogamisca chopardi*	Hawke and Farley (1973) Edney et al. (1974) Grandcolas (1995a)
Aquatic	*Litopeltis sp.* *Poeciloderrhis cribrosa verticalis* *Opisthoplatia maculata*	Seifert and Seifert (1976) Rocha e Silva Albuquerque et al. (1976) Takahashi (1926)

children. At times they "bite savagely," leaving permanent scars (Roth and Willis, 1957; Denic et al., 1997). Most reports are from ships, nursing homes, unhygienic urban settings, and primitive tropical living quarters. See Roth and Willis (1957) for a full roster of these horror stories.

Many cockroaches are equipped for predation: they are agile, are aggressive in other contexts, have powerful mandibles, and possess spined forelegs to help secure prey. The recorded victims of cockroaches include ants, parasitic wasps, *Polistes* larvae, centipedes, dermestids, aphids, leafhoppers, mites, and insect eggs (Roth and Willis, 1960). Both *B. vaga* and *B. asahinai* eat aphids and are considered generalist predators (Flock, 1941; Persad and Hoy, 2004). *Periplaneta americana* has been observed both catching and eating blowflies in a laboratory setting (Cooke, 1968), and pursuing and capturing termite de-alates in and around dwellings. They pounced on termites from a distance of 5 cm, and followed them into crevices in the floor (Annandale, 1910; Bowden and Phipps, 1967). Cockroaches that feed on guano, leaf litter, or epiphylls also ingest the invertebrate microfauna that inhabit their primary food source (WJB, pers. obs). Dead invertebrates are scavenged by *Blattella karnyi* (Roth and Willis, 1954b), *Parcoblatta pennsylvanica* (Blatchley, 1920), and *P. fuliginosa* (Appel and Smith, 2002), among others. "The insect collector will often find that cockroaches, particularly in the tropics, will play sad havoc with his dead specimens" (Froggatt, 1906).

There are a few instances of cockroaches harvesting the secretions and exudates of heterospecific insects. Several are known to feed on honeydew (e.g., *Eurycotis* spp. sipping it from fulgorids—Naskrecki, 2005). *Parcoblatta pennsylvanica* has been observed feeding on cercopid spittle (Gorton, 1980). Recently two species of Costa Rican *Macrophyllodromia* were observed grazing the white, waxy secretion on the tegmina of at least two species of Fulgoridae (Fig. 4.6) (Roth and Naskrecki, 2001).

Conspecifics as Food Sources

The remaining cases of animal-based food pertain to fellow cockroaches. This fits the profile of other detritivores, as intraguild predation and cannibalism are widespread within decomposer food webs (Scheu and Setälä, 2002). There are a few cases of cockroaches preying on other cockroach species, like *N. cinerea* killing and eating *D. punctata* (Roth, 2003a). A more significant source of animal tissue, however, originates from same-species interactions (Nalepa, 1994). Most records of cockroach cannibalism come from domestic pests in lab culture (e.g., *Periplaneta* spp.—Pope, 1953; Roth, 1981a; *B. germanica*—Gordon, 1959), and it is the vulnerable that are most often taken as prey. Hatchlings, freshly molted nymphs, and the weak or wounded are the most frequent victims. It is usually the abdomen that is eaten first, to take advantage of the uric acid pool stored in the fat body (Cochran, 1985). Adult cockroaches in culture (Abbott, 1926) and in caves (Darlington, 1970) often have their wings extensively nibbled (although this may also be the result of aggressive interactions). The most ubiquitous ecological factor favoring cannibalism is the quality and quantity of available food, which depends to varying degrees upon population density (Elgar and Crespi, 1992).

Egg eating is a form of cannibalism, although in some cases the ingested eggs may be unfertilized or unviable (Joyner and Gould, 1986). In cockroaches, oothecae may be partially or entirely eaten prior to hatch (Roth and Willis, 1954b; Nalepa, 1988a), and oothecae carried by fe-
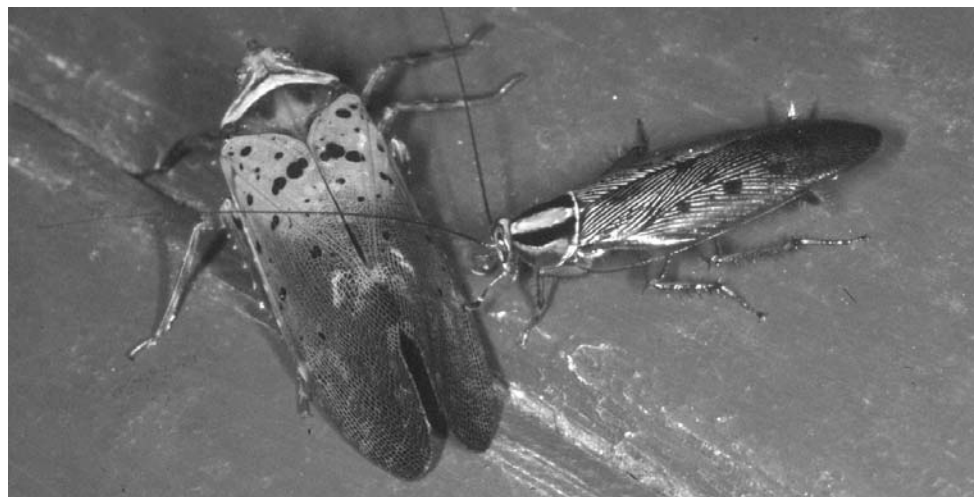

Fig. 4.6 The Costa Rican cockroach *Macrophyllodromia maximiliani* palpating the elytron of the fulgorid *Copidocephala guttata.* From Roth and Naskrecki (2001), courtesy of Piotr Naskrecki, with permission from the Journal of Orthoptera Research.

Table 4.5. Organic composition of exuvia from adult ecdysis and oothecae from several cockroach species, as determined by ^{13}C-NMR analyses. Reprinted from Kramer et al., "Analysis of cockroach oothecae and exuvia by solid state ^{13}C-NMR spectroscopy," *Insect Biochemistry* 21 (1991): pp. 149–56; copyright (1991), with permission from Elsevier.

Species	Relative amount (%) in/on exuvia			
	Protein	Chitin	Diphenol	Lipid
Periplaneta americana	49	38	11	2
Blattella germanica	59	30	9	2
Gromphadorhina portentosa	53	38	8	1
Blaberus craniifer	52	42	5	1
Rhyparobia maderae	61	35	4	1
Species	Relative amount (%) in/on post-hatch oothecae			
	Protein	Oxalate	Diphenol	Lipid
Periplaneta americana	87	8	4	1
Periplaneta fuliginosa	86	7	6	1
Blatta orientalis	88	7	4	1
Blattella germanica	95	< 1	3	1

males are not immune to biting and cannibalism by conspecifics (Roth and Willis, 1954b; Willis et al., 1958). After hatch, neonates of ovoviviparous cockroaches eat the embryonic membranes and the oothecal case (Nutting, 1953b; Willis et al., 1958); the sturdier oothecal cases of oviparous species are probably eaten by older nymphs or adults. After hatch in *Cryptocercus,* for example, oothecal cases are occasionally found still embedded in wood, but chewed flush with the surface of the gallery; hatching oothecae isolated from adults always remain intact (Nalepa and Mullins, 1992). It is estimated that females of *Cryptocercus* may be able to recover up to 59% of the nitrogen invested into a clutch of eggs by consuming the oothecal cases after hatch, but it is unknown how much of this nitrogen is assimilated (Nalepa and Mullins, 1992). Cannibalism may be part of an evolved life history strategy in young families of *Cryptocercus* (Nalepa and Bell, 1997; Chapter 8).

Cast skins are a prized food source and are eaten quickly by the newly molted nymph or by nearby individuals. In *P. americana* the cast skin is usually consumed within an hour after molt (Gould and Deay, 1938), and the older the nymph, the more quickly the skin is eaten (Nigam, 1932). Nymphs of *B. germanica* are known to force newly emerged individuals away from their cast skins and "commence to eat the latter with great gusto" (Ross, 1929). A nymph of *E. posticus* usually eats its exuvium immediately after molt, before the new cuticle has hardened. Nearby cockroaches also eat fresh exuvia, and occasionally the molting cockroach as well (Darlington, 1970). Competition to feed on exuvia has been observed

in both *Macropanesthia* (M. Slaytor, pers. comm. to CAN) and *Cryptocercus* (CAN, unpubl. obs.). In the latter, "snatch and run" bouts can occur where an exuvium changes ownership a half dozen times or more before it is completely consumed. The competition is understandable in that a cast skin is a considerable investment on the part of a growing nymph; exuvia from young instars of *E. posticus,* for example, comprise nearly 16% of their dry weight (Darlington, 1970). The cuticle is made up of chains of a polysaccharide, chitin, embedded in a protein matrix. Protein and chitin are 17% and 7% nitrogen by mass, respectively (Chown and Nicolson, 2004), and together these may account for 95% or more of the organic materials in an exuvium or oothecal case (Table 4.5).
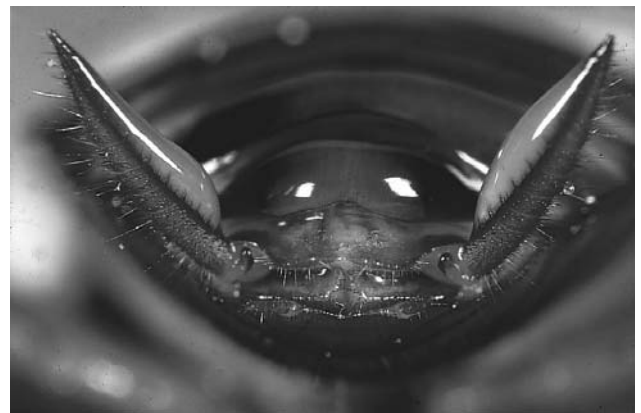

Fig. 4.7 Rear view of a male nymph of *Periplaneta australasiae,* showing the proteinaceous secretion that accumulates on the cerci and terminal abdominal tergites. Photo courtesy of Thomas Eisner.

Cockroaches apparently have the enzymes required to break down the chitin polysaccharide chain; endogenous chitinase is distributed throughout the gut of *P. americana* (Waterhouse and McKellar, 1961). Exuvium consumption appears directly related to nitrogen budget in *P. americana;* the behavior occurs more commonly in females, in insects reared on a low-protein diet, and in those deprived of their fat body endosymbionts (Mira, 2000).

In addition to the direct consumption of bodies, body parts, and reproductive products, cockroaches feed on materials exuded from the body of conspecifics in several contexts (Table 4.6). A form of nuptial feeding occurs in most cockroach species whose mating behaviors have been studied. Tergal glands are common in mature male cockroaches (Chapter 6). The secretions they produce attract the female during courtship, and as she climbs onto the male's back to feed on them she is properly positioned for genital contact (Roth, 1969; Brossut and Roth, 1977). Tergal secretions are general phagostimulants, and gravid, unreceptive females as well as males and nymphs feed on the gland of a courting male (Roth and Willis, 1952a; LMR, unpubl. obs.; Nojima et al., 1999b). In at least two blattellid species, *B. germanica* and *X. hamata,* males use the secretion of the uricose (accessory) gland as a nuptial gift (Mullins and Keil, 1980; Schal and Bell, 1982). During auto- and allogrooming cockroaches may ingest cuticular waxes, as well as anything else on the body surface; they spend a significant amount of time grooming antennae, legs, feet, and wings (Bell, 1990). Fe-

males and nymphs of both sexes in a variety of oviparous species produce a grayish viscous secretion on the cerci and terminal abdominal segments (Fig. 4.7). The material reappears 5–10 min after molt or the removal of the secretion. During autogrooming of the glandular area, the upper layer of the secretion is removed by the hind tibia; the leg is then cleaned by drawing it through the mouthparts (Naylor, 1964). The material is primarily (90%) proteinaceous and may serve as supplemental food (Roth and Stahl, 1956). Nymphs have been observed ingesting it from each other (D. Abed and R. Brossut, pers. comm. to CAN). Newly molted cockroaches eat their exuvium together with the glandular material accumulated on it (Roth and Stahl, 1956). The secretion also serves in defense, by mechanically impairing small predatory arthropods (Roth and Alsop, 1978; Ichinosé and Zennyoji, 1980). Allogrooming has been observed in *Pane. cribrata* (Rugg, 1987) and *Cryptocercus punctulatus* (Seelinger and Seelinger, 1983), neither of which produce this type of exudate. Neonates in at least six cockroach subfamilies feed on body fluids or glandular secretions of the mother (Chapter 8). These originate from a variety of locations on the adult body and have been analyzed only in the viviparous *Diploptera punctata* (Chapter 7).

CAVES

Caves are almost entirely heterotrophic; they depend on the transfer of energy and nutrients from the surface environment. Food is brought in with plant roots, water (i.e., organic material brought in with percolating rainwater, flooding, streams), and animals, particularly those that feed in the outside environment but return to the cave for shelter during their inactive period (Howarth, 1983; Gnaspini and Trajano, 2000; Hüppop, 2000). Although caves are generally considered food deficient, there is tremendous variation among and within caves. Food scarcity may be considered general, periodic (variation in time), or patchy (variation in space) (Hüppop, 2000). The best examples of the latter are guano beds that can be several meters deep and support tremendous populations of invertebrates. These islands of life, however, "are surrounded by desert, as most of the underground space is severely oligotrophic and sparsely populated" (Gilbert and Deharveng, 2002).

Guano

Vertebrate excrement is by far the most important nutritional base for cave Blattaria; cockroaches that feed on guano are apparently found on all main continents (Gnaspini and Trajano, 2000). If the vertebrates use the same roosting areas year round, then guano deposition is

Table 4.6. Conspecifics as food sources (modified from Nalepa, 1994).

Feeding behavior	Selected references
Cannibalism/necrophagy	Gordon (1959), Roth (1981a)
Oophagy (oothecae/ oothecal cases)	Nutting (1953b), Roth and Willis (1954b), Willis et al. (1958), Nalepa (1988a)
Consumption of exuvia	Roth and Willis (1954b), Willis et al. (1958)
Male-female transfer	
Tergal glands	Nojima et al. (1999b), Kugimiya et al. (2003)
Accessory glands	Mullins and Keil (1980), Schal and Bell (1982)
Cuticular secretions (from grooming and cercal exudates)	Roth and Stahl (1956), Seelinger and Seelinger (1983)
Parental feeding	Stay and Coop (1973), Roth (1981b), Perry and Nalepa (2003)
Coprophagy	Cruden and Markovetz (1984), Lembke and Cochran (1990)

predictable in space as well as time and can support very large, persistent groups of cockroaches (guanobies). This occurs primarily in the tropics, because there food is available for bats throughout the year (Poulson and Lavoie, 2000). Cave cockroaches feed on the droppings of birds and of frugivorous, insectivorous, and haematophagous bats, but not carnivorous bats (Table 13.1 in Gnaspini and Trajano, 2000). The abundance and quality of guano varies not only in relation to the diet of a vertebrate guano source, but also seasonally, depending on roosting sites and the availability of food items (Darlington, 1995a). Communities that develop on guano can be very distinct. In one Australian cave, guano may be inhabited by mites, pseudoscorpions, beetles, and maggots, while in a nearby cave the guano is dominated by cockroaches (*Paratemnopteryx* sp.) and isopods (Howarth, 1988). *Eublaberus distanti* living in Tamana Cave, Trinidad, wait nightly buried under the surface of guano, with their antennae extended above the surface. When the insectivorous bat *Natalus tumidirostris* begins to return from foraging at about 3:00 a.m., the cockroaches emerge to feed on the fresh droppings raining from above. The frugivorous bat *Phyllostomus hastatus hastatus* is found in the same cave, and though *Eub. distanti* may burrow through their droppings, the cockroaches do not feed on them (Hill, 1981). None of the six cockroach species found in the caves of the Nullarbor Plain in south Australia are associated with bat guano, but *Paratemnopteryx rufa* and *Trogloblattella nullarborensis* utilize bird droppings (Richards, 1971).

Most cockroaches that live on the surface of guano appear highly polyphagous (Richards, 1971) and will take advantage of any animal or vegetable matter present in the habitat. Indeed, species able to benefit from all types of food present in caves have more aptitude for colonizing the subterranean environment (Vandel, 1965). The gut contents of *Eub. posticus* are indistinguishable from guano, but Darlington (1970, 1995a) considers both *Eub. distanti* and *Eub. posticus* primarily as scavengers on the guano surface. These cockroaches are not indiscriminant feeders, however, as they will pick out the energy-rich parts of food presented to them (Darlington, 1970). The cave floor in Guanapo is covered with bat droppings, dead bats, live and dead invertebrates, as well as fruit pulp, seeds, nuts, and other vegetable fragments defecated by the bats (Darlington, 1995–1996). In cave passages remote from guano beds the choices are much more restricted. Leaves, twigs, and soil that wash or fall into caves generally form the food base for troglobites (Poulson and White, 1969). There also may be occasional bonanzas of small mammals that blunder into caves but cannot survive there (Krajick, 2001). The ability of many cockroaches to endure long intervals without food, particu-

larly if water is available (Table 4.3), may allow for exploitation of the deep cave environment. This starvation resistance is based at least in part on the capacity to binge at a single meal when food is available, together with the bacteroid-assisted ability to mete out stored reserves from the fat body when times are lean.

Plant Food in Caves

Cavernicolous cockroaches that depend on plant litter transported by water (Roth and McGavin, 1994; Weinstein, 1994) are attracted to traps baited with wet leaves (Slaney and Weinstein, 1996). While sinking streams may be continual, low-level sources of flotsam, seasonal flood debris supplies the bulk of the plant litter in most tropical caves (Howarth, 1983; Gnaspini and Trajano, 2000). In Australia, some caves may receive an influx of water and associated organic matter only once every 5 yr (Humphreys, 1993). Seeds defecated by frugivorous bats and the seeds of palm and other plants regurgitated by oilbirds commonly sprout in guano beds (Darlington, 1995b). The "forests of etiolated seedlings" (Poulson and Lavoie, 2000) that emerge may serve as food to cave cockroaches, but this is unconfirmed. *Periplaneta, Blaberus,* and other genera that feed on the guano of frugivorous bats also take advantage of fruit pieces dropped onto the floor (e.g., Gautier, 1974a). Fruit bats in Trinidad bring the fruit back to the caves, eat part of it, and then drop the remainder (Brossut, 1983, p. 150).

Live/Dead Vertebrates as Food in Caves

Those cockroaches that live in bat guano opportunistically feed on live, dead, and decomposing bats. Juveniles in maternity roosts that lose their grip and fall to the cave floor are particularly vulnerable (Darlington, 1970). *Blaberus* sp. have been observed rending the flesh of a freshly fallen bat, starting with the eyes and lips (D.W., 1984). Among the species recorded as feeding on dead bats are *Blattella cavernicola* (Roth, 1985), *Gyna caffrorum, Gyna* sp., *Hebardina* spp., *Symploce incuriosa* (Braack, 1989), and *Pycnoscelus indicus* (Roth, 1980). Cockroaches that live in the guano of oilbirds are treated to fallen eggs and occasional bird corpses (Darlington, 1995b). LMR once placed a dead mouse into a large culture of *Blaberus dytiscoides* and it was skeletonized overnight; he suggested to his museum colleagues that the cockroaches might be used to clean vertebrate skeletons.

Live/Dead Invertebrates as Food in Caves

Many cave cockroaches scavenge dead and injured invertebrates including conspecifics, and several have been re-

ported to take live victims. Both *B. cavernicola* (Roth, 1985) and *Pyc. indicus* (Roth, 1980) prey on the larvae of tinead moths; *Pyc. indicus* also appears to be the main predator of a hairy earwig (*Arixenia esau*) found on the guano heap. Crop contents of both *Trog. nullarborensis* and *Para. rufa* consisted of numerous small chitinous particles and setae. In *Trog. nullarborensis* it was possible to identify small dipterous wing fragments and lepidopterous scales (Richards, 1971).

Geophagy in Caves

True troglobites are rarely associated with guano but little information is available regarding their food sources. At least two cockroach species appear geophagous. Roth (1988) found clay in the guts of five nymphs of *Nocticola australiensis,* and suggested that *Neotrogloblattella chapmani* subsists on the same diet (Roth, 1980). The latter is confined to remote passages away from guano beds. Clays and silts in caves contain organic material, protists, nematodes, and numerous bacteria that can serve as food for cavernicoles. Chemoautotrophic bacteria may be particularly important in that they are able to synthesize vitamins (Vandel, 1965). Cave clay is a source of nutrition in a number of cave animals, including amphipods, beetles, and salamanders (Barr, 1968). One species of *Onychiurus* (Collembola) survived over 2 yr on cave clay alone (Christiansen, 1970).

Microbivory in Caves

As with detritivores in the epigean environment, the primary food of cave cockroaches may be the decay organisms, rather than the organic matter itself (Darlington, 1970). This may be particularly true for cockroaches that spend their juvenile period or their entire lives buried in guano. In *Sim. conserfarium,* for example, groups of all ages are found at a depth of 5–30 cm in the guano of fruit bats in West African caves (Roth and Naskrecki, 2003). What better microbial incubator than a pile of feces, leaf litter, or organic soil in a dark, humid environment in the tropics? In addition to ingesting microbial cytoplasm and small microbivores together with various decomposing substrates, it is possible that some cave cockroaches directly graze thick beds of bacteria and fungi that live off the very rocks. These include stalactite-like drips of massed bacteria, and thick slimes on walls (Krajick, 2001). In Tamana cave, fungi dominate the guano of insectivorous bats. The low pH combined with bacteriocides produced by the fungi is responsible for the low number and diversity of bacteria. The pH of frugivorous bat guano, on the other hand, favors bacterial growth, which supports a dense population of nematodes (Hill, 1981). Recent surveys using molecular techniques indicate that even oligotrophic caves support a rich bacterial community able to subsist on trace organics or the fixation of atmospheric gases (Barton et al., 2004).