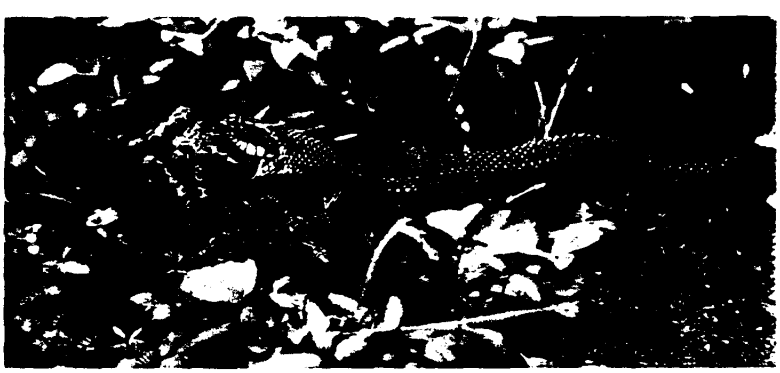
COSTA RICAN NATURAL HISTORY

Edited by Daniel H. Janzen

With 174 Contributors



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Bittacus banksi (Bitacido, Bittacid, Hanging Fly)

G. W. Byers

Three genera of Bittacidae (Insecta: Mecoptera) occur in Costa Rica: *Bittacus*, *Kalobittacus*, and *Pazius*. The only fairly common species is *Bittacus banksi* Esben-Peterson, which has been found along the western coast of Mexico, in Yucatan, and in much of lowland Central America. The following comments pertain to Bittacidae generally because, of the nine species now known from Costa Rica (1980), six are still undescribed and unnamed. We have virtually no observations of the behavior of any species, almost no detailed habitat information, and no knowledge whatever of the immature forms of any Central American species.

Adult bittacids may be found in low, shaded, herbaceous growth or grasses but, unless hunted in these habitats, are most likely to be seen around lights at night. They are fairly large insects with long, slender abdomens, long legs, and four elongate, many-veined, often hyaline and iridescent wings. *Bittacus* includes the largest and most robust species, *B. banksi* (fig. 11.11) being about 22 mm in overall length with a wingspan of approximately 45 mm. At rest, *Bittacus* species fold the wings alongside the abdomen. The one known species of *Pazius* is large but more slender, about 25 mm long and 37 mm across the outspread wings. Species of *Kalobittacus* are only about 13 mm in length with a 32-mm wingspan; they rest with the wings held out to the sides. The legs terminate in a single large claw that with the last tarsal segment folds back against the more basal part of the tarsus to form a raptorial appendage. Occasionally bittacids are seen carrying insect prey grasped in one of the hind legs, since these legs are most frequently used in prey capture. The bittacid feeds by inserting its slender beak (a prolongation of the head, bearing scissorlike mandibles at its tip) into the prey organism and consuming the contents, leaving the hollow exoskeleton.

In flight, bittacids are slow and awkward, giving somewhat the impression of a large crane fly with an extra pair of wings. When not flying, the insects suspend themselves from a twig or the edge of a leaf, usually by means of the front and middle legs. When alarmed, they ordinarily fly only a few meters and come to rest in low vegetation (that is, they are not likely to fly up into trees that are shading their habitat). Males offer prey insects to females as a nuptial meal. They may also evert two pale-colored, rounded pheromone-dispersing vesicles from the back of the abdomen to attract females from distances up to several meters, then display the nuptial prey. *Kalobittacus* and *Pazius* are active mainly by day, while *Bittacus* is chiefly nocturnal and may ascend into the foliage of trees at night.

Larval bittacids, as far as is known, are terrestrial and saprophagous, feeding particularly on dead insects. They move only slowly along the ground surface in search of food and are occasionally collected in pitfall traps at night. They have somewhat the appearance of sordid-whitish caterpillars with branched, fleshy projections from most body segments. These projections are often encrusted with soil placed on them by the larvae.

Records of bittacids from Costa Rica are mainly from the Pacific lowlands, less often from montane environments. *Bittacus* and *Kalobittacus* probably occur throughout the country, but *Pazius* has so far been found only at Golfito (but ranges through Panama into northwestern South America). There are collection records for every month from May to September, with a distinct peak of abundance in July for all three genera. Readers are urged to record observations and collect specimens of these insects to the extent permitted, and to make these available to taxonomists of Mecoptera.

Blaberus giganteus (Cucaracha, Giant Cockroach, Giant Drummer, Cockroach of the Divine Face) and ***Xestoblatta hamata*** (Cucaracha)

C. Schal

The Blattaria are diverse behaviorally, ecologically, and physiologically, yet the higher classification is well established and the phylogenetic relationships are well worked out. Hence the group is amenable to comparative and evolutionary studies. Of the approximately four thousand described species of cockroaches, a very small percentage share man's domicile. The vast majority occur in the tropics, where in some habitats the most abundant species are undescribed (Fisk and Schal 1981). Like other animals and plants, they are experiencing range reduction and possibly extinction as man extends his range into the tropical forests.

I have chosen to present a comparative approach to two Costa Rican species. The reader should bear in mind that although the physiological and behavioral literature based on laboratory studies is rather large, field ecological data are sparse and limited to enclosed natural

FIGURE 11.11. *Bittacus banksi*. *a*. Adult resting at blacklight; note fully extended hind tarsi. *b*. Adult eating small fly caught at blacklight; note curled and grasping position of hind tarsi. Santa Rosa National Park, Guanacaste Province, Costa Rica, June 1980 (photos, D. H. Janzen).

habitats such as caves, hollow trees, and decomposing logs.

Blaberus giganteus (= *B. colosseus*) is a large cockroach (fig. 11.12*a*) that has been widely collected in all seven provinces of Costa Rica. It and its close relative *Archimandrita* sp. are probably the largest Neotropical cockroaches by weight. *B. giganteus* is a nocturnal insect occasionally seen at lights. At the La Selva field station, and in La Pacifica and Santa Rosa in Guanacaste, it is commonly found in hollow trees, sharing the habitat with bats, opossums, and various arthropods. The cockroaches within the tree stratify vertically along micrometeorological gradients. Small nymphs occur in the bat guano at the base of the tree. At night they are active aboveground in the exposed moist sections, but during the day they retreat to the drier, more protected portion of the substrate. They are adept at burrowing (Crawford and Cloudsley-Thompson 1971), a behavior that has important adaptive value in light of the common raids on such trees by army ants. Larger instars occur higher in the tree, and adults occupy perches above them. By day, both adults and large nymphs hide in crevices in the inner wall of the tree.

Males of *B. giganteus* exhibit an interesting behavior toward attractive odors. Males engage in escalated agonistic encounters and increase their searching along the floor of the cage when a sexually receptive, virgin female is introduced. This behavior may be related to the ecological stratification of the age classes. Since nymphs occur below the adult males, a newly ecdysed female will most probably approach males from below. Also, since oviposition occurs in the guano, postoviposition receptive females move upward from the base of the tree. The male enhances his chances of encountering receptive females by directing his search downward. Nothing is known about the diurnal variation in micrometeorological profiles that may produce directional air flow to enhance chemical communication (as in forest habitats, Schal 1982; see below).

The social behavior of *B. giganteus* has been examined both in the laboratory and in the field (Gautier 1974*a*,*b*; pers. obs.). The social structure is plastic, describing a continuum between territoriality and hierarchy. At low densities, most males occupy perches without temporal or spatial changes in site occupancy. As the density increases and the number of preferred unoccupied sites

FIGURE 11.12. *a, Blaberus giganteus,* adults feeding. *b, Xestoblatta hamata,* adults copulating. Finca La Selva, Sarapiquí District, Costa Rica (photos, C. Schal).

decreases, a territorial/hierarchical system emerges, with more males meandering without site specificity. At even higher densities, males, females, and large nymphs clump together in preferred areas, leaving large regions unoccupied. Top-ranking males are distinguishable by their erect posture and aggressiveness.

Sexually receptive females passing near groups of males disrupt the territorial or hierarchical structure. Aggressive behavior is escalated, and males engage in hoarding, a combination of sexual displays directed at the female and agonistic acts directed at other males. Recent studies have attempted to delineate the male social system with regard to the ontogeny and physiological correlates of agonistic behavior. However, it is not known

whether hierarchies and territories in this species confer greater mating success on the dominant male, as in the cockroach *Nauphoeta cinerea* (Schal and Bell 1982*b*).

In contrast to *Blaberus*, *Xestoblatta hamata* (fig. 11.12*b*) is a forest-dwelling Costa Rican cockroach. It is similar in size and appearance to *Periplaneta americana* but is not known to occur outside tropical forests. Like the giant cockroach, this species exhibits age-class and sexual-height stratification (Schal 1982). Nymphs occur in the leaf litter. Adults migrate from the leaf litter to occupy nocturnal perches in the understory, then move back to the forest floor before sunrise. In an extensive study at the La Selva field station I found that males oriented to chemical signals (pheromones) emitted by females. Temperature and wind-profile data provide evidence for a vertical ascent of air in the forest understory. Thus directional transport of airborne pheromone molecules may explain the observed sexual stratification with males perching higher than females (Schal 1982).

Unlike *Blaberus*, an ovoviviparous cockroach that incubates about forty eggs internally for 60 days, the oviparous *Xestoblatta* female is an efficient reproductive machine, ovipositing approximately twenty-five eggs every 8 to 10 days. *Xestoblatta* females rely on two kinds of food resources in addition to an opportunisitc food habit that allows them to exploit "seasonal food" (fruits, seeds, flowers; *Blaberus* has a superabundant food resource in bat guano). One such food source is the shed bark of a legume, *Inga coruscans*. At La Selva, marked females return to shedding *Inga* trees at regular intervals that correlate well with early stages of the ovarian cycle immediately following oviposition. Chemical analysis of the sequestered materials indicates that the bark has low nitrogen and high lipid content. Hence, *Inga* may provide *Xestoblatta* females with energy reserves and materials to be used in vitellogenesis (providing the eggs with food reserves). These materials are acquired in the first 4 days after oviposition. At other stages in the ovarian cycle other foods are taken, depending on their chemical composition. Thus lipids are preferred early in the gonadotrophic cycle, then proteins are taken, and carbohydrates are selected before oviposition.

An important nitrogen source is provided by males. After copulation (on the 4th night of the ovarian cycle), the male empties the contents of his uricose accessory sex glands into his genital region. The female feeds on this material. Labeled uric acid injected into males is recovered in the female's eggs after mating; that is, paternal material is utilized for nymphal development (Schal and Bell 1982*a*). The quantity of uric acid taken by the female and sequestered in the eggs depends on the female's nutritional state. More male-derived uric acid is recovered from females on nitrogen-deficient diets than from females on high-protein diets (Schal and Bell 1982*a*).

Unlike most cockroaches, *Xestoblatta* females mate repeatedly during their adult life. The contribution of male urates to the female probably constituted an important factor in the evolution of this mating system.

Blaberus and *Xestoblatta* are very different in their ecological niches, mating systems, social structures, nutritional requirements, and morphology. The forests and plantations of Costa Rica include a large diversity of cockroaches: brightly colored wasp and beetle mimics, diurnally active species, acoustically communicating species, semiaquatic species in ephemeral bromeliad pools, species possessing noxious chemical defenses, others that share the nests of ants and termites, cave dwellers with antennae several times as long as their bodies, flat species well adapted for life under tree bark, and saltatory species that provide a serious challenge to the diverse forest herpetofauna that preys upon them. Reproductively, the cockroaches have oviparous, ovoviviparous, viviparous, and parthenogenic representatives, which fit well into ecological reproductive strategy classifications of r- and K-selected species.

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Blastophaga and Other Agaonidae (Avispita del Higo, Fig Wasp)

D. H. Janzen

Fig flowers (*Ficus* spp.) are pollinated by 1–2 mm long wasps in the Agaonidae (chalcidoid parasitic Hyme-