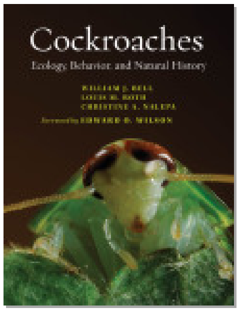
TWO: Locomotion: Ground, Water, and Air



Published by

Wilson, Edward O., et al.
Cockroaches: Ecology, Behavior, and Natural History.
Johns Hopkins University Press, 2007.
Project MUSE. https://dx.doi.org/10.1353/book.3295.

TWO

Locomotion: Ground, Water, and Air

i can walk on six feet
or i can walk on four feet
maybe if i tried hard enough
i could walk on two feet
but i cannot walk on five feet
or on three feet
or any odd number of feet
it slews me around
so that i go catercornered

—archy, "a wail from little archy"

Cockroaches were once placed in the suborder Cursoria (Blatchley, 1920) (Lat., runner) because the familiar ones, the domestic pests, are notorious for their ground speed on both horizontal and vertical surfaces. Indeed, the rapid footwork of these species has made cockroach racing a popular sport in a number of institutions of higher learning. Like most animal taxa, however, cockroaches exhibit a range of locomotor abilities, reflecting ease of movement in various habitats. On land, the limits of the range are mirrored in body designs that maximize either speed or power: the lightly built, long-legged runners, and the bulkier, more muscular burrowers. There is a large middle ground of moderately fast, moderately powerful species; however, research has focused primarily on the extremes, and it is on these that we center our discussion of ground locomotion. We touch on cockroach aquatics, then address the extreme variation in flight capability exhibited within the group. Finally, we discuss ecological and evolutionary factors associated with wing retention or loss.

GROUND LOCOMOTION: SPEED

Periplaneta americana typifies a cockroach built to cover ground quickly and is, relative to its mass, one of the fastest invertebrates studied. It has a lightly built, somewhat fragile body and elongated, gracile legs capable of lengthy strides. The musculature is typical of running insects, but the orientation of the appendages with respect to the body differs. The middle and hind pairs point obliquely backward, and the leg articulations are placed more ventrally than in most insects (Hughes, 1952; Full and Tu, 1991). *Periplaneta americana* has a smooth, efficient stride, and at most speeds, utilizes an alternating tripod gait, that is, three legs are always in contact with the ground. The insect can stop at any point in the walking pattern because its center of gravity is always within the support area provided by the legs. At a very slow walk the gait grades into a metachronal wave, moving from back to front, that is, left 3-2-1, then right 3-2-1 (Hughes, 1952; Del-

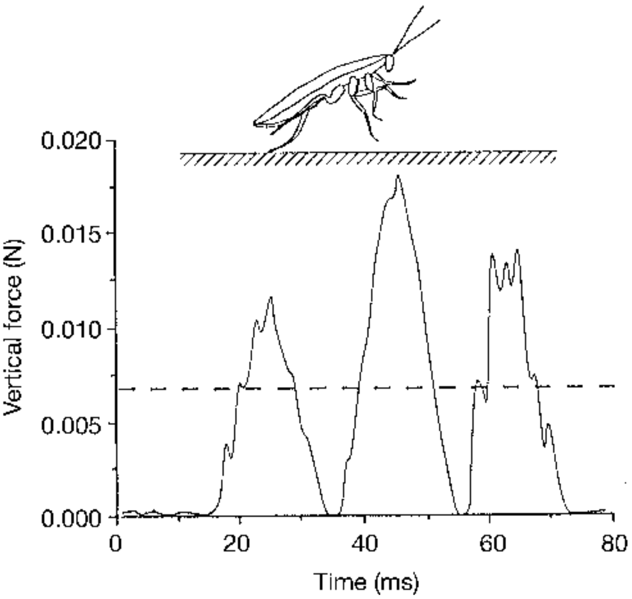


Fig. 2.1 Ground reaction force pattern for *Periplaneta americana* running bipedally, with the metathoracic legs propelling the body. Vertical forces periodically decrease to zero, indicating that all six legs are off the ground in an aerial phase. From Full and Tu (1991), with the permission of Robert J. Full and Company of Biologists Ltd.

comyn, 1971; Spirito and Mushrush, 1979). At its highest speed, *P. americana* shifts its body weight posteriorly and becomes bipedal by sprinting on its hind legs. The body is raised well off the ground and an aerial phase is incorporated into each step in a manner remarkably similar to bipedal lizards (Fig. 2.1). *Periplaneta* can cover 50 body lengths/sec in this manner (Full and Tu, 1991). As pointed out by Heinrich (2001), by that measure they can run four times faster than a cheetah. Other studied cockroaches are slower and less efficient. The maximum speed for *Blaberus discoidalis,* for example, is less than half of that of *P. americana.* The former is a more awkward runner, with a great deal of wasted motion (Full and Tu, 1991). Speed is known to vary with temperature (*Blab. discoidalis*), substrate type, sex, and developmental stage (*B. germanica*) (Wille, 1920; Full and Tullis, 1990). Hughes and Mill (1974) note that it is the ability to change direction very rapidly that often gives the impression of great speed. The ability to run swiftly and to fly effectively are not mutually exclusive. *Imblattella panamae,* a species that lives among the roots of epiphytic orchids, is fast moving both on wing and on foot (Rentz, 1987, pers. comm. to CAN). Hebard (1916a) noted that *Cariblatta,* a genus of diminutive insects, "ran about with great speed and took wing readily, though usually flying but short distances. When in flight, they appeared very much like small brownish moths." As a group, blattellids are generally very fast moving, especially when pursued. Most are long-legged with the ventral surfaces of the tarsi spined (Rentz, 1996).

Stability and Balance

Impressive locomotor performances are not limited to flat surfaces; cockroaches can scamper over uneven ground and small obstacles with agility and speed. Their vertically oriented joint axes act in concert with a sprawled posture to allow the legs to perform like damped springs during locomotion. As much as 50% of the energy used to displace a leg is stored as elastic strain energy, then returned (Spirito and Mushrush, 1979; Dudek and Full, 2000; Watson et al., 2002). In experiments on rough terrain, running *P. americana* maintained their speed and their alternating tripod gait while experiencing pitch, yaw, and roll nearly 10-fold greater than on flat surfaces (Full et al., 1998). *Blaberus discoidalis* scaled small objects (5.5 mm) with little change in running movements. Larger (11 mm) objects, however, required some changes in kinematics. The insects first assessed the obstacle, then reared up, placed their front tarsi on it, elevated their center of mass to the top of the object, then leveled off. The thorax was capable of substantial ventral flexion during these movements (Watson et al., 2002).

In a remarkable and no doubt entertaining series of experiments, Jindrich and Full (2002) studied self-stabilization in *Blab. discoidalis* by outfitting cockroaches with miniature cannons glued to the thorax. They then triggered a 10 ms lateral blast designed to knock the cockroach suddenly off balance in mid-run (Fig. 2.2). The insects successfully regained their footing in the course of a single step, never breaking stride. Stabilization occurred too quickly to be controlled by the nervous system; the mechanical properties of the muscles and exoskeleton were sufficient to account for the preservation of balance.

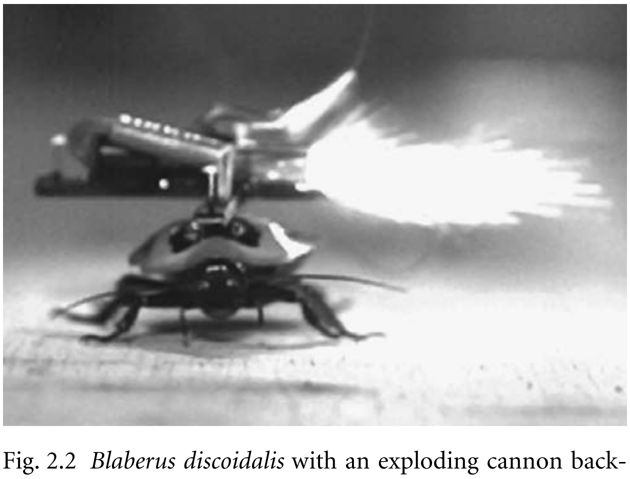


Fig. 2.2 *Blaberus discoidalis* with an exploding cannon backpack attempting to knock it off balance. Photo courtesy of Devin Jindrich.

There is some concern over gangs of these armed research cockroaches escaping and riddling the ankles of unsuspecting homeowners with small-bore cannon fire (Barry, 2002).

A healthy cockroach flipped onto its back is generally successful in regaining its footing. In most instances righting involves body torsion toward one side, flailing movements of the legs on the same side, and extension of the opposite hind leg against the substrate to form a strut. The turn may be made to either the right or left, but some individuals were markedly biased toward one side. In some cases a cockroach will right itself by employing a forward somersault, a circus technique particularly favored by *B. germanica* (Guthrie and Tindall, 1968; Full et al., 1995). If flipped onto its back on a smooth surface *Macropanesthia rhinoceros* is unable to right itself and will die (H. Rose, pers. comm. to CAN).

Aging cockroaches tend to dodder. There is a decrease in spontaneous locomotion, the gait is altered, slipping is more common, and there is a tendency for the prothoracic leg to "catch" on the metathoracic leg. The elderly insects develop a stumbling gait, and have difficulty climbing an incline and righting themselves (Ridgel et al., 2003).

The recent spate of sophisticated research on mechanisms of cockroach balance and control during locomotion is in part the result of collaborative efforts between robotic engineers and insect biologists to develop blattoid walking robots. The ultimate goal of this "army of biologically inspired robots" (Taubes, 2000) is to carry sensory and communication devices to and from areas that are difficult or dangerous for humans to enter, including buildings collapsed by earthquakes, bombs, or catastrophic weather events. In some cases living cockroaches have been outfitted with small sensory and communication backpacks ("biobots"), and their movement steered via electrodes inserted into the bases of the antennae (Moore et al., 1998). *Gromphadorhina portentosa* was the species selected for these experiments because they are large, strong enough to carry a reasonable communications payload, easy to maintain, and "no one would get too upset if we were mean to them" (T. E. Moore, pers. comm. to LMR). One limitation is that biobots could be employed only in the tropics or during the summer in temperate zones. Perhaps engineers should start thinking about making warm clothing for them, modeled after spacesuits (LMR, pers. obs.).

Orientation by Touch

Like many animals active in low-light conditions, cockroaches often use tactile cues to avoid obstacles and guide their locomotion. The long filiform antennae are positioned at an angle of approximately 30 degrees to the body's midline when the insect is walking or running in open spaces (*P. americana*). These serve as elongate probes that "cut a sensory swath" approximately 5.5 cm wide (Camhi and Johnson, 1999). The antennae are also used to maintain position relative to walls and other vertical surfaces. One antenna is dragged along the wall, and when it loses touch the cockroach veers in the direction of last contact. The faster they run the closer their position to the wall. Experimentally trimming the antennae also results in a path closer to the wall. The insects quickly compensate for projections or changes in wall direction, but depart from convex walls with diameters of less than 1 m (Creed and Miller, 1990; Camhi and Johnson, 1999). German cockroaches placed in a new environment tend to follow edges, but wander more freely in a familiar environment (Durier and Rivault, 2003).

GROUND LOCOMOTION: CLIMBING

The ability of a cockroach to walk on vertical and inverted horizontal surfaces (like ceilings) is predicated on specific features of the tarsi. The tarsus is comprised of five subsegments or tarsomeres. Each of the first four of these may bear on its ventral surface a single, colorless pad-like swelling called the euplanta, plantula, or tarsal pulvillus. At the apex of the fifth tarsal subsegment is a soft adhesive lobe called the arolium, which lies between two large articulated claws (Fig. 2.3). The surface of the arolium is sculptured and bears a number of different types of sensillae. Both arolia and euplantae deform elastically to assure maximum contact with a substrate and to conform to the microsculpture of its surface. Little cockroach footprints left behind on glass surfaces indicate that secretory material aids in forming a seal with the substrate. Generally, when a cockroach walks on a smooth or rough surface, some of the euplantae touch the substrate, but the arolia do not. The tarsal claws function only when the insect climbs rough surfaces, sometimes assisted by spines at the tip of the tibiae. The arolium is employed primarily when a cockroach climbs smooth vertical surfaces such as glass; the claws spread laterally and the aroliar pad presses down against the substrate (Roth and Willis, 1952b; Arnold, 1974; Brousse-Gaury, 1981; Beutel and Gorb, 2001). These structures can be quite effective; an individual of *Blattella asahinai* that landed on a car windshield was not dislodged until the vehicle reached a speed of 45 mph (= 72 kph) (Koehler and Patterson, 1987).

Cockroach species vary in the way they selectively employ their tarsal adhesive structures. *Diploptera punctata*, for example, stands and walks with the distal tarsomeres raised high above the others, and lowers them only when climbing, but in *Blaberus* the distal tarsomeres are always

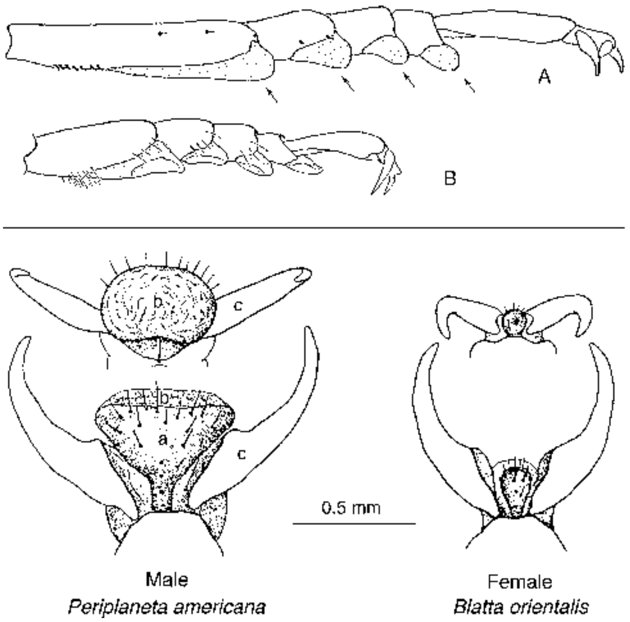


Fig. 2.3 Adhesive structures on the legs of cockroaches. *Top,* euplantae (arrows) on tarsal segments of two cockroach species. (A) Hind tarsus of male *Opisthoplatia orientalis;* (B) hind tarsus of male *Comptolampra liturata.* From Anisyutkin (1999), with permission of L.N. Anisyutkin. *Bottom,* apical and dorsal view of the pretarsi of the prothoracic legs in two cockroach species, showing the claws and arolia. *Left,* a cockroach able to walk up a vertical glass surface (male *Periplaneta americana*); *right,* one unable to do so (female *Blatta orientalis*). a = arolium; b = aroliar pad; c = tarsal claw. After Roth and Willis (1952b).

in contact with the substrate (Arnold, 1974). Within a species, there may be ontogenetic differences. Unlike adults, first instars of *B. germanica* are 50% faster on glass than they are on rough surfaces, probably because they use euplantae more than claws or spines during locomotion (Wille, 1920). Variation in employing adhesive structures is related to the need to balance substrate attachment with the need to avoid adhesion and consequent inability to move quickly on various surfaces. Both *Blatta orientalis* and *Periplaneta australasiae* walk readily on horizontal glass surfaces if they walk "on tiptoe" with the body held high off the substrate. If the euplantae of the mid and hind legs are allowed to touch the surface, they become attached so firmly that the cockroach can wrench itself free only by leaving the tarsi behind, clinging to the glass (Roth and Willis, 1952b).

Tarsal Morphology: Relation to Environment

Cockroaches vary in their ability to climb (i.e., escape) glass containers (Willis et al., 1958). This is due principally to the development of the arolium, which varies in size, form, and sculpturing and may be absent in some species (Arnold, 1974). *Blatta orientalis,* for example, has subobsolete, nonfunctional arolia and is incapable of climbing glass (Fig. 2.3). Euplantae may also differ in size and shape on the different tarsomeres, be absent from one or more, or be completely lacking. The presence or absence of these adhesive structures can be used as diagnostic characters in some genera (e.g., the genus *Allacta* has euplantae only on the fourth tarsomere of all legs), but are of minor taxonomic significance in others (e.g., the genera *Tivia, Tryonicus, Neostylopyga, Paratemnopteryx*) (Roth, 1988, 1990b, 1991d). Intraspecifically, variation may occur among populations, between the sexes, and among developmental stages (Roth and Willis, 1952b; Mackerras, 1968a). In *Paratemnopteryx* (= *Shawella*) *couloniana* and *Neotemnopteryx* (= *Gislenia*) *australica* euplantae are acquired at the last ecdysis (Roth, 1990b).

Although arolia and euplantae are considered adaptive characters related to functional requirements for climbing in different environments (Arnold, 1974), it is not currently obvious what habitat-related features influence their loss or retention in cockroaches. Adhesive structures are frequently reduced or lost in cave cockroaches, perhaps because clinging mud or the surface tension of water on moist walls reduces their effectiveness (Mackerras, 1967c; Roth, 1988, 1990b, 1991a). It would be instructive to determine if the variation in adhesive structures exhibited by different cave populations of species like *Paratemnopteryx stonei* can be correlated with variation among surfaces in inhabited caves. Arolia are absent in all Panesthiinae (Mackerras, 1970), and the two cockroaches listed by Arnold (1974) as having both arolia and euplantae absent or "only vaguely evident"—*Arenivaga investigata* and *Cryptocercus punctulatus*—are both burrowers. Nonetheless, the loss of arolia and euplantae is not restricted to cave and burrow habitats (Roth, 1988); many epigean species lack them. Arnold (1974) found it "surprising" that the tarsal features are so varied within cockroach families and among species that inhabit similar environments. A number of authors, however, have emphasized that it is the behavior of the animal within its habitat, rather than the habitat itself, that most influences locomotor adaptations (Manton, 1977; Evans and Forsythe, 1984; Evans, 1990). The presence and nature of appendage attachment devices is thought to be strongly associated with a necessity for negotiating smooth, often vertical plant surfaces (Gorb, 2001). Thus in a tropical forest, a cockroach that perches or forages on leaves during its active period may retain arolia and euplantae, but these structures may be reduced or lost in a species that never ventures from the leaf litter. Pulvilli and arolia are very well developed, for example, in *Nyctibora acaciana,* a species that oviposits on ant-acacias (Deans and Roth,

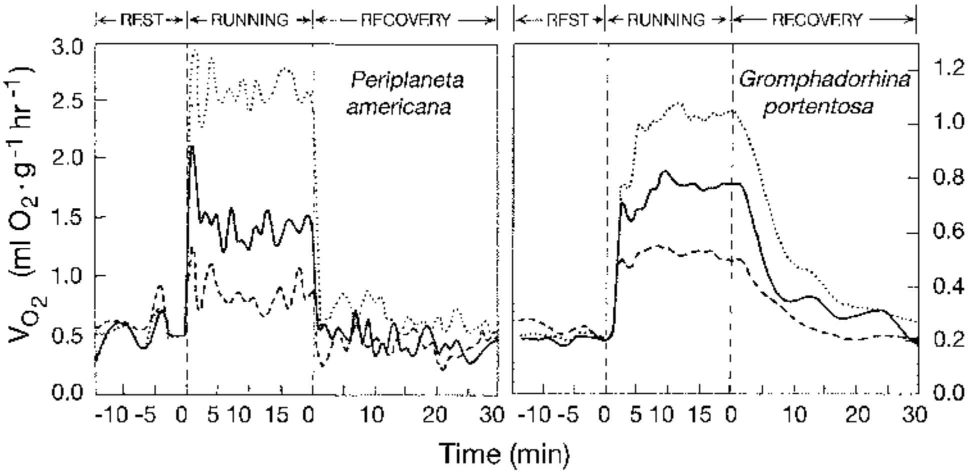


Fig. 2.4 Oxygen consumption while running on a treadmill: a cockroach built for speed (*Periplaneta americana*) versus one built for power (*Gromphadorhina portentosa*). Oxygen peaks rapidly in *P. americana,* and afterward the insect recovers rapidly. There is a lag time before oxygen peaks in *G. portentosa,* and a slow recovery time while the insect "catches its breath." Note difference in scale of y-axis. Reprinted from Herreid and Full (1984), with permission from Elsevier.

2003). In cockroaches that possess them, variation in sculpturing on the arolia may function in maximizing tenacity and agility on specific plant surface morphotypes (Bernays, 1991). Many species of tropical cockroach do not run when on leaves, but instead stilt-walk (WJB, pers. obs.). The slow leg movements produce little vibration in the substrate, and may allow them to ease past spiders without eliciting an attack, a phenomenon called "vibrocrypticity" (Barth et al., 1988).

GROUND LOCOMOTION: POWER

At the other end of the spectrum from sleek, fast-running cockroaches such as *P. americana* are the muscular, shorter-legged species that burrow into soil or wood. Their legs are usually ornamented with sturdy spines, particularly at the distal end of the tibiae; these function to brace the insect against the sides of the burrow, providing a stable platform for the transmission of force. Fossorial cockroaches are built for power, not speed. When forced to jog on a treadmill, all tested cockroach species exhibited a classic aerobic response to running; oxygen consumption (VO_2) rapidly rose to a steady state that persisted for the duration of the workout. When exercise was terminated, the recovery time of *P. americana* and *Blab. discoidalis* rivaled or exceeded the performance of the best vertebrate runners (Fig. 2.4). Among the slowest to recover was the heavy-bodied *G. portentosa,* which took 15–45 min, depending on the speed of the run (Herreid et al., 1981; Herreid and Full, 1984). Some individuals of *G. portentosa* exhibited obvious signs of fatigue. They stopped, carried their body closer to the substrate, and had a hard time catching their breath: respiratory movements were exaggerated and the insects maintained their spiracles in a wide-open position.

Burrowing

Digging behavior in cockroaches has not been studied, but the little, mostly anecdotal information we have indicates substantial variation, both in the behavior employed and in the body part used as a digging tool. There are at least two modes of creating tunnels in a hard substrate (soil, wood), both of which are accomplished by moving the substrate mechanically from in front of the insect and depositing it elsewhere. There are also two methods of digging into more friable material (guano, leaf litter, sand), achieved by insinuating the body into or through preexisting spaces. Cockroaches use refined excavation and building techniques in burying oothecae (Chapter 9).

Scratch-Digging (Geoscapheini)

All members of the uniquely Australian Geoscapheini excavate permanent underground living quarters in the compact, semi-arid soils of Queensland and New South Wales. The unbranched burrows of *M. rhinoceros* can reach a meter beneath the surface (Chapter 10); the tunnel widens near the bottom into a compartment that functions as a nursery and a storage chamber for the dried vegetation that serves as food. The distal protibiae are impressively expanded to act as clawed spades, driven by the

Fig. 2.5 *Macropanesthia rhinoceros,* initiating descent into sand; photo courtesy of David Rentz. *Inset:* Detail of mole-like tibial claw used for digging; photo courtesy of Kathie Atkinson.

large muscles of the bulky body (Fig. 2.5). The hard, stout spines flick the soil out behind the cockroach as it digs. When the insect is moving through an established burrow, the spines fold neatly out of the way against the shank of the tibia. The tarsi are small and dainty (Park, 1990). The large, scoop-like pronotum probably serves as a shovel. Tepper (1894) described the behavior of *Geoscapheus robustus* supplied with moist, compressed soil: "they employ not only head and forelegs, but also the other two pairs, appearing to sink into the soil without raising any considerable quantity above the surface, nor do they appear to form an unobstructed tunnel, as a part of the dislodged soil appears to be pressed against the sides, while the remainder fills up the space behind the insect. A few seconds suffice them to get out of sight." Soil texture and compaction no doubt determine the energetic costs of digging and whether burrows remain open or collapse behind the excavator.

Tooth-Digging (Cryptocercidae)

Cryptocercus spp. chew irregular tunnels in rotted logs, but the tunnels are clearly more than a by-product of feeding activities. Numerous small pieces of wood are obvious in the frass pushed to the outside of the gallery. When entering logs, the cockroaches often take advantage of naturally occurring crevices (knotholes, cracks), particularly at the log-soil interface. Burrows then generally follow the pattern of moisture and rot in individual logs. Rotted spring wood between successive annual layers is often favored. In well-rotted logs, the cockroaches will in part mold their living spaces from damp frass. In fairly sound logs, galleries are only slightly larger than the diameter of the burrower, and may be interspersed with larger chambers (Nalepa, 1984, unpubl. obs.).

Adult *Cryptocercus* have been observed manipulating feces and loosened substrate within galleries. The material is pushed to their rear via a metachronal wave of the legs. The insect then turns and uses the broad surface of the pronotum to tamp the material into place. The tarsi are relatively small, and stout spines on the tibiae serve to gain purchase during locomotion. The cockroach is often upside down within galleries, and like many insects living in confined spaces (Lawrence, 1953), frequently walks backward, allowing for a decrease in the number of turning movements. The body also has a remarkable degree of lateral flexion, which allows the insect to bend nearly double when reversing direction in galleries (CAN, unpubl. obs).

Sand-Swimming (Desert Polyphagidae)

During their active period, fossorial desert Polyphagidae form temporary subsurface trails as they "swim" through the superficial layers of the substrate. Their activities generate a low rise on the surface as the loosely packed sand collapses in their wake. The resultant serpentine ridges look like little mole runs (Fig. 2.6) (Hawke and Farley, 1973). During the heat of day, the cockroaches (*Arenivaga*) may burrow to a depth of 60 cm (Hawke and Farley, 1973). The bodies of adult females and nymphs are streamlined, with a convex thorax and sharp-edged pronotum. Tibial spines on the short, stout legs facilitate their pushing ability and serve as the principal digging tools. These spines are often flattened or serrated, with sharp tips. Anterior spines are sometimes united around the apex in a whorl, forming a powerful shovel (Chopard, 1929; Friauf and Edney, 1969). *Eremoblatta subdiaphana,* for example, has seven spines projecting from the front tibiae (Helfer, 1953). Also aiding subterranean move-

Fig. 2.6 Tracks (2–3 cm wide) of *Arenivaga* sp. at the base of a mesquite shrub near Indigo, California. Females and nymphs burrow just beneath the surface at night. From Hawke and Farley (1973), courtesy of Scott Hawke. *Inset:* Ventral view of female *Arenivaga cerverae* carrying an egg case. The orientation of the egg case is likely an adaptation for carrying it while the female "swims" through the sand. Note well-developed tibial spines. Photo by L.M. Roth and E.R. Willis.

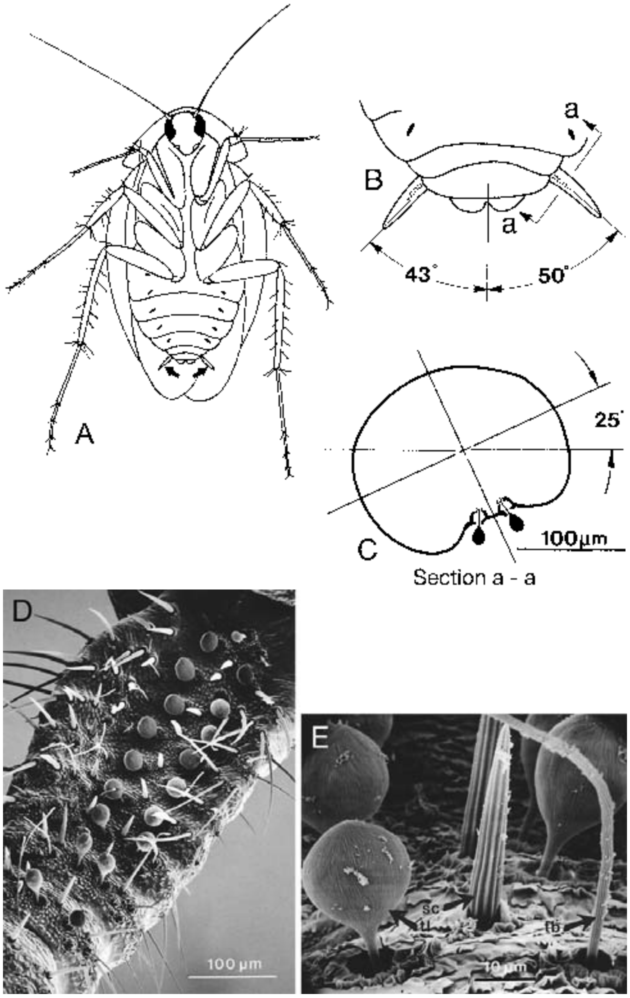


Fig. 2.7 Sensory organs on cerci of adult male *Arenivaga* sp. (A) Ventral view of insect, with the cerci indicated by arrows. (B) Posterior end of the abdomen showing the orthogonal position of the cerci and rows of tricholiths. (C) Cross section through the left cercus to illustrate that the cerci are rotated laterally from the horizontal plane. (D–E) Scanning electron micrographs showing details of tricoliths on the cerci. (D) Ventral view of left cercus; note two parallel rows of tricholiths. (E) View from the distal end of the tricholith (tl) rows showing sensilla chaetica (sc) and a trichobothrium (tb). Courtesy of H. Bernard Hartman. From Hartman et al. (1987), with permission from Springer Verlag.

ments are large spherical sense organs (tricholiths) on the ventral surface of the cerci in *Arenivaga* and other polyphagids (Roth and Slifer, 1973). These act like tiny plumb bobs in assisting orientation of the cockroaches while they move through their quasifluid environment (Walthall and Hartman, 1981; Hartman et al., 1987) (Fig. 2.7). First instars of *Arenivaga* have only one tricholith on each cercus; new ones are added at each molt. Adult females have six pairs and males have seven pairs (Hartman et al., 1987).

Head-Raising (*Blaberus craniifer*)

In studying the burrowing tendencies of *Blab. craniifer,* Simpson et al. (1986) supplied the cockroaches with a mixture of peat moss and topsoil, then filmed them as they dug into the substrate. The insects were able to bury themselves in just a few seconds using a rapid movement of the legs, combined with a stereotyped dorsal-ventral flexion of the head and pronotum. The combined head-raising, leg-pushing behavior seems well suited to digging in light, loose substrates (litter, dust, guano), but may also facilitate expanding existing crevices, like those in compacted leaf litter or under bark. This digging technique does not require the profound body modifications exhibited by cockroaches specialized for burrowing in hard substrates, and is therefore compatible with the ability to run rapidly. Indeed, the behavior seems well suited to the "standard" cockroach body type displayed by *Blab. craniifer:* an expanded, hard-edged pronotum, inflexed head, slick, flattened, rather light body, and moderately strong, spined legs.

SWIMMING

It seems logical that cockroaches are not easily drowned, as they are members of a taxon whose ancestors were associated with swamp habitats and "almost certainly able to swim" (North, 1929). As anyone who has tried to flush a cockroach down the toilet can verify, these insects have positive buoyancy and will bob to the surface of the water if forced under. A water-repellent cuticle aids surface tension in keeping them afloat (Baudoin, 1955). *Periplaneta americana* is a fine swimmer, and can move in a straight line at 10 cm/sec. The body is usually arched, with the antennae held clear of the water and moving in normal exploratory fashion. If the antennae touch a solid substrate, the insect turns toward the source of stimulation and swims faster. While swimming, the legs are coordinated in the same alternating tripod pattern seen while walking on land; this differs from the pattern of synchronous leg pairs seen in other terrestrial and aquatic insects in water. Articulated spines on the tibia of each leg are strongly stimulated by movement through water and may provide feedback in regulating swimming behavior. All developmental stages can swim, but the youngest instars are hampered by surface tension (Lawson, 1965; Cocatre-Zilgein and Delcomyn, 1990).

Most *P. americana* isolated on an artificial island will escape within 10 min, with escape more rapid in experienced insects (Lawson, 1965). Two strategies are employed, reminiscent of those seen in humans at any swimming pool. (1) Gradual immersion (the "wader"): the surface of the water is first explored with the forefeet (Fig.

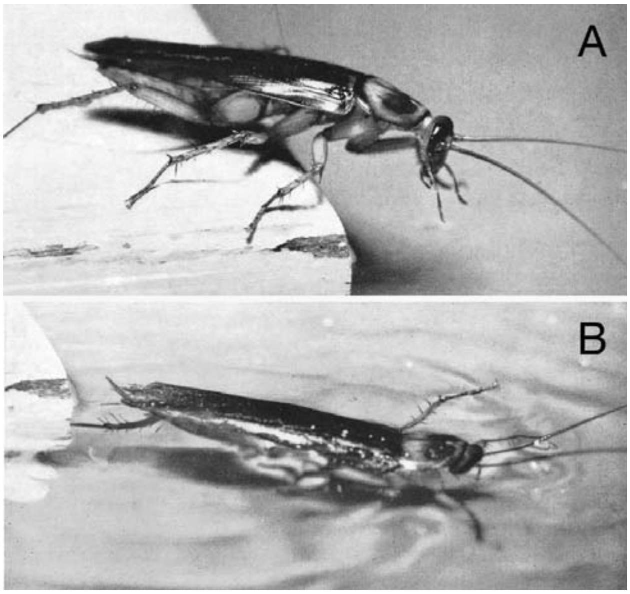


Fig. 2.8 (A) *Periplaneta americana* testing the water with forelegs before (B) taking the plunge. Courtesy of R.M. Dobson.

2.8). The middle legs then attempt to reach the bottom beneath the water, while clinging to the island with the rear legs and with the front of the body afloat. Finally, the cockroach releases the hind legs, enters completely, and swims away. (2) The "cannonball" strategy: after initial exploration, the insect retires slightly from the edge, crouches, then jumps in, often while fluttering the wings.

The legs of amphibious cockroaches do not exhibit any morphological adaptations for swimming and are no different from those of non-aquatic species (Shelford, 1909; Takahashi, 1926). Nymphs of many *Epilampra* spp. swim rapidly below the surface (Crowell, 1946; Wolcott, 1950); newborn nymphs as well as adults of *Ep. wheeleri* (= *Ep. abdomennigrum*) swim easily and remain under water a good deal of the time (Séin, 1923). Individuals of *Poeciloderrhis cribrosa verticalis* can swim against a current velocity of 0.15 m/sec (Rocha e Silva Albuquerque et al., 1976). *Opisthoplatia maculata,* on the other hand, rarely swims, but instead walks on submerged rocks along stream bottoms (Takahashi, 1926).

WINGS AND FLIGHT

Adult cockroaches with fully developed flight organs have two sets of wings that reach or surpass the end of the abdomen, completely covering the abdominal terga. The hindwings are membranous, but the forewings (tegmina) are somewhat sclerotized. In most species the tegmina cross each other, with the left tegmen covering a portion of the right, and with the covered portion of a different texture and color. There are also cases where the forewings are transparent and similar in size and texture to the hindwings (e.g., *Paratemnopteryx suffuscula, Pilema cribrosa, Nocticola adebratti, Cardacus* (= *Cardax*) *willeyi*), or hardened and elytra-like (e.g., *Diploptera* and other beetle mimics).

The entire wing apparatus of cockroaches shows clear adaptations for a concealed lifestyle (Brodsky, 1994). Dorsoventral flattening has altered the structure of the thoracic skeleton and musculature, and when at rest the wings are folded flat against the abdomen. One exception is *Cardacopsis shelfordi,* whose wings do not lie on the abdomen with the tips crossing distally, but diverge as in flies (Karny, 1924 in Roth, 1988). Elaborate mechanisms of radial and transverse folding allow the delicate hindwings to fit under the more robust tegmina. In repose, the anal lobe of the hindwing is always tucked under the anterior part of the wing (remigium). Polyphagids accomplish this with a single fold line (Fisk and Wolda, 1979), but in other cockroaches this area is folded along radial lines into a simple fan. There may be apical rolling (e.g., *Prosoplecta nigrovariegata, Pr. coccinella, Choristima* spp.) or folding (e.g., *Anaplecta*) of the remigium. In some species (e.g., *D. punctata*), this crease is in the middle of the wing, allowing for a folded wing with only half the length and a quarter of the area of the unfolded wing (Fig. 2.9). These more elaborate strategies of wingfolding are common in beetle mimics, as it allows for the protection of hindwings that exceed the length of the tegmina (Shelford, 1912a; Roth, 1994). Patterns of wingfolding, together with other wing characters, can be useful in cockroach classification (Rehn, 1951; Haas and Wootton, 1996; Haas and Kukalova-Peck, 2001). A number of generic names originate from wing characters, for example, *Plecoptera* (Gr., plaited + wing), *Chorisoneura* (Gr., separate + veins), *Symploce* (Gr., woven together), *Ischnoptera* (Gr., slender + wing) (Blatchley, 1920).

Cockroaches are "hindmotor" flyers. The hindwing is

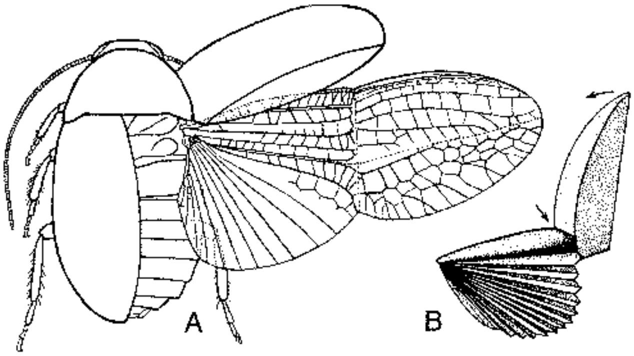


Fig. 2.9 Wing folding in *Diploptera punctata;* (A) dorsal view, right tegmen and wing expanded, longitudinal and transverse folds marked as dotted lines; from Tillyard (1926). (B) Posterodorsal view of a wing in the process of folding. Drawing by Robin Wootton, courtesy of Robin Wootton and Fabian Haas.

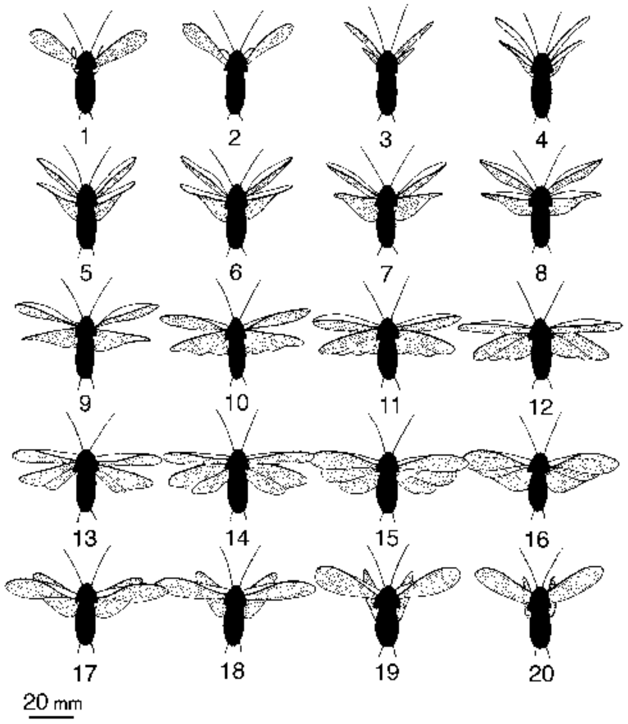


Fig. 2.10 Flight in *Periplaneta americana;* consecutive film tracings of a single wingbeat. The forewings reach the top of the stroke just as the hindwings pass the top of the stroke and begin to pronate (#3). As a result, both pairs pronate nearly simultaneously (#4), so that the hindwings, moving faster, are ahead of the forewings (#5), approach the bottom of the stroke, supinate, and go up (#12–20). From Brodsky (1994), by permission of Oxford University Press.

the main source of propulsion (Brodsky, 1994), and the two pairs of wings operate independently and slightly out of phase (Fig. 2.10). In basal cockroaches the tegmina seem to be an integral part of the flight mechanism, but in the more derived species their direct use in flight is less common (Rehn, 1951). During flight, aerodynamically induced bending of the cerci serves as a feedback in regulating wingbeat frequency (Lieberstat and Camhi, 1988). It is generally believed that the majority of winged cockroaches are rather inept fliers and lack the ability to sustain long-distance flight (Peck and Roth, 1992). Flight ability within the group varies, of course, and even weak fliers can be quite maneuverable in the air, with various strategies for evading predators. A number of small tropical species are known to be strong fliers, capable of sustained flights in a straight line or with slight lateral curves. They are able to increase altitude but cannot hover (Farnsworth, 1972).

Wing Reduction and Flightlessness

All taxonomic groups of cockroaches include species with variably reduced or absent tegmina and hindwings, exposing all or part of the dorsal surface of the abdomen. The exceptions are those groups in which the distal portion of the hindwing is set off by a transverse fold (e.g., Diplopterinae, Ectobiinae, Anaplectinae—Rehn, 1951). Wing reduction typically affects the hindwings more than the tegmina (Peck and Roth, 1992). Even when they are reduced, wings are always flexibly joined to the thorax. Adults with reduced wings can be distinguished from older nymphs, then, because the wing pads of the latter are nonflexible extensions of the posterior margins of the wing-bearing thoracic segments (Fisk and Wolda, 1979). Although in some cockroach groups apterous species are tiny and may be passed over by collectors because they resemble nymphs (Mackerras, 1968a), some of the largest known cockroaches (*Macropanesthia*) also lack wings.

Based on information in Rehn (1932b) and Roth and Willis (1960), Roff (1990, Table 8) estimated that more than 50% of all cockroaches and 50–60% of temperate species lack the ability to fly. Vastly different figures also have been published. Roff (1994) indicated that just 4% of cockroaches are flightless in both sexes, and 24% are sexually dimorphic, with males flying and females flightless (data from North America, French Guiana, Africa, and Malagasy). There are reasons to be cautious when assessing cockroach flight ability. First, only a fraction of the more than 4000 known cockroach species are included in these estimates; volant canopy species in particular may be underestimated. Second, flight capability in cockroaches is typically based on published descriptions of wing morphology in museum specimens. The possession of fully developed wings, however, does not necessarily mean that a cockroach can fly (Farnsworth, 1972; Peck and Roth, 1992).

A more accurate measure of cockroach flight capability may lie in the color of the thoracic musculature of freshly killed insects. Kramer (1956) found that the pterothoracic musculature of apterous, brachypterous, and flightless or feebly flying macropterous cockroaches appears hyaline white, while that of strong fliers is opaque and conspicuously pink (Table 2.1). These color differences are correlated with distinct metabolic differences, as reflected in enzymatic activity and oxygen uptake (Kramer, 1956). Consequently, cockroaches with white musculature may not be able to release energy rapidly enough to sustain wing beating (Farnsworth, 1972). In cockroaches with pink musculature, the muscles of the mesothorax and metathorax are equally pigmented. One exception is the "beetle" cockroach *D. punctata* (= *dytiscoides*), which derives its common name from the fact that the somewhat reduced, hardened tegmina resemble elytra and cover a pair of long hindwings (Fig. 2.9). In this species the mesothoracic muscles are hyaline white, but the metathorax bearing the elongated hindwings con-

Table 2.1. Wing development and its relationship to pigmentation of the thoracic musculature. Based on Kramer (1956) and Roth and Willis (1960).

Cockroach species	Color of pterothoracic musculature	
	Mesothorax (wing condition)[1]	Metathorax (wing condition)
Blaberus craniifer	Pink (M)	Pink (M)
Blaberus giganteus	Pink (M)	Pink (M)
Blatta orientalis	White (R)	White (R)
Blattella germanica	White (M)	White (M)
Blattella vaga	Pink (M)	Pink (M)
Cryptocercus punctulatus	White (A)	White (A)
Diploptera punctata	White (R)	Pink (M)
Eurycotis floridana	White (R)	White (R)
Nauphoeta cinerea	White (R)	White (R)
Neostylopyga rhombifolia	White (R)	White (R)
Parcoblatta pennsylvanica		
Male	Pink (M)	Pink (M)
Female	White (R)	White (R)
Parcoblatta virginica		
Male	Pink (M)	Pink (M)
Female	White (R)	White (R)
Periplaneta fuliginosa		
Male	Pink (M)	Pink (M)
Female	White (M)	White (M)
Periplaneta brunnea		
Male	Pink (M)	Pink (M)
Female	White (M)	White (M)
Periplaneta australasiae		
Male	Pink (M)	Pink (M)
Female	White (M)	White (M)
Pycnoscelus surinamensis[2]	Pink (M)	Pink (M)
Rhyparobia maderae	Pink (M)	Pink (M)
Supella longipalpa		
Male	Pink (M)	Pink (M)
Female	White (R)	White (R)

[1]M = macropterous, R = reduced, A = absent.
[2]Female morphs with reduced wings exist.

tains pigmented muscle (Kramer, 1956). Macropterous adults with white musculature include *Blattella germanica*, females of *Supella longipalpa* (= *supellectilium*), and three species of *Periplaneta*. Both sexes of *B. germanica* and *Blattella vaga* have fully developed wings (see Plate 5 of Roth and Willis, 1960), but *B. germanica* is incapable of sustained flight (Brenner et al., 1988).[2] The rosy flight muscles of *B. vaga* are an indication that it is volant, but its flight behavior is unknown. The Asian cockroach *Blattella asahinai* is morphologically very similar (Lawless, 1999) and very closely related (Pachamuthu et al., 2000) to *B. germanica*, but flies readily and strongly (Brenner et al., 1988); presumably, dissections would indicate that it has pigmented flight muscles. Males of *Su. longipalpa* are fleet runners and can take to the air for short distances, but females are unable to fly (Hafez and Afifi, 1956). Another example of a macropterous but flightless species is *Thorax porcellana* (Epilamprinae). Both sexes are fully winged, but only the male uses them for short flights and only rarely (Reuben, 1988).

The correlation between flight muscle pigmentation and the physiological ability to sustain flight has been examined most extensively in *P. americana*. In tests on laboratory strains tethered females (white flight muscles) could sustain no more than a 3–12 sec flight, compared to 5–15 min in males (pink flight muscles). Moreover, freshly ecdysed male *P. americana* have white pterothoracic muscles and flight behavior similar to that of adult females: they flutter weakly or plummet when tossed into the air. The flight behavior of these young males changes in conjunction with the postmetamorphic development of pink pigmentation in their musculature (Kramer, 1956; Farnsworth, 1972; Stokes et al., 1994). In the tropics *P. americana* is reportedly an excellent flyer, and is known in some locales as the "Bombay canary." It has been observed flying out of sewers and into buildings. It was also spotted in a German zoo flying distances of up to 30 m, in fairly straight lines or in flat arcs about 0.5 to 1.5 m above the ground (Roth and Willis, 1957). It is unclear, however, whether these volant *P. americana* are males only, or if both sexes in natural populations can fly. Rehn (1945) indicated that the flying ability of *Periplaneta* (species unspecified) is "often exercised and by both sexes." Female *P. americana* from laboratory cultures in two U.S. locations and one in Germany, however, remained earthbound during flight tests (Kramer, 1956). Appel and Smith (2002) report that *P. fuliginosa* females with fully formed oothecae are capable of sustained flight on warm, humid evenings in the southern United States, but laboratory-reared females of this species sank like rocks when tossed in the air (Kramer, 1956). Perhaps females lose the ability to fly when raised in culture. At least one study demonstrated that flight initiation in *P. americana* was significantly affected by the temperature at which they were reared (Diekman and Ritzman, 1987), and flight performance in other insects is known to quickly suffer under laboratory selection (Johnson, 1976).

A physiological change in flight musculature no doubt precedes or accompanies morphological wing reduction, but may be the only modification if the tegmina and wings have a functional significance other than flight. Full-sized wings may be retained in flightless species be-

---

2. It is, however, a frequent flier on airplanes (Roth and Willis, 1960).

cause they may act as parachutes, controlling the speed and direction of jumps and falls. German cockroaches, for example, will glide short distances when disturbed (Koehler and Patterson, 1987). Tegmina and wings may be used as tools in territorial or sexual signaling; males in several species flutter their wings during courtship. They also may serve as stabilizers during high-speed running, as physical protection for the abdomen and associated tergal glands, in visual defense from enemies (crypsis, mimicry, aposematicism), and, in rare cases, as shelter for first instars.

Ecological Correlates of Flight Condition

A number of papers have focused on the ecological determinants that may select for wing retention versus loss in various insect groups. Chopard (1925) was the first to examine the phenomenon in cockroaches, and divided cockroach genera into one of three wing categories: (1) tegmina and hindwings developed in both sexes; (2) wings short or absent in females only; and (3) wings short or absent in both sexes. He then arranged genera by collection locality and concluded that flightlessness was correlated with certain geographic locations. Rehn (1932b), however, demonstrated that each of the three listed conditions can be displayed by different species within the same genus, and refuted the idea that flightlessness was correlated with geography. Rehn could find no single factor that selected for wing reduction in the cockroaches he studied (New World continental and West Indian species), but thought that "altitude and possibly humidity or aridity under special conditions" might be involved. More recently, Roff (1990, Table 1) surveyed the literature and concluded that cockroaches as well as other insects that live in deserts, caves, and social insect nests have a higher than average incidence of flightlessness. He also found that a lack of flight ability was not exceptionally high on islands, in contrast to conventional thought.

Generalizations on the correlation between flight ability and habitat are difficult to make for cockroaches. With few exceptions, conclusions are based on wing length, and habitat type is inferred from daytime resting sites or baited traps. As discussed above, the possession of full-sized wings is not always a reliable index of flight ability, and the location of diurnal shelter is only a partial indication of cockroach habitat use. Although it is safe to assume that cockroaches attracted to light traps have some degree of flight ability, the traps collect only night-active species that are attracted to light, and the ecological associations of these remain a mystery. Males of *Neolaxta*, for example, are very rarely seen in the field, but can be collected in considerable numbers from light traps (Monteith, in Roth, 1987a). Given those caveats (there will be more later), we will here examine wing trends in some specific habitat categories.

Islands

Darwin (1859) first suggested that the isolation imposed by living on an island selects for flightless morphologies, because sedentary organisms are less likely to perish by being gusted out to sea. More recent authors, however, have questioned the hypothesis (e.g., Darlington, 1943). For one thing, scale is not taken into account. Conditions are different for a large insect on a small island versus a tiny insect on a substantial one (Dingle, 1996). Roff (1990) analyzed the wing condition of insects on oceanic islands versus mainland areas (corrected for latitude) and found no correlation between island life and a sedentary lifestyle. Denno et al.'s (2001a) work on planthoppers in the British Virgin Islands also supports this view.

The observation that a flightless cockroach lives on an island does not necessarily mean that the wingless condition evolved there. Cockroaches have greater over-water dispersal powers than is generally assumed, because they raft on or in floating debris and vegetation (Peck, 1990; Peck and Roth, 1992). Moreover, cockroaches that live under bark or burrow in wood or other dead vegetation may be the most likely sailors; this category includes a relatively high percentage of wing-reduced species (discussed below). Trewick (2000) recently analyzed DNA sequences in the blattid *Celatoblatta*, a flightless genus found in New Zealand and in the Chatham Islands, habitats separated by about 800 km of Pacific Ocean. The island populations were monophyletic, and probably dispersed from New Zealand to the islands by rafting sometime during the Pliocene (2–6 mya). Members of this genus are known to shelter in logs during the day.

When six small mangrove isles off the coast of Florida were experimentally sterilized, *Latiblattella rehni* and an undescribed species in the same genus were early re-invaders on several of them (Simberloff and Wilson, 1969). Males of *Lat. rehni* have fully developed, "very delicate" (Blatchley, 1920) wings; those of the female are slightly reduced, but it is unknown if they are functional. Colonization, then, could have been by active or passive flight, or by rafting. The Krakatau Islands offered a unique opportunity to study the reintroduction of cockroaches into a tropical ecosystem from a sterile baseline after a series of volcanic eruptions in 1883 stripped them of plant and animal life. A 1908 survey found a few cockroach species already present, with a subsequent steep colonization curve that flattened out after the 1930s (Thornton et al., 1990). The 17 species reported from the islands by 1990 include pantropical species (*P. americana, Blatta orientalis*) probably introduced by humans, fully winged species (e.g., *Balta notulata, Haanina major*), those with reduced wings (*Lobopterella dimidiatipes*), and species in which there is a great deal of variation in wing reduction in both sexes (e.g., *Hebardina concinna*). *Neostylopyga picea,* which has short tegminal pads and lacks wings, also is present on the islands and probably arrived by rafting. It is generally found in humus and decaying wood (Roth, 1990a).

Studies in the Galapagos offer the best evidence that the evolution of flightlessness may occur on islands. Eighteen species are reported on the Galapagos (Peck and Roth, 1992). Of these, the introduced or native (naturally occurring tropical American and Galapagos) cockroaches are fully winged as adults, except for female *Symploce pallens.* The five endemic species are all partially or wholly flightless. Peck and Roth (1992) suggest that three natural colonization events took place. First, an early colonization by *Ischnoptera* and loss of flight wings in three descendent species, a later colonization by *Chorisoneura* and partial reduction of flight wings in two descendent species, and lastly, a recent colonization by *Holocampsa nitidula* and perhaps another *Holocampsa* sp. These authors give a detailed analysis of the process of wing reduction in the studied cockroaches, and conclude that their data fit the generalization that loss of flight capability often accompanies speciation on islands. The authors do note, however, that the flightless condition "may not be a result of island life per se, but may be a specialization for life in more homogenous leaf litter or cave habitats at higher elevations on the islands."

Mountains

There are several indications that wing reduction or loss in cockroaches may be correlated with altitude. On Mt. Kilimanjaro in Africa, for example, fully alate *Ectobius africanus* females were collected only below 1000 m (Rehn, 1932b). In Australia, males in the genus *Laxta* may be macropterous, brachypterous, or apterous, but all known females lack wings. In the two cases where males are not fully winged, both were collected at altitude: *Lax. aptera* (male apterous) from the Brindabella Ranges and Snowy Mountains, and *Lax. fraucai* (male brachypterous) from northeastern Australia at 670–880 m (Mackerras, 1968b; Roach and Rentz, 1998; Roth, 1992). Although most *Ischnoptera* species are fully winged, the flightless *Ischnoptera rufa debilis* occurs at high altitude in Costa Rica (Fisk, 1982). The metabolic cost of flight may be substantial at the cold temperatures typical of high elevations (Wagner and Liebherr, 1992).

Deserts

Females of desert cockroach species are generally apterous or brachypterous, but males are fully alate (Rehn, 1932b). The high cost of desiccation during flight may account for many cases of wing reduction in desert insects (Dingle, 1996), but may be less of a problem for night-active insects like many Blattaria. Rehn (1932b) noted that the number of brachypterous and subapterous cockroaches in deserts was comparable to that of humid rainforest areas of tropical America. It has been suggested that the strong tendency for wing reduction among all families of Australian cockroaches (Mackerras, 1965a) is a response to desert conditions (Chopard, in Rehn, 1932b). Almost all of the large Australian group Polyzosteriinae are brachypterous or apterous, but not all live in the desert. *Scabina antipoda,* for example, is brachyterous and found under bark in the rainforests of eastern Australia (Roach and Rentz, 1998).

Insect Nests

Cockroaches adapted to living in the nests of social insects are always apterous or have wings reduced to varying degrees. *Pseudoanaplectinia yumotoi,* associated with *Crematogaster* sp. ants in canopy epiphytes in Sarawak, is among those with the longest wings. The tegmina and wings reach to about the sixth tergite in the female, and to about the supra-anal plate in the male (Roth, 1995c); it is unknown as to whether these allow for flight. Females of *Nocticola termitofila,* from nests of *Termes* sp. and *Odontotermes* sp. termites, are apterous (Fig. 1.16C). Males are brachypterous, with transparent wings about half the length of the abdomen (Silvestri, 1946); these are fringed around the edges (like thrips) and may allow for passive wind transport. *Attaphila* living in the fungus gardens of leaf-cutting ants have apterous females and brachypterous or apterous males (Gurney, 1937; Roth, 1991a). Both *Att. fungicola* and *Att. bergi* have evolved a unique solution for moving between nests—they are phoretic on ant alates leaving the nest on their mating flight (Fig. 2.11) (Wheeler, 1900; Bolívar, 1901; Moser, 1964; Waller and Moser, 1990). These myrmecophiles have large arolia (Gurney, 1937) that may assist them in clinging to their transport. Several questions arise concerning this phoretic relationship. Do both male and female cockroaches disperse with the alates, or only fertilized females? Since the nuptial flight of male ants is invariably fatal (Hölldobbler and Wilson, 1990), do the cockroaches choose the sex of their carrier? If cockroaches do choose male alates, perhaps they can transfer to female alates while the ants are copulating. The vast majority of the thousands of released virgin queens die within hours of leaving the nest (Hölldobbler and Wilson, 1990); do their associated cockroaches subsequently search for nests on foot? Because they disperse together, would molecular analysis reveal a co-evolutionary relationship between this myrmecophile and its host? A comparison of *Attaphila* to *Myrmecoblatta wheeleri* also

Fig. 2.11 Phoretic female of *Attaphila fungicola* attached to the wing base of *Atta* sp. host. The cockroach is about 2.7 mm in length. Courtesy of John Moser.

would be of interest. The latter lives in the nests of a variety of ant genera (*Campanotus, Formica, Solenopsis*), but have no arolia or pulvilli on the tarsi, and there are no records of host transport (Fisk et al., 1976).

Arboreal

Species that live in trees are generally expected to be good fliers, because the alternative is a long down-and-up surface trip when moving between limbs or trunks (Roff, 1990; Masaki and Shimizu, 1995). Fisk (1983) identified the cockroaches that fell during canopy fogging experiments conducted in rainforests in Panama and Costa Rica. Of the 25 species for which wing condition is known in both males and females, 23 (92%) are winged in both sexes, one (*Nesomylacris asteria*) has reduced tegmina and wings in both sexes, and one (*Compsodes deliculatus*) has winged males and apterous females (analyzed by LMR). Small blattellid species were the most abundant and diverse group collected during the study. These data support the notion that cockroaches that spend the day in trees are generally flight-capable. Further support comes from behavioral observations in Costa Rica. Flight between perches was noted in all winged species observed during their active period (Schal and Bell, 1986). Some cockroach species, however, spend their entire lives within specialized arboreal niches, are unlikely to be collected during canopy fogging, and are not necessarily volant. These include cockroaches that live under bark, in epiphytes, in arboreal litter, and in insect and bird nests. Of the 31 species of Brazilian cockroaches collected in bromeliads by Rocha e Silva Albuquerque and Lopes (1976), 55% were apterous or brachypterous.

Caves

As discussed in the following chapter, caves are at one end of a continuum of subterranean spaces frequented by cockroaches, with the border between caves and other such habitats often vague. Variation in wing reduction, as well as associated morphological changes, may reflect different degrees of adaptation to these specialized habitats. In Australian *Paratemnopteryx*, species found in caves usually exhibit some degree of wing reduction (Table 2.2). Several species in this genus are intraspecifically variable; both macropterous and reduced-wing morphs of *Para. howarthi* can even be found in the same cave (Roth, 1990b). Epigean species in the genus living under bark or in leaf litter are often macropterous, but also may exhibit wing reduction. The area of the cave inhabited (deep cave versus twilight zone), nutrient availability (is there a source of vertebrate excrement?), and length of time a population has been in residence all potentially influence the morphological profiles of the cave dwellers. Like other invertebrates, cockroaches that are obligate cavernicoles (troglobites) typically exhibit wing reduction or loss.

Table 2.2. Wing development in cavernicolous and epigean species of the Australian genus *Paratemnopteryx*, based on Roth (1990b), Roach and Rentz (1998), and Slaney (2001). Those species described as epigean were found under bark and in litter.

Species	Habitat	Wing condition
Para. atra	Cavernicolous, in mines	Slightly reduced
Para. australis	Epigean, one record from termite nest	Reduced
Para. broomehillensis	Epigean	Macropterous
Para. centralis	Epigean	Macropterous
Para. couloniana	Epigean, in houses	Variably reduced, some males macropterous
Para. glauerti	Epigean	Male macropterus, female reduced
Para. howarthi[1]	Cavernicolous and epigean	Macropterous and reduced males, females reduced
Para. kookabinnensis	Cavernicolous	Reduced
Para. rosensis	Epigean	Male macropterous, female reduced
Para. rufa	Cavernicolous and epigean	Reduced
Para. stonei	Cavernicolous and epigean	Variably reduced[2]
Para. suffuscula	Epigean	Macropterous
Para. weinsteini	Cavernicolous	Reduced, female more so

[1] Brachypterous and macropterous morphs can be found in same cave.
[2] Female wings slightly longer than male's.

Wing Variation within Closely Related Groups

A number of closely related cockroach taxa unassociated with caves can show as much variation as *Paratemnopteryx*. Wing condition is therefore of little value as a diagnostic generic character unless it occurs in conjunction with one or more stable and distinctive characters (Hebard, 1929; Rehn, 1932b). The three native species of the genus *Ectobius* in Great Britain clearly depict an evolutionary trend in female wing reduction. Males are macropterous in all three species. Females of *E. pallidus* also have fully developed wings, but in *E. lapponicus* the tegmina of the female are about two-thirds the length of the abdomen and the wings are reduced. In *E. panzeri* the tegmina of the female are just a little longer than wide and the wings are micropterous (Kramer, 1956). The subfamily Tryonicinae illustrates the degree of wing variation that can occur at higher taxonomic levels. Table 2.3 displays the genera of these blattids arranged to exhibit a detailed gradient of wing development from one extreme (macropterous) to the other (apterous).

Case Study: Panesthiinae

Those members of the Panesthiinae for which we have ecological information are known to burrow in soil (Geoscapheini) or rotted wood (the remainder). They therefore illustrate the range of wing variation possible within an ecologically similar, closely related taxon (Table 2.4). Many species in the subfamily have fully developed tegmina and wings, and are heavy bodied but able flyers (Fig. 2.12A). Male *Panesthia australis*, for example, have been collected at lights in Australia (Roth, 1977; CAN, pers. obs.). Some genera include sexually dimorphic species, with winged males and wingless females (*Miopanesthia*), and a number of species in the genus *Panes-*

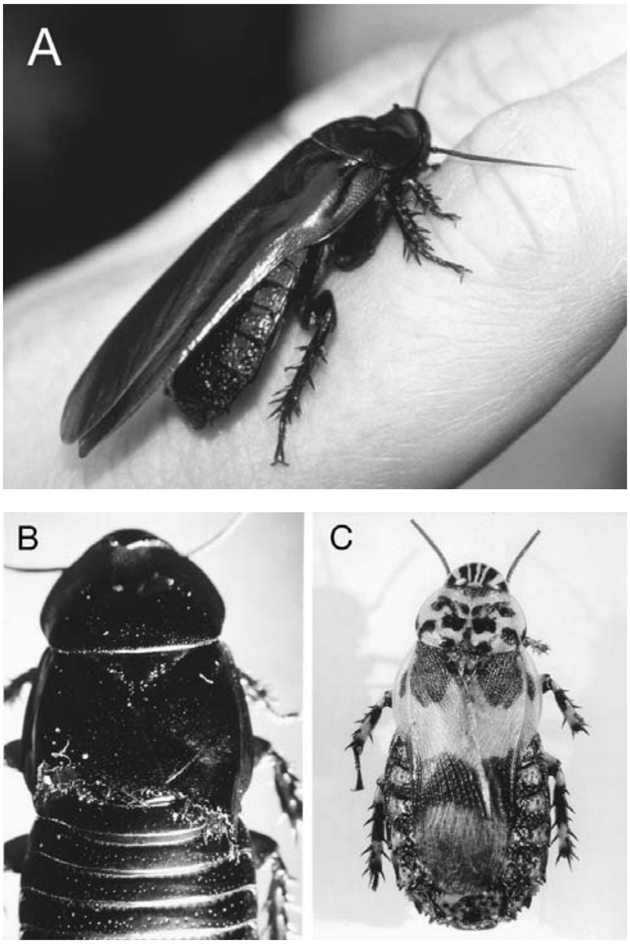


Fig. 2.12 Wing condition in wood-feeding Panesthiinae. (A) Fully winged adult of Australian *Panesthia australis;* photo by C.A. Nalepa; (B) detail of adult Australian *Panesthia cribrata* showing ragged wing bases after dealation; photo courtesy of Douglas Rugg; (C) strikingly patterned winged female of *Caeparia donskoffi* from Vietnam, body length approximately 3.5 cm; photo by L.M. Roth.

Table 2.3. Tryonicinae (Blattidae) illustrate the complete range of wing development, from fully developed wings to completely apterous, with intermediate stages (LMR, pers. obs.).

Wing characters	Genus (no. species)	Country
Fully winged, but wings may not reach the end of the abdomen	*Methana* (10)	Australia
Tegmina reduced, elongated, lateral, completely separated from the mesonotum, reaching a little beyond hind margin of second abdominal tergite, hindwings present, vestigial, lateral, completely covered by the tegmina	*Tryonicus* (3) (female apterous)	Australia
Tegmina small, lateral lobes completely separated from the mesonotum, not reaching the first abdominal tergite, wings absent	*Punctulonicus* (2) *Angustonicus* (2) *Rothisilpha* (2)	New Caledonia
Tegmina lateral, but not completely separated from the mesonotum, wings absent	*Pellucidonicus* (2) *Pallidionicus* (5) *Angustonicus* (1) *Punctulonicus* (1) *Rothisilpha* (1)	New Caledonia
Completely apterous	*Lauraesilpha* (4)	New Caledonia

Table 2.4. Extent of development of tegmina and wings in 10 genera of Panesthiinae; after Table 6 in Roth (1982b). The "reduced" wing category includes brachypterous morphs, micropterous morphs, and those with reduced tegmina and absent wings. One genus includes polymorphic species (*Panesthia*). Sexual dimorphism is found only in the genus *Miopanesthia*.

	Number of species + subspecies with tegmina and wings				
Genus	Fully developed (macropterous)[1]	Fully developed + reduced-wing morphs	Reduced	Absent	Total
Panesthia[2]	23 + 1	5 + 1	15 + 2	11 + 1	54 + 9
Miopanesthia[2]					
Male	6	0	0	2	8
Female	1[3]	0	0	7	8
Ancaudellia[2]	15 + 1	0	3 + 3	0	18 + 4
Salganea[2]	26 + 3	0	12 + 1	4	42 + 4
Caeparia[2]	4	0	0	0	4
Microdina	0	0	1	0	1
Parapanesthia[4]	0	0	0	1	1
Neogeoscapheus[4]	0	0	0	2	2
Geoscapheus[4]	0	0	0	2 + 2	2 + 2
Macropanesthia[4]	0	0	0	4	4

[1] A number of these eventually shed their wings.

[2] Wood-feeding cockroaches; information on the diet of *Miopanesthia, Caeparia,* and *Ancaudellia* from a pers. comm. from K. Maekawa to CAN.

[3] The original description of *M. sinica* Bey-Bienko did not indicate the wing condition of the female; the implication is that they have tegmina and wings (Roth, 1979c).

[4] Soil-burrowing cockroaches (Geoscapheini).

thia are intraspecifically variable. Of these, both males and females may have either well-developed or variably reduced wings. In some species (e.g., *Pane. australis*), the reduced-wing form is uncommon (Roth, 1977).

Uniquely among cockroaches, some macropterous members of this subfamily shed their wings. In some species of *Panesthia, Salganea,* and *Ancaudellia* only the basal region of the tegmina and wings remains intact. The wings are not cleanly snapped at a basal suture, as in termites, but have a raggedy, irregular border (Fig. 2.12B) (Roth, 1979c; Maekawa et al., 1999b). Some early observers thought that dealation resulted from the chewing action of conspecifics (Caudell, 1906), that they "solicit the assistance of their comrades to gnaw them off close to the base." Others, however, suggested that the wings were broken off against the sides of their wood galleries, because dealation occurs even in isolated individuals and because the proposed gnawing action was never observed (McKeown, 1945; Redheuil, 1973). The wings are most likely lost by a combination of both behaviors. In laboratory studies of *Panesthia cribrata,* Rugg (1987) saw adults moving rapidly backward, rubbing the wings against the sides of the cage, and also observed a male chewing the wing of a female, then dragging off a tattered portion and eating it. Rugg illustrates obviously chewed wings, with distinct semicircular portions removed. Individuals are unable to chew their own wings (D. Rugg, pers. comm. to CAN). Like termites and some other insects, Panesthiinae with deciduous wings restrict flight activity to the prereproductive stage of their adult life. It would therefore be of interest to determine if flight muscle histolysis accompanies wing loss, and if so, how it relates to fecundity. In crickets, dealation induces histolysis of the wing muscles and a correlated rapid production of eggs (Tanaka, 1994).

A well-corroborated estimate of relationships among 20 species of Panesthiinae inferred from a combined analysis of 12S, COII, and 18S is illustrated in Fig. 2.13 (Maekawa et al., 2003). We mapped four wing-related character states onto the depicted tree: wing morphology (macropterous, reduced wings, or apterous), and in macropterous species, whether the wings are permanent or deciduous. The apterous condition appears to have evolved three times, in *Miopanesthia deplanata, Panesthia heurni,* and the Geoscapheini. Deciduous wings arose twice, in *Salganea* and in the lineage that includes *Panesthia* and *Ancaudellia.* Within *Salganea,* reduced wings seem to be derived from the macropterous, deciduous state. Maekawa et al.'s (2003) phylogeny is not fully resolved and shows the genus *Panesthia* as poly- or paraphyletic. It is nonetheless obvious that the morphological wing condition and the behaviors associated with removing deciduous wings are evolutionarily labile in these cockroaches. Wings are generally dull and uniformly colored in the Panesthiinae that eventually shed them. Un-

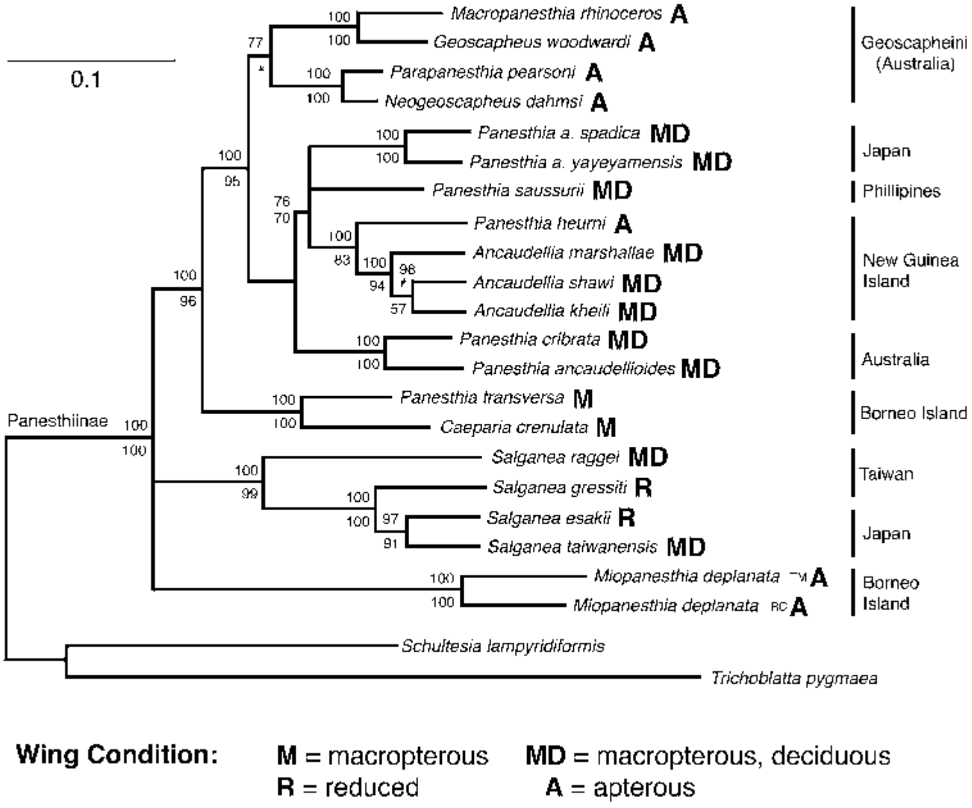


Fig. 2.13 Phylogenetic distribution of wing condition in the Panesthiinae. The phylogenetic tree is inferred from a combined analysis of 12S, COII, and 18S, obtained using Bayesian inference of phylogeny with the GTR + I + G model of substitution. Posterior probabilities (PP), expressed as percentages, are shown above branches to indicate the level of support for each node. Branches with less than 50% PP were collapsed to form polytomies. Bootstrap values (expressed as percentages) from an MP analysis are shown below the nodes. The asterisk indicates a node that was not supported in more than 50% of bootstrap replicates; however, an analysis in which COII third codon transitions were downweighted by a factor of 4 resulted in 70% support. The scale bar indicates the number of inferred substitutions per site. From Fig. 3 (p. 1305) in Maekawa et al. (2003), courtesy of K. Maekawa and with permission of the Royal Society of London. Wing conditions based on Roth (1979b, 1979c) and the observations of K. Maekawa (pers. comm. to CAN).

like the other macropterous species, *Panesthia transversa* and *Caeparia crenulata* (as well as other species of *Caeparia*) have strongly colored and patterned wings and retain them throughout their adult life (Fig. 2.12C). This reinforces the idea that cockroach wings have functional significance in contexts other than flight; in this case it is likely that retained wings have signal value to predators, conspecifics, or both. A comparison of the population genetics of apterous or brachypterous wood-feeding species to those that have remained flight capable might yield data relevant to dispersal distances.

Intraspecific Wing Variation

A similar reduction in tegmina and wings often occurs in both sexes of a species. Sexual dimorphism is common, however, and it is most often the female that exhibits the greater degree of wing reduction. At one extreme are species with fully winged males and apterous females. Examples include the African genus *Cyrtotria* (= *Agis*) (Rehn, 1932a), *Trichoblatta sericea*, living on and under the bark of *Acacia* trees in India (Reuben, 1988), and many desert Polyphagidae. In *A. investigata*, for example, females are wingless, but at night fully winged males emerge from the sand and fly (Edney et al., 1974). Females of *Escala circumducta* have "almost discarded their organs of flight" and live their entire lives beneath the bark of trees. The fully winged males associate with the females only during a brief pairing season (Shaw, 1918). In cockroaches with extreme wing dimorphism females are often burrowers or crevice fauna, but the habitats of males are unknown, because they have been collected only at lights. Some cases of sexual dimorphism are so extreme that they are problematic to taxonomists trying to associate the two sexes (Roth, 1992). Females of *Laxta* (= *Onisco-*

soma) *granicollis* are flattened and wingless, resembling "an enormous wood louse," while males are winged and "of more graceful shape" (Swarbeck, 1946). Similarly, males of several species of *Perisphaeria* and *Pseudoglomeris* are slender, winged insects, while the females are apterous and broader (Hanitsch, 1933). More moderate cases of wing dimorphism include species where both sexes have reduced wings but the female more so, and those species discussed above, where both sexes are fully winged, but the female is nonetheless flightless. We are not aware of cases of macropterous females and apterous males, but when wing reduction occurs in both sexes, sometimes the wings of the male are shorter (e.g., *Para. stonei*—Roth, 1990b).

Wing development within a species is not always a fixed character. In some cockroaches, only one sex exhibits variation, for example, *Neotemnopteryx fulva* males are macropterous, but the females may be macropterous or brachypterous (Roth, 1990b). Likewise, *E. africanus* males are macropterous, but female wing reduction varies with altitude (Rehn, 1932b). In other cockroaches, the reduction of tegmina and wings is variable in both sexes. These include at least five species of *Panesthia* (Roth, 1982b), *H. concinna* in the Galapagos (Roth, 1990a), and the Australian *Para. couloniana* (Roth, 1990b). The latter generally has brachypterous tegmina and micropterous wings, but the degree of reduction varies, and there are males whose flight organs are fully developed. This species lives in litter and under bark, but there are also records of it infesting houses (Roach and Rentz, 1998).

Migration

Intraspecific variation in the wing form of insects is usually associated with migratory flight, that is, dispersal or migration from the habitat, as opposed to trivial flight, activity associated with routine behavior such as feeding, mate finding, or escaping from enemies. As such, the environmental cues known to influence wing form are those that signal seasonal habitat deterioration (photoperiod, temperature) or less predictable, density-dependent habitat changes (poor nutrition, stress, crowding) (Travis, 1994; Masaki and Shimizu, 1995). High population density is known to induce a number of morphological and physiological changes in studied cockroach species, for example, *Blab. craniifer* (Goudey-Perriere et al., 1992) and *Eublaberus distanti* (Rivault, 1983), but to date, wing form has not been one of them.

Mass migrations and dispersals have been recorded in cockroaches, though not in wing-polymorphic species. Surface activity in *C. punctulatus* occurs following rainfall, during daylight hours in spring (Nalepa, 2005). Soil-burrowing Australian Geoscapheini undertake spectacular pedestrian migrations after rains—sometimes seen by motorists crossing roads every few yards for 32 km at a stretch (Monteith, pers. com. to LMR). There are two intriguing reports of possible long-distance movement by flight. On a sunny morning in Venezuela at an elevation of 1100 m, Beebe (1951) observed a "flurry" of at least 30 *Blaberus giganteus* fluttering slowly up a gorge used as a flyway for migrating insects. Under the hot sun in an Arizona desert, Wheeler (1911) watched two separate swarms of male *Homoeogamia subdiaphana* alternately flying and quickly running over the sand in a southwesterly direction; he likened their quick movements to those of tiger beetles (Cicindelidae). Overpopulated buildings or sewers have been known to spawn natural migrations in several species of urban pests (Roth and Willis, 1957). It is unusual that many of these movements occur during daylight hours in otherwise nocturnal insects. Stein and Haschemi (1991) report that German cockroaches emigrating from a garbage dump used solar cues for orientation. Most walked directly toward the sun, with their bearing shifting from east to west over the course of the day.

Evolution of Flightlessness

Macropterism is clearly the primitive condition in cockroaches (Rehn, 1932b). Because no fossil cockroaches are known with abbreviated organs of flight (R.J. Tillyard, in Shaw, 1918), it is assumed that Paleozoic cockroaches were swift-flying and diurnal (Brodsky, 1994). Flight may have been advantageous in Carboniferous swamps, as it would allow movement between patches of habitat surrounded by water. On the other hand, the possession of wings does not assure the ability to fly, and apterous and brachypterous cockroaches are less likely to leave fossil evidence than their more volant relatives. There are indications of wing sexual dimorphism in the fossil record. Schneider (1977, 1978) concluded that the wings of Carboniferous females were broader than those of males, and Laurentiaux (1963) demonstrated that there were intersexual differences in both the length and the shape of wings.

It is possible to induce alary reduction experimentally in a normally winged species (e.g., *Blab. craniifer*), but attempts to produce fully developed wings in an apterous cockroach have been unsuccessful; Lefeuvre (1971) therefore concluded that the evolutionary loss of wings is irreversible. On the other hand, Masaki and Shimizu (1995) suggested that wing reduction is possible without elimination of the genetic background for macropterous development, and potential evolutionary reversal of wing loss has been demonstrated in the Hemiptera-Heteroptera (Anderson, 1997) and in the Phasmatodea (Whiting et al., 2003). As robust phylogenetic trees become available for varying cockroach taxa, the possibility of the re-evolution of wings in the Blattaria can be put to the test.

Habitat Factors Associated with Wing Loss

Flight loss in insects is most often associated with environmental stability (Southwood, 1962; Harrison, 1980; Roff, 1990; Denno et al., 1991, 2001b; Wagner and Liebherr, 1992; Zera and Denno, 1997, among others). The logic is that flightless morphotypes are inclined to persist in spatially homogeneous, temporally stable habitats where food, shelter, and mates are continuously accessible to pedestrians. Conversely, flight is retained in insects living in temporary habitats, so that fluctuating levels of resource quality and abundance may be tracked. Although a number of studies support this hypothesis (e.g., Roff, 1990; Denno et al., 1991), the association of cockroaches with their habitat is not as clear as it is in insects such as stenophagous herbivores on annual plants, or waterstriders that live in temporary versus permanent ponds. Few cockroaches are exclusively associated with ephemeral or periodically disturbed habitats, although they may utilize them if available. Some species exhibit seasonal habitat shifts, but there are no known cockroaches with seasonal variation in wing morphology.

Several hurdles to understanding the role of habitat in structuring cockroach wing morphology must be added to those noted earlier. First, there can be a great deal of intraspecific variation in habitat choice. A good example is *Chorisoneura carpenteri* from the Galapagos, a species with both brachypterous and macropterous forms. The fully winged morphs have been collected at elevations of 30–1000 m in agricultural areas, arid zones, pampa, humid forest, and *Scalesia* forest; the brachypterous form has been collected at 120–700 m in all of the listed habitats but one—the agricultural zone (Peck and Roth, 1992). Second, many cockroaches defy being described by just one aspect of their habitat, and it is difficult to tease apart the relative importance of a hierarchy of overlapping ecological levels. Is a canopy cockroach more likely to be wingless if the forest is on a mountain? Is it valid to compare a list of wingless cockroaches found in caves to a list of wingless cockroaches found in Texas (Roff, 1990, p. 395)? Finally, the fact that so many cockroaches in different habitats utilize the same microhabitats confounds analysis. Whether they are found in a desert, grassland, forest, or elsewhere, many cockroaches are associated with a continuum of dark, humid, enclosed spaces that they find or make.

The strength of the association of a given cockroach species with these subterranean and other spaces appears influential in wing development. Cockroaches that live their entire lives in burrows, galleries, or crevices, except for a brief dispersal period at the subadult or young adult stage or when the habitat becomes unsuitable, seem most prone to winglessness. It is apparent from an examination of the Panesthiinae (Fig. 2.13) that the habit of burrowing in wood or soil may be connected to the prevalence of reduced, absent, or deciduous wings in this subfamily. Cockroach species that spend their lives in the loose spaces beneath bark also fall into this category. Shaw (1918) noted that flightless cockroaches are generally cryptic in their habits, and that there was a “definite correlation” between a flattened morphology and the absence of wings. In deserts, cockroach microhabitats include the base of grass tufts and the spaces beneath debris and boulders. The majority of desert cockroaches, however, live a partially or entirely subterranean existence. Half of the 28 desert cockroaches listed by Roth and Willis (1960) live in the burrows of small vertebrates, and additional species burrow into loose sand. It should be noted that obligate cavernicoles are an extreme case of this same continuum. The ecological influences that promote wing loss in all these cockroaches, then, may differ more in degree than in type.

Several characteristics of crevices and burrows may influence wing loss in the cockroaches that permanently or periodically inhabit them. First, these are temporally stable habitats. Logs, leaf litter, and other rotting vegetable matter are continuously or periodically replenished from source plants, and migration to fresh resources, if required, is often a local trip. Second, these are homogeneous microhabitats, in that they are interchangeable dark, moist, protected quarters. If leaf litter on the forest floor loses moisture during the tropical dry season, for example, cockroaches normally found in ground-level litter are known to move into moist, arboreal accumulations of leaves (Young, 1983). Third, these are chiefly two-dimensional microhabitats, particularly for cockroach species that either rarely venture from shelters or have a modest ambit around them. Schal and Bell (1986) found that many of the flightless cockroach species in Costa Rican rainforest ground litter did not move very far in vertical space during their active period. Recent evidence suggests that it is the interaction of habitat dimensionality and habitat persistence that may have the most significant effect on insect wing morphology (Waloff, 1983; Denno et al., 2001a, 2001b). Finally, these cockroaches are able to feed within their shelter (in logs, under bark, in leaf litter, in vertebrate burrows, in social insect nests, in caves), or the shelters are situated in the immediate vicinity of potential food (soil burrowers, under rocks, under logs). The proximity of widespread, persistent, often abundant but low-quality food has two potential implications for the evolution of cockroach wing morphology. First, the insects are less tied to the seasonality of their food source. Flightlessness in insects tends to be positively correlated with their ability to remain throughout the year in their developmental habitat (Anderson, 1997; Denno et al., 2001a). Second, wing reduction and loss is often associated with nutrient limitation (Jarvinen and Vepsalainen, 1976; Kaitala and Hulden, 1990), and cockroaches that rely on rotting vegetable matter as a primary food source may be living close to their nutritional threshold. In caves, wing loss and associated morphological changes occur more frequently in organisms that rely on plant debris than those that rely on bat or bird guano (Culver et al., 1995).

Wing Loss and Life History Trade-offs

Food abundance and quality cannot be divorced from wing morphology because it is costly to produce and maintain the wings and their muscular and cuticular support (Roff and Fairbairn, 1991); insect flight muscle is one of the most metabolically active tissues known (e.g., Weis-Fogh, 1967). Flight behavior is also energetically demanding, and can alter the composition of hemolyph for up to 24 hr afterward in *P. americana* (King et al., 1986). These metabolic expenses place a significant demand on an insect's overall energy budget, and compete with other physiologically demanding life history processes. The best documented of these is egg production. Any easing of the selective pressure to maintain wings allows a female to divert more resources to egg production, increasing her fitness more than if she remained volant ("flight-oogenesis syndrome") (Roff, 1986, 1990; Roff and Fairbairn, 1991). Flight capability can diminish rapidly under the right conditions (Denno et al., 1991; Marooka and Tojo, 1992), and may account for the lack of functional flight muscle in laboratory-reared females of *Periplaneta* (Table 2.1). The flight-oogenesis syndrome also may account for the prevalence of flightless females, rather than males, in cockroach species exhibiting sexual dimorphism in flight ability. The relationship between wing morphology and fecundity has been demonstrated in a number of insect species, including orthopteroids (e.g., Cisper et al., 2000), but is as yet unstudied in cockroaches. The fact that there are numerous cockroach species with males possessing reduced or absent wings suggests that there is a cost to the retention of wings even in males. In some insects, short-winged males have a mating advantage over macropterous males, or a gain in testes and body size (Dingle, 1996; Langellotto et al., 2000). Macroptery in males is most often related to the distribution of females in the habitat, and whether they are accessible to males on foot (Roff, 1990; Denno et al., 2001a). This is likely the case in cockroaches, because in many species females produce volatile sex pheromones; males use these chemical cues to actively seek mating partners (Gemeno and Schal, 2004). The degree of wing development may affect longevity in both sexes (Kaitala and Hulden, 1990; Roff and Fairbairn, 1991). It may be relevant, then, that among the longest-lived of the known cockroaches are apterous species that burrow in wood or soil (Chapter 3).

Wing Loss, Paedomorphosis, and Population Structure

A lack of functional wings is at the heart of two obstacles to understanding the evolutionary biology of some earthbound cockroaches. First, aptery and brachyptery are associated with a developmental syndrome that reduces morphological complexity, making it difficult to distinguish among closely related taxonomic groups. Second, the loss of mobility associated with aptery can result in complex geographic substructuring of these morphologically ambiguous groups.

Wing reduction or loss is the best indicator of paedomorphosis, defined as the retention of juvenile characters of ancestral forms in the adults of their descendents (Matsuda, 1987; Reilly, 1994). Not all short-winged insects retain juvenile characters, but in other cases, it is clear that many so-called adult characters are absent in short-winged or apterous morphs (Harrison, 1980). The diminishment or loss of structures such as ocelli, compound eyes, antennal and cercal segments, and some integumental structures such as sensilla often accompanies aptery and brachyptery (Matsuda, 1987). These reductions are common in cockroaches (Nalepa and Bandi, 2000), and like other animals (Howarth, 1983; Juberthie, 2000b; Langecker, 2000) occur most often in species that inhabit relatively safe, stable environments, such as caves, burrows, logs, social insect nests, leaf litter, and other cryptic environments. Lefeuvre (1971) found that some cockroach species with reduced wings have fewer developmental stages than macropterous relatives, and that juvenile features can be retained in the tracheal system, peripheral nervous system, and integument. Warnecke and Hintze-Podufal (1990) concluded that the reduced wings of female *Blaptica dubia* are the result of larval characters that persist into maturity, rather than the growth inhibition of adult wings. Other examples include the retention of styles in wingless adult females of *Noc. termitophila* (female cockroaches normally lose their styles prior to the adult stage) (Matsuda, 1979), and the reduced sensory and glandular systems of the myrmecophile *Att. fungicola* (Brossut, 1976). *Cryptocercus* has reduced eyes and cercal segmentation, and exhibits marked paedomorphic traits in its genital morphology (Walker, 1919; Crampton, 1932; Klass, 1995). Females of the desert cockroach *A. investigata* are "generally nymphlike," lack the wings and ocelli seen in the male, and have shorter antennae and cerci (Friauf and Edney, 1969). Because wing loss in cockroaches is female biased, it is most often females that exhibit correlated paedomorphic characters.

The systematics of paedomorphic organisms can be frustrating. Because many structures never develop or develop variably within a group, they cannot be used to delimit taxa, or to infer phylogenetic relationships. Independent losses of ancestral postmetamorphic features is an important source of homoplasy and can confound cladistic analysis (Wake, 1991; Brooks, 1996; Hufford, 1996). The morphological homogeneity of the Polyphagidae has caused quite a few problems with attribution, not only to species but also to genera (Failla and Messina, 1987). Members of the genus *Laxta* "vary so much in color and size and have genitalia so similar as to make distinguishing taxa difficult" (Roth, 1992). Paedomorphic characters and mosaic evolution in the wood-feeding cockroach *Cryptocercus* strongly contribute to problems in determining the phylogenetic relationships of this genus at all taxonomic levels (Klass, 1995, 1998a; Nalepa and Bandi, 1999, 2000; Nalepa et al., 2002). Cave cockroaches, like other cave dwellers (Howarth, 1983; Juberthie, 2000a; Langecker, 2000), are prone to taxonomic problems associated with paedomorphosis. Roth (1990b) noted that *Para. stonei* from different caves all had reduced hindwings but varied in body size, in the development of pulvilli, and in length of tegmina. The genitalia were so similar, however, that he assigned them to different races within the species. A morphometric study by Slaney and Weinstein (1997b) subsequently supported Roth's conclusions.

Molecular and chemical tools are increasingly required to provide characters to distinguish among these morphologically ambiguous cockroach taxa. Humphrey et al. (1998), for example, used protein electrophoresis to propose that morphologically similar populations of *M. rhinoceros* are comprised of three genetic species. Slaney and Blair (2000) used the ITS2 gene region of nuclear ribosomal DNA in the *Para. stonei* group, and their results supported conclusions based on morphology. Molecular phylogenetic relationships, however, are not always completely congruent with relationships based on morphological characters. Basal relationships among species of the wood-feeding blaberid *Salganea* are poorly resolved by molecular analysis, probably because of rapid and potentially simultaneous radiation of the group (Maekawa et al., 1999a, 2001).

In flightless animals the pool of potential mating partners is limited to those that can be found within walking distance, resulting in restricted levels of gene flow. Populations may become subdivided and isolated to varying degrees, resulting in complex genetic substructuring and the formation of local species, subspecies, and races. This is common in caves, where subterranean spaces can be isolated or locally connected via mesocaverous spaces (Barr and Holsinger, 1985). It is also common on mountains, where endemic races and subspecies may be wholly restricted to single peaks (Mani, 1968). *Cryptocercus primarius,* for example, is found in an area of China with a dissected topography characterized by high mountain ridges sandwiched between deep river gorges, forming various partitioned habitats (Nalepa et al., 2001b). This genus of montane cockroaches is also dependent on rotting logs, which ties their distribution to that of mature forests. Any event that has an impact on the distribution of forests, including glaciation (Nalepa, 2001; Nalepa et al., 2002) and deforestation (Nalepa et al., 2001b) will affect the population structure of the cockroach. Consequently the geographic distribution of genetic populations and species groups in both Northeast Asia (Park et al., 2004; Lo et al., 2000b) and the eastern United States (Nalepa et al., 2002) can be unexpected. *Cryptocercus* found in southern Korea, for example, are more closely related to populations in Northeast China than they are to all other Korean members of the genus.