

include assassin bugs (Reduviidae), ground beetle larvae (Carabidae), rove beetles (Staphylinidae), ant lions (Myrmeleontidae), and worm lions (Diptera: Rhagionidae: *Vermileo*). Sphecid wasps in the genera *Aphilanthops* and *Clypeadon* provision their nests exclusively with ants (Evans 1962, 1977). In Costa Rica, windscorpions (Solifugae) run along and within nocturnal foraging columns of the leaf-cutting ant *Atta cephalotes*, probably preying on single workers (Bukowski 1991). Spiders that specialize on ants are often striking visual mimics of their prey, presumably as camouflage against small vertebrate predators that have learned to avoid the ants (Oliveira and Sazima 1984; Oliveira 1988). Although most vertebrates studiously avoid ants because of their stings and noxious chemical deterrents, vertebrate ant specialists include anteaters and some toads, lizards, snakes, and birds (Bequaert 1922; Weber 1972b).

Symbioses

Symbioses between ants and other animals (particularly arthropods) constitute a vast and fascinating subject, the far-flung literature of which has yet to be exhaustively catalogued (but see Kistner 1979, 1982, and Hölldobler and Wilson 1990 for excellent reviews).

ANT-HOMOPTERAN ASSOCIATIONS. The tending of homopterans by ants is well known, no doubt because of the striking parallel with the husbandry of cattle by humans. The majority of homopteran-tending ant species occur in the subfamilies Dolichoderinae, Formicinae, and Myrmicinae, although some ponerines (notably in the Ecatommini) also obtain significant nutrition through such interactions. In addition to Aphidae, ants also tend homopterans in the families Cercopidae, Cicadellidae, Coccidae, Fulgoridae, Membracidae, Pseudococcidae, and Psyllidae. Ants feed on "honeydew," a by-product of homopteran phloem-feeding consisting

largely of carbohydrate but also containing amino acids that in some cases are added by the homopteran (Dixon 1985). In return, the ants protect homopterans from predators and parasitoids.

Most ant-homopteran associations are facultative mutualisms. However, ants in the North American genus *Acanthomyops* (Formicinae) appear to be obligately dependent on their root coccid symbionts (Wing 1968), as are species of the pantropical genus *Acropyga* (Formicinae). A virgin queen of an *Acropyga* species departs on her nuptial flight carrying in her mandibles a coccid symbiont to serve as the parthenogenetic progenitor of a future "herd" (Silvestri 1925; Wheeler 1935; Bünzli 1935; Brown 1945; Buschinger et al. 1987). This behavior has also been observed in a Sumatran *Cladomyrma* species (Roepke 1930). The Malaysian ant *Hypoclinea cuspidatus* (Dolichoderinae), an obligate symbiont of the mealybug *Malaicoccus formicarii* (Pseudococcidae), is a true "nomadic herdsman." The entire colony (which can consist of more than 10,000 workers and 5000 pseudococcids) is constantly on the move as old feeding sites are depleted and new ones required (Maschwitz and Hänel 1985).

Ants also tend caterpillars in the butterfly family Lycaenidae (Hinton 1951; Atsatt 1981; Pierce 1987). In this case, nourishment is provided to the ants via specialized glands, and, as in the homopteran case, protection from predation and parasitism is provided by the ants (Malicky 1969; Pierce and Mead 1981; Pierce and Easteal 1986).

GUESTS IN ANT NESTS. Many thousands of arthropod species make their homes and/or earn their livings in the stable environment afforded in or near ant nests, including members of the Acari (Chelicerata), Araeneae, Collembola, Diplopoda, Isopoda (Crustacea), Pseudoscorpionida, and, within the insects, of the orders Blattaria, Coleoptera, Diptera, Homoptera, Hymenoptera,