



Ant Ecology

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Foreword by E.O. Wilson



Box 6.1 'Berry' ants: an eye-popping symbiosis from the rainforest canopy

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Successful transmission to a terminal host is one of the biggest challenges in a parasite's life cycle. Consequently, parasites have evolved a variety of mechanisms to change the behaviour and appearance of intermediate hosts to facilitate their consumption by the subsequent hosts. Several remarkable examples of this phenomenon involve ants as intermediate hosts, including the grass-climbing behaviour of *Formica* spp. infected with the fluke *Dicrocoelium dendriticum*, the yellow colour of cestode-infected *Leptothorax* spp., and the distended gasters of fluke-infected *Camponotus* spp. These and many other examples are summarized in reviews by Schmid-Hempel (1998) and Moore (2002). Evolutionarily, these changes in host appearance or behaviour are often interpreted as extended phenotypes of the parasites (Dawkins 1982; Hughes *et al.* 2008).

Recently, a striking case of ant manipulation by a parasite was uncovered in the rainforest canopies of Panama and Peru. Workers of the arboreal ant *Cephalotes atratus* infected by the nematode *Myrmeconema neotropicum* have red gasters containing several hundred worm eggs (Poinar and Yanoviak 2008; Yanoviak *et al.* 2008b). The life cycle of the nematode is closely linked to the life cycle and temporal polyethism of the ant; peak redness occurs when the ant is spending large amounts of time outside the nest, and coincides with the presence of infective nematode larvae within the eggs. The colour change is not caused by the deposition of red pigments. Rather, it results from localized exoskeletal thinning or leaching of pigments by the developing worms. This dramatic change in appearance is accompanied by continuous gaster-flagging and a substantially weakened postpetiole, characteristics not found in healthy ants. During the latter stages of infection, the parasitized ant becomes sluggish and assumes an erect posture (Plate 4).

In combination, these changes likely facilitate the consumption of ant gasters by frugivorous or omnivorous birds, which presumably mistake

the red gasters for ripe fruit (Yanoviak *et al.* 2008b). Unlike the examples mentioned earlier, ants are the final hosts for this parasite, and birds function as paratenic hosts (i.e. animals that transmit parasites to new hosts without becoming infected themselves; Moore 2002). Unfortunately, direct evidence for bird predation on infected gasters is lacking. However, given what is known of the natural history of *C. atratus* (especially their frequent foraging on bird faeces; reviewed by de Andrade and Baroni-Urbani 1999) and circumstantial evidence from field experiments (Yanoviak *et al.* 2008b), fruit mimicry remains the most parsimonious explanation. Many Neotropical angiosperms have small red fruits available at different times of year, and it is logical that a bird foraging on such fruits would sample any similar red object in its vicinity.

A plausible alternative hypothesis to fruit mimicry is that the red gasters make *C. atratus* workers more conspicuous to predators. Such 'increased conspicuousness' strategies are common among parasites, although few have been studied experimentally (Moore 2002). Increased conspicuousness is not supported in this case for at least two reasons. First, *C. atratus* is already one of the most conspicuous arboreal ant species in Neotropical lowland rainforests. Aside from non-selective foraging by tropidurid lizards, the workers are generally ignored by insectivorous vertebrates (de Andrade and Baroni-Urbani 1999; S. Yanoviak, personal observation). Thus, although infected workers stand out from healthy workers, this difference is unlikely to greatly increase predation on a common but unpalatable ant that is already an easy prey.

Second, the colour red is generally aposematic in insects. To overcome this strong negative signal, infected ants should resemble non-insects, or red gasters should provide a tasty reward. At the peak of infection (Plate 4), parasitized workers are practically immobile. They resemble ants morphologically, but not behaviourally. Given that nematode eggs pass through birds undigested (Yanoviak *et al.*

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Box 6.1 continued

2008), there is no obvious reward (nor penalty, excluding effort) associated with consuming an infected ant. Thus, a fundamental assumption of the increased conspicuousness hypothesis – that an attractive signal is associated with valuable resources – is not supported. Likewise, if there is no negative consequence of gaster consumption (a sting or noxious chemical), this mistake should persist in the bird's behavioural repertoire.

Symbioses between ants and other organisms are common and well documented;

ant–plant and ant–fungal mutualisms support entire research programs, books, and conference symposia. In contrast, ant symbioses with nematodes (Poinar *et al.* 2006) are under-investigated. Such parasitism is frequently overlooked or mistaken as a taxonomic variety, as occurred with red-gastered *C. atratus* over a century ago (Poinar and Yanoviak 2008). 'Berry' ants exemplify the remarkable interconnectedness of species in tropical forests, and hopefully will stimulate additional research on ant–parasite interactions.

dependency in these interactions (Section 6.5), and put this variation in the context of macroevolutionary variation (Section 6.6). Finally, we highlight the utility of these interactions for addressing questions fundamental to the field of ecology (Section 6.7) and conclude (Section 6.8) by identifying promising areas of future research.

6.2 Ants providing protection for food

Trophobiotic interactions involve the consumption of a food reward, often in return for protection from natural enemies. For ant-loving hemipterans, caterpillars, and most plants, these rewards almost invariably involve a sugary and/or nutrient-rich liquid, one that is collected by the foragers that patrol the area surrounding the resource (Plate 3). Highly specialized ant-plants (myrmecophytes) offer additional food rewards and provide ants with a domicile.

6.2.1 Sap-feeding hemipterans

Many ant species engage in mutualisms with herbivorous hemipterans (Stadler and Dixon 2005; Way 1963), and 41% of ant genera include trophobiotic species (Oliver *et al.* 2008). 'Myrmecophily' (ant-loving) occurs within most families of the Sternorrhyncha and Auchenorrhyncha (Hemiptera), including aphids (Aphididae), coccids and scales (Coccoidea), and membracids (Membracidae) (Sta-

adler and Dixon 2005). Within aphids, 40% of species are ant-tended, and many aphid genera include both tended and untended species (e.g. Mooney *et al.* 2008). These hemipterans tap into host plant phloem sap, which is rich in carbohydrates but relatively poor in nutrients and amino acids. As a consequence, sap-feeding hemipterans must dispose of large quantities of processed, but nonetheless sugar-rich, fluid. Many ants collect this sugary liquid waste, commonly referred to as honeydew. Ant attendance often results in larger hemipteran colonies (Way 1963) and greater fecundity (Bristow 1983; Del-Claro and Oliveira 2000). Ants that otherwise prey upon arthropods do not attack the sap-feeding herbivores, or at least do so more rarely. However, the incentives to view some proportion of an aphid colony as prospective prey rather than mutualistic partners may increase as honeydew-supplied carbohydrates become less limiting with colony growth (Cushman 1991; see Figure 6.1). In addition to this occasional predation, hemipterans may also bear yet unrevealed ecological or physiological costs from their mutualisms with ants. For example, in the absence of predators, ants can reduce aphid reproduction (Stadler and Dixon 1998, Yao *et al.* 2000).

The mechanism of ant benefits to tended hemipterans is most often presumed to occur via protection from natural enemies (Buckley and Gullan 1991; Stadler and Dixon 2005; Way 1963). Ants provide protection against enemies that are frequently