OXFORD BIOLOGY

Ant Ecology

Edited by Lori Lach | Catherine L. Parr | Kirsti L. Abbott

Foreword by E.O. Wilson

Box 12.2 The directed aerial descent of arboreal ants

Stephen P. Yanoviak

The evolution of winged flight in insects is unresolved due to a lack of fossil intermediate forms, but was likely preceded by directed aerial descent (i.e. gliding) in an arboreal setting (Dudley *et al.* 2007). Whereas a variety of vertebrates exhibit aerial gliding, the behaviour was unknown in wingless arthropods until it was recently documented in arboreal ants (Yanoviak *et al.* 2005, 2008a). Given that ants are a derived group among insects and are secondarily wingless, their gliding behaviour, while interesting and unexpected, is not directly relevant to the origins of winged flight in insects. However, their abundance in tropical forest canopies, their large variation in body size and morphology, and recent improvements to their phylogenetic resolution make ants an excellent focal group for investigating the selective pressures and aerodynamic mechanisms associated with this remarkable behaviour.

Arboreal ants forage in a relatively exposed physical setting. They may be accidentally dislodged from trees (e.g. Haemig 1997), or may voluntarily drop from branches when provoked (Yanoviak and Dudley 2006; Yanoviak *et al.* 2008a). In preliminary studies in Peru, worker ants composed 66% of wingless arthropods collected in ten passive funnel traps suspended in the forest canopy (Yanoviak, unpublished data). Thus, significant numbers of workers fall as 'ant rain' in tropical forests.

Lost workers are costly to ant colonies, and landing in the unfamiliar understory may have grave consequences for arboreal ants. Seasonally flooded forests are common in the tropics and present the most extreme circumstances — fallen insects are immediately consumed by surface-feeding fish. But even dry understory litter may pose a significant hazard. For example, up to 100% of arboreal ants released in the litter were attacked, and up to 40% were killed by the resident litter fauna in preliminary trials conducted in Peruvian terra firme forest (Yanoviak, unpublished data). Thus, the likelihood of a fallen arboreal ant returning to its point of origin after landing in the understory is presumably low, and gliding reduces this loss (Yanoviak *et al.* 2005).

Most research on gliding ants to date has focused on the myrmicine genus *Cephalotes*, especially the common Neotropical species *C. atratus* (Figure 12.2.1). However, at least six other ant genera include gliding species: *Camponotus*, *Cataulacus*, *Daceton*, *Nesomyrmex*, *Procryptocerus*, and *Pseudomyrmex*. Glide performance is generally size-dependent within and among species (Yanoviak *et al.* 2005, 2008a). Specifically, smaller workers within colonies, and smaller species within genera, tend to have larger glide indices (glide index = the horizontal distance travelled per unit vertical drop distance). The consistency of these size-

a b

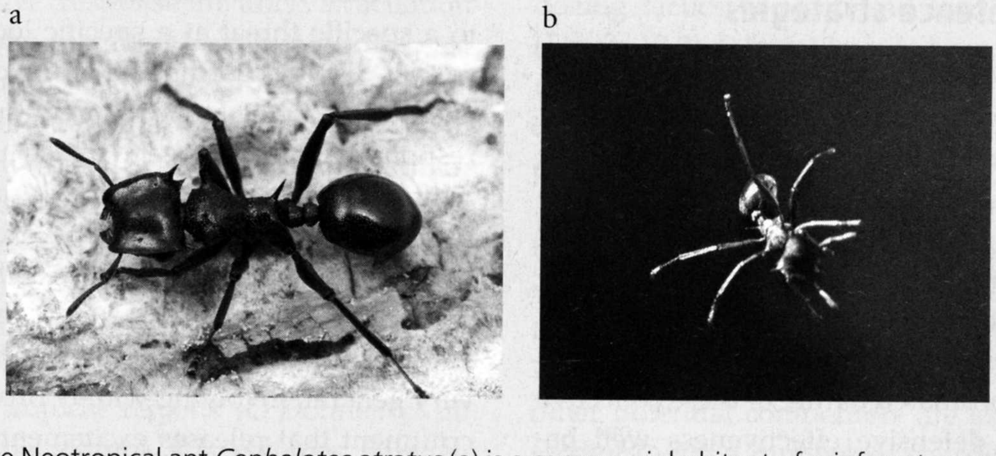

Figure 12.1.2 The Neotropical ant *Cephalotes atratus* (a) is a common inhabitant of rainforest canopies across South America. If a worker of this species is dislodged from the tree trunk it is able to (b) direct its aerial descent back to the tree trunk. (Photos: Alex Wild)

Box 12.2 continued

based patterns largely results from basic physics (i.e. smaller ants reach terminal velocity earlier in a fall). In contrast, mechanisms of aerodynamic stability and glide control are predominately behavioural and differ markedly among taxa. For example, *Camponotus* workers glide toward tree trunks head-first, whereas *Cephalotes* and *Cataulacus* glide abdomen-first (Yanoviak *et al*. 2005, 2008a). The aerodynamic relevance of different appendages during a fall also differs among taxa. Experiments with *C. atratus* suggest that the hind legs are necessary for aerodynamic stability in a fall, whereas field observations indicate that the forelimbs may serve this function in some *Camponotus* (Dudley and Yanoviak, unpubl. data).

Given that not all arboreal ants glide, and not all ants glide in the same manner, what traits can be associated with this behaviour? Gliding taxa share four characteristics: (*a*) costly workers (relatively small colony size and large per-worker investment); (*b*) arboreal nesting (ground-nesting arboreal ants like *Atta* and *Paraponera* do not glide); (*c*) good vision; and (*d*) diurnal activity (Yanoviak *et al*. 2005). The latter two characteristics are necessary for targeting during a fall. No nocturnal ants are known to glide, and falling *C. atratus* depend on visual cues to orient to light-coloured objects (e.g. lichen-covered tree trunks; Yanoviak and Dudley 2006). All available evidence indicates that gliding has multiple independent origins in ants. Comparative phylogenetic analyses and more information regarding the ecology, natural history, and morphology of arboreal ants will clarify the selection pressures associated with the behaviour.

In sum, ants provide an excellent model for studying gliding in small, wingless arthropods because they are abundant and experimentally tractable. However, ongoing research shows that gliding is not limited to ants — indeed, directed aerial descent is widespread among arboreal arthropods, some of which may support hypothesized terrestrial origins of insect flight (Dudley *et al*. 2007). Uncovering the mechanisms and constraints associated with the behaviour in ants will facilitate research on less common taxa that are relevant to understanding the evolution of winged flight in insects.

directed descent, returning them to their home tree or nearby vegetation with great reliability (Yanoviak *et al*. 2005; Box 12.2).

12.6 Group defence strategies

While individual defences may improve the survival and resource acquisition of individual ants, they must be put in the broader context of the defensive strategies of the colony as a whole. These group defences, while benefiting from individual defences, can be defined as those that require coordination of more than one individual for success, often at the cost of some of the individuals involved. The coordinated nature of these collective actions achieves defensive effectiveness well beyond the sum of the capabilities of the participating individuals.

12.6.1 Coordinated group defence at the nest

Coordinated group defences are defined here as strategies that use recruitment (pheromonal, tactile, or acoustic) to mobilize a mass defensive response to a specific threat at a specific location. Most ant species display coordinated group defence when an enemy is detected at the nest, but the strength of the response and the degree to which a colony relies on fight or flight depends on the species, life stage of the colony, and the enemy. The universal self-sacrificing behaviour of ant workers is the key in coordinated fight responses because it can increase their overall potency. In many taxa, a fight response is very general, involving widely broadcast alarm recruitment that releases excitement and aggression (Hölldobler and Wilson 1990). However, these responses can be more sophisticated, involving