

Box 10.1 Ants in the intertidal zone: colony and behavioural adaptations for survival Simon Robson

The nests of *Polyrhachis sokolova* are restricted to the mangrove mud of northern Australia and nearby tropical countries, where colonies survive despite seemingly inhospitable conditions (Kohout 1988; Nielsen 1997). The intertidal zone of mangroves, situated at the interface between land and ocean, constantly changes with the tidal cycle. Nests are frequently covered by incoming tides, can remain submerged for up to 3.5 h during a normal tidal cycle (Nielsen 1997) and during extreme spring tides can be covered by as much as two metres of water (Shuetrim 2001). Foraging areas can therefore rapidly change from sand and mud to pools of hot salty water, and the nests themselves face a constant risk of invasion via the burrowing activity of numerous mangrove organisms such as crabs and mudskippers.

Ongoing studies are revealing how *P. sokolova* manage to survive these conditions, but a great deal remains unknown. The nests appear to be of a typical structure for subterranean ants, based on a series of chambers and inter-connecting tunnels. There are no obvious structural modifications that might reflect their intertidal location. The nest entrance collapses when the tide comes in and possibly forms a fairly water tight plug against further flooding, though the lower nest chambers become inundated with the rising water table. The colony itself is thought to survive submersion by individuals collecting in those chambers that continue to hold pockets of air (Nielsen 1997). Carbon dioxide levels become elevated during tidal submersion and reach some of the highest levels known for ant colonies. The processes enabling ants to survive these high CO₂ concentrations (up to 11%) must be impressive, but the actual physiological mechanisms involved remain unknown (Nielsen *et al.* 2003). Colonies can be polydomous and may consist of up to four nests, but there appears to be no relationship between the degree of polydomy and ecological factors such as the frequency with which individual nests are inundated (Shuetrim 2001).

Perhaps the most obvious and novel response to these inhospitable conditions is the ability of ants to swim. Individual foragers encountering a body of water simply stretch themselves out on the surface of the water and swim across (Kohout 1988; Nielsen 1997). Recent high-speed digital imaging and ultrastructural studies reveal that swimming is achieved through behavioural rather than morphological modifications. Individuals do not possess the elongated hairs and appendages or flattened smooth bodies often found in swimming arthropods (*P. sokolova* looks like a typical ant!), but they do display a modified gait when swimming: they do not simply continue 'walking' when they reach the water. Power when swimming is provided by the first two pairs of legs, which break the water surface and move in a rhythm similar to that used when walking. Movement of the hind legs, however, is suppressed. These legs are extended straight out across the surface of the water where they appear to maintain surface tension, prevent the ant from sinking, and may even act as a rudder (Fig. 10.1.1). Individuals do not swim in random directions, but are capable of changing course while swimming if need be, and can successfully navigate back to their colonies even when forced to both walk and swim (Raj 2007).



Figure 10.1.1. A *Polyrhachis sokolova* worker swimming across the surface of the water. (Photo: Ajay Narendra)

Active swimming is an extremely unusual behaviour for ants. Their relatively small size and the physical dynamics of the air—water

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Box 10.1 continued

interface mean that individuals falling into water typically stick to the surface or eventually sink, but a few species have derived novel solutions. Colonies of some species that become inundated with flooding (such as *Wasmannia auropunctata* and *Solenopsis invicta*) are able to form large rafts of interlocked individuals that float away until dry land is

reached, and an unusual species of *Camponotus* is able to not only enter and walk through the liquid within a pitcher plant to forage for dead insects, but is able to extricate itself and its prey as well (Clarke and Kitching 1995). But as far as we are aware, *P. sokolova* is the only ant species that has successfully bridged the land—water interface.

permanent adaptations, for example in *Formica* wood ants (Seifert 2007). Polydomy can be favoured as a feature increasing the number of solaria, as in *Myrmica sulcinodis* (Pedersen and Boomsma 1999). In cold winters, thermoregulation and desiccation prevention are critical to reduce losses of colony members (Heinze and Hölldobler 1994). Probably as a strategy to avoid losses due to desiccation, and triggered by a decline in temperature in autumn, several monogynous colonies can aggregate into a larger polygynous one for winter, with subsequent fragmentation in spring, as in *Leptothorax acervorum* (Seifert 2007 and references therein). Habitat temperature probably also influences queen number (Elmes and Petal 1990), the investment in reproductives of either sex (sex allocation) and caste determination (through effects on larval growth rates), though these effects await quantification (Liautard *et al.* 2003).

10.3.6 Pathogen and parasite load

As ubiquitous and eternal plagues of ant colonies, pathogens and parasites (henceforth just ‘pathogens’) influence colony structure under ecological time scales and likely influenced its evolution. Interest in ecological immunology of social insects has increased in recent years (Cremer *et al.* 2007).

For species that are at a high risk of infection, colony spatiality is expected to evolve to yield polydomy and gallery systems, both of which adaptations decrease pathogen transmission (Cremer *et al.* 2007; Schmid-Hempel 1998). Leaf-cutting ants provide two examples. Founding queens use platforms to cultivate their incipient fungus gardens, reducing infec-

tion of the fungus by soil-borne diseases (Fernández-Marín *et al.* 2007), and parasitic fungi are deposited far from the fungus garden in waste dumps (Hart and Ratnieks 2001). Pathogen load also influences worker task allocation. Once a leaf-cutting worker begins work at the waste dump, she remains there and is thus confined to the task of garbage worker (Hart and Ratnieks 2001). The previous example might suggest that pathogen load also accelerates the evolution of worker polymorphism. However, Schmid-Hempel (1998) tentatively suggests the reverse – namely, that polymorphism imposes a cost that opens species to increased numbers of parasite species, perhaps by providing an increased number of niches within the colony for the parasites.

Pathogens also are of interest when we consider factors that shape mating frequency. Multiple mating provides more opportunities for a founding queen to contract infection (Cremer *et al.* 2007). On the other hand, herd immunity, the higher resistance of genetically variable groups compared to less variable ones (Serfling 1952), should be increased by queen multiple mating, so that selection by disease is also plausible as a selective force in favour of polyandry. These competing hypotheses await further testing.

10.3.7 Cooperation and conflict in the colony

Cooperation within the colony is the undisputed foundation of the ecological success of eusocial insects (Bourke and Franks 1995; Crozier and Pamilo 1996; Hölldobler and Wilson 1990). However, there is another reason why this topic deserves special