

# Extended Phenotype: Nematodes Turn Ants into Bird-Dispersed Fruits

A recent study has discovered a novel extended phenotype of a nematode which alters its ant host to resemble ripe fruit. The infected ants are in turn eaten by frugivorous birds that disperse the nematode's eggs.

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In the rainforest canopy of Central and South America an exceptional ant has become even more intriguing following the discovery of its novel interaction with a parasite. Previously, the giant turtle ant *Cephalotes atratus*, which nests in tree trunks and large branches, was literally flung into the spot-light when researchers found that, when dropped from the canopy, the ants can glide and return to their own tree and thereby avoid getting lost on the forest floor far below [1]. The same group of researchers now report that a nematode parasite occupying the ant's gaster (the ant-specific term for the terminal part of the abdomen) causes it to shift from its normally matt black appearance to resemble a ripe, red fruit (Figure 1) [2,3]. This colour morph is so striking that it initially received taxonomic recognition when Emery described it as a variety in 1894. However, the true story of fruit mimicry has now turned out to be a compelling example of the extended phenotype, a concept introduced by Dawkins [4] to conceptualise the phenotype beyond the organism's own body — in this case, parasite genes having their phenotypic effect on the ant's body.

The story begins when ant larvae become orally infected by juvenile nematodes contained in bird faeces that are fed to them by foraging ants, and it ends with nematode eggs being eaten by duped frugivorous birds that deposit nematode laden faeces close to new ant colonies where the cycle repeats. Nematodes mate in the gaster of callow workers — those that have just emerged from the pupal stage. Males die and the female nematodes produce yellow eggs which mature over time. At the same time the cuticle of the ant thins to become amber rather than the usual matt black and the combined effect is a red, fruit-like gaster that is particularly splendid in the sunshine of the high canopy (Figure 1).

So as to leave little to chance, the parasite alters ant behaviour to increase the likelihood that birds will ingest the eggs. Unlike uninfected individuals, parasitized worker ants show nearly constant gaster-flagging, a behaviour where the gaster is held up when walking (Figure 1). Infected ants are also less aggressive: they do not bite or produce alarm pheromones when disturbed. These behavioural changes are positively associated with the degree of redness: that is, the effect is greatest in ants containing more transmissible stages of the parasite. Such a correlation between the degree of manipulation and parasite development occurs in other host-parasite systems: in malaria for example, humans with infective stages (gametocytes) are more attractive to the mosquito vector, and conversely mosquitoes containing transmissible stages (sporozites) bite more people [5–7].

The manipulation of the hapless ant does not end there, however. By now, the ants are moving around the canopy holding their gaster, packed with nematode eggs, into the air for passing birds. However, as this ant is heavily armoured with a thick cuticle (not for nothing has it been christened the giant turtle ant) and has formidable spines along its head and thorax (Figure 1), then the meal is likely to be an unpleasant one for a bird more used

to tender fruit. Remarkably, however, the parasites have weakened the joint between the ant's gaster and thorax. The gaster when pulled detaches before the ant is dislodged from the tree trunk. In fact, it can be removed with 14-times less force than that required to remove the gaster of an uninfected ant: it seems that picking this 'fruit' is easy.

The demonstration of fruit mimicry by a parasite has a strong wow factor. It certainly is among the more impressive examples of host manipulation by parasites (reviewed in [8]), a field already replete with weird and wonderful adaptations such as parasitoid wasps causing their spider hosts to spin post-mortem cocoons for developing wasp pupae [9], or nightly legions of suicidal crickets that jump, lemming-like, into water so their hairworm parasites can find a partner [10]. But what can fruit mimicry add to our conceptual understanding of the evolutionary biology of parasite manipulation of hosts and the wider topic of extended phenotypes?

The study of parasite manipulation of host behaviour is undergoing a renaissance following the publication in 2005 of a special issue of the journal *Behavioural Processes* (volume 68, issue 3) in which 31 scientists engaged in such research appraised the state of the field. This self-examination was prompted by the need to look beyond descriptions of manipulated behaviours to more integrated studies that would examine the proximate mechanisms and ecological significance of manipulation [11]. The wider topic of the extended phenotype is also coming under re-examination. Originally the concept referred only to the expression of genes beyond the body of the organism containing

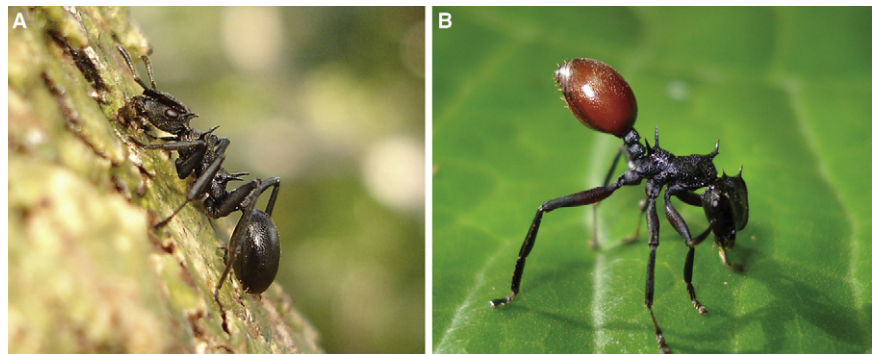


Figure 1. An uninfected (left) and infected turtle ant. Note the spines on both ants and the aloft red gaster of the latter. (Photos: Stephen Yanoviak.)

those genes [4] and three types were considered: animal architecture, parasite manipulation of host behaviour and action at a distance. More recently, the concept has been expanded upon by niche constructionists [12] and community geneticists [13], which has led to some controversy [14–17]. What novel insight can this story of forbidden fruit in a rainforest canopy contribute?

It adds greatly to empirical investigations of the proximate mechanisms by which parasites gain control of their host's body. The authors [3] provide evidence that targeted neuronal atrophy (ventral nerve cord) and structural changes in the cuticle are mechanisms by which the parasite gains a gaster-bobbing, red-berry vehicle. Because the ants are very abundant, often with several thousand individuals per colony, easy to keep in the laboratory (D.P.H., personal observation) and, best of all, the infective stage of the parasite can be easily collected by feeding chickens with infected gasters, this ant–nematode interaction has the potential to become an attractive model system. Also, since another manipulating parasite, the fungus *Cordyceps*, causes this same ant to descend to the understory and bite onto the bark of trees before it dies [18], the scene is set to examine how two parasites with widely diverging manipulator strategies can control the same host.

When considering the evolutionary biology of the extended phenotype there are potentially rich pickings from this system. The authors suggest that the habit of being eaten by a frugivorous bird that defecates on tree trunks patrolled by other colonies serves to disperse nematodes between patchily distributed hosts. That is, by manipulating the phenotype of one host (from black to red) a nematode gains the use of another organism's phenotype (bird wings) to achieve dispersal. Such a vehicle-centred view [4,19] is useful because it allows us to ask if evolutionary constraints imposed by an organism's bauplan on regular phenotype evolution also apply to extended phenotypes, since the nematode has sidestepped the constraints that exist for the evolution of flight in nematodes by taking advantage of bird wings. Also, it seems worth asking whether the expressed extended phenotype can be optimal for

both the male and female genes. As multiple males co-exist with multiple females in a single gaster (Steve Yanoviak, personal communication) is there conflict among, or between, the sexes over the timing of manipulation? Or do the aligned interests of having, literally, all the eggs in one (fruit) basket mean conflict is absent? Clearly this system has great potential for obtaining answers to such questions. Coming as it does at a time of some controversy over the original formulation of extended phenotype principles, this fruit-mimicking nematode does underline that some extended phenotypes can hardly be considered to be anything else than that.

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DOI: 10.1016/j.cub.2008.02.001

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## Multimodal Integration: Visual Cues Help Odor-Seeking Fruit Flies

Olfactory stimuli are uniquely devoid of directional information, so that multimodal cues are typically required for their localization. A clever new experimental paradigm with flying *Drosophila* has shown that accurate heading into an odor plume requires panoramic visual cues.

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Olfaction is an unusual sensory modality. The vast number of olfactory receptors enables perception of a staggering complexity of qualitatively distinct stimuli [1]. Even more unusual compared to other sensory modalities is the paucity of spatial information in the perceived

olfactory signal. Spatial information about the source of a stimulus is present at the receptor surface for most sensory systems, such as vision, electroreception, taste and touch, or can be quickly computed for systems that are not organized somatotopically, such as audition. Spatial orientation to odors in a mobile medium, however, typically requires integration of