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Behavioral mechanisms and morphological symptoms of zombie ants dying from fungal infection

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Abstract

Background: Parasites that manipulate host behavior can provide prominent examples of extended phenotypes: parasite genomes controlling host behavior. Here we focus on one of the most dramatic examples of behavioral manipulation, the death grip of ants infected by *Ophiocordyceps* fungi. We studied the interaction between *O. unilateralis s.l.* and its host ant *Camponotus leonardi* in a Thai rainforest, where infected ants descend from their canopy nests down to understory vegetation to bite into abaxial leaf veins before dying. Host mortality is concentrated in patches (graveyards) where ants die on sapling leaves *ca.* 25 cm above the soil surface where conditions for parasite development are optimal. Here we address whether the sequence of ant behaviors leading to the final death grip can also be interpreted as parasite adaptations and describe some of the morphological changes inside the heads of infected workers that mediate the expression of the death grip phenotype.

Results: We found that infected ants behave as zombies and display predictable stereotypical behaviors of random rather than directional walking, and of repeated convulsions that make them fall down and thus precludes returning to the canopy. Transitions from erratic wandering to death grips on a leaf vein were abrupt and synchronized around solar noon. We show that the mandibles of ants penetrate deeply into vein tissue and that this is accompanied by extensive atrophy of the mandibular muscles. This lock-jaw means the ant will remain attached to the leaf after death. We further present histological data to show that a high density of single celled stages of the parasite within the head capsule of dying ants are likely to be responsible for this muscular atrophy.

Conclusions: Extended phenotypes in ants induced by fungal infections are a complex example of behavioral manipulation requiring coordinated changes of host behavior and morphology. Future work should address the genetic basis of such extended phenotypes.

Keywords: extended phenotype behavioral manipulation, ants, fungi, convergent evolution, parasites

Background

Some parasites can adaptively take over and completely control the behavior of their hosts leading to positive fitness returns for parasite genes [1-4]. Host behavior is an extended phenotype of the parasite [5]. The degree of behavioral manipulation varies greatly across parasites from very slight alterations of pre-existing behaviors [6] to the expression of wholly novel behaviors that are never seen in healthy hosts [7]. Extended phenotypes have gained considerable prominence in community- [8], evolutionary- [9] and behavioral ecology [10].

Early studies of extended phenotypes focused on detailing behavioral changes and inferring whether they represent adaptations for parasites or should rather be interpreted as adaptive defense mechanisms of the host or as by-products of infection [11-13]. Recently, more integrative approaches have emerged which includes a greater focus on the mechanisms by which behavioral changes occur. An important component is a fuller understanding of the biology of particular study systems and the timing

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