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Commentary

Parasitic manipulation: a theoretical framework may help

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The study of parasitic manipulation is an endless source of fascinating biological stories (Moore, 2002). After reviewing some of the most documented examples, Thomas et al. (2005) discuss the state of the field and define new perspectives of research. A large part of this review is devoted to the mechanistic processes allowing a parasite to manipulate its host behaviour. *How* do parasites manipulate? Answering this question clearly requires a closer look at the intimate relationship between the parasite and its host, and new methods like proteomics may help to get new insights. But Thomas et al. (2005) are also interested in the evolutionary processes leading to parasitic manipulation. *Why* do parasites manipulate? In the most publicised examples of parasitic manipulation, the answer to this question seems obvious. For example, ants (intermediate host) infected with *Dicrocoelium dendriticum* ascend blades of grass to facilitate transmission towards sheep (definitive host). In this case, there is clearly a conflict of interest between the host and the parasite (transmission kills the intermediate host) and manipulation makes perfect sense for the parasite. Actually, it is not that simple. The parasite that manipulates the behaviour of the host dies without leaving descendants in the definitive hosts and one needs to invoke kin selection (related parasites infecting the same ant may benefit from the manipulation) to explain this behaviour (Wilson, 1977; Sober and Wilson, 1998). Thomas et al. (2005) did not discuss in great length the *D. dentriticum* example but they did raise the point that in many situations the evolutionary understanding of parasitic manipulation is complex. I believe that in most of these cases, insights could be gained from some theory. Indeed, the explicit formalisation of parasite and host life cycles would yield expressions for their respective fitness, which could then be used to evaluate the adaptive nature of specific strategies.

In the *D. dentriticum* example discussed above, the explicit description of the parasite's life cycle may help to construct a kin selection model and ultimately to understand when parasitic manipulation is adaptive (Wilson, 1977; Sober and Wilson, 1998). Modelling parasite life cycle may also be useful whenever parasites exploit different types of hosts (the rule rather than the exception in parasitic manipulation) and where some hosts may be less suitable than others (Gandon, 2004). An extreme situation occurs when predators which are not suitable definitive hosts feed on manipulated intermediate hosts (Mouritsen and Poulin, 2003). Here, as pointed out by Thomas et al. (2005), the host–parasite interaction has to be placed in its full

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ecological context to reveal the effect of the quality and the quantity of different hosts on parasite evolution. Another problematic situation emerges when parasite transmission occurs both horizontally and vertically (e.g. virus particles that modify the superparasitism behaviour of *Leptopilina boulardi*, Varaldi et al., 2003). In these cases, because of vertical transmission, both the host and the parasite may benefit from host reproduction. Thus, host manipulation that enhances horizontal transmission may not always be beneficial for the parasite (Varaldi et al., 2003; Reynolds and Hardy, 2004). In such situations, a theoretical approach may help take into account the complexity emerging from parasite life cycles (Choisy et al., 2003; Parker et al., 2003; Gandon, 2004).

A theoretical approach could also help understand host evolution. For example, Thomas et al. (2005) suggest that the host may gain from being manipulated if parasites adopt a mafia-like behaviour (i.e. the parasite retaliates if the host resists). A life-history model including the different stages of the host's life cycle could be used to explore under which conditions the hosts should try to resist the manipulation or, on the contrary, cooperate with the parasite. Such a model could also be used to investigate the evolutionary consequences of parasitism for uninfected hosts. Indeed, one may expect that uninfected hosts may evolve different life-history strategies in infected and uninfected populations. For example, it has been shown that parasitism may select for earlier reproductive maturity (Lafferty, 1993). One may thus expect similar life-history and/or behavioural shifts in hosts that have a risk of being infected by parasites affecting their behaviour.

In summary, the understanding of parasitic manipulation could benefit from being placed in the theoretical framework used to study more classical traits in host–parasite interactions (after all parasitic manipulation is only one component of parasite virulence). This theoretical approach could be used to analyse the dynamics of these complex systems but also to better understand the evolution of both the parasite and its host.

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