# Evolution and phylogeny of behavioural manipulation of insect hosts by parasites

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## SUMMARY

The literature contains many examples of changes induced by parasites in the behaviour and/or other phenotypic traits of insects. From an evolutionary perspective, the nature of these changes is usually difficult to assess. Parasite-induced changes in host behaviour can be adaptations of either host or parasite, or they can be mere pathological consequences of infection. Of the many criteria and experimental tests necessary to distinguish between adaptations and non-selected consequences, two are particularly important: the demonstration of fitness benefits for either host or parasite associated with the behavioural change, and the elucidation of the proximate mechanism responsible for the behavioural change. Another approach can serve to identify adaptive changes in behaviour: mapping specific behavioural alterations on a phylogeny of either hosts or parasites. The usefulness of this approach is illustrated with two examples, acantho-cephalan–cockroach associations and insect–fungus associations. The adaptive nature of parasite-induced behavioural changes will always be difficult to evaluate because they are the product of two distinct but interacting genotypes. However, experimental and phylogenetic approaches can provide valuable insights into the evolutionary history of insect–parasite interactions.

Key words: adaptation, constraints, behavioural modification, entomogenous fungi, fitness benefits.

## INTRODUCTION

Parasites of all kinds induce various alterations in the physiology and behaviour of their hosts. This is an unavoidable consequence of the exploitation of host tissues and resources by the parasite, and of the defensive actions taken by the host in response. The literature now contains numerous examples of insect hosts displaying altered morphology (Wülker, 1964), physiology (Hurd, 1990; Beckage, 1993), or behaviour (Horton & Moore, 1993) following infection by parasites. There are many explanations for parasite-induced changes in behaviour. They range from simple pathology, in which altered behaviour is a non-adaptive, proximate side-effect of infection, to adaptation of the host or parasite, where the behavioural changes are the ultimate product of selection. By far the most attractive explanation, and not surprisingly the most popular one, is that changes in host behaviour are the result of direct manipulation by the parasite. For example, the parasite could alter the behaviour of its insect intermediate host to facilitate its transmission to its definitive host. Alternatively, the parasite could alter the behaviour of its insect host to increase its chances of reaching an appropriate microhabitat for further development, or to facilitate the dispersal of its propagules. Such scenarios have been proposed as clear illustrations of the extended phenotype concept, in which genes in one organism have phenotypic effects on another organism (Dawkins, 1982); they will also be the focus of this review.

The widespread use of the 'adaptive manipulation' label for parasite-induced changes in host behaviour has been criticized on several grounds (Moore & Gotelli, 1990; Poulin, 1995). For instance, fitness benefits for the parasites are rarely quantified even though demonstrating these benefits is a prerequisite for the behavioural alteration to be adaptive. From a theoretical perspective, we may expect host manipulation by parasites to be restricted to certain host–parasite systems only. Manipulation should only evolve if the increase in transmission success or survival it provides outweighs the costs of manipulation, if any. These costs can include the production of secretions to alter host behaviour; any energy invested in producing these secretions is unavailable for other parasite functions such as growth. Some key ecological parameters, such as parasite abundance and prevalence, or the basic transmission rate of non-manipulative parasites, can determine whether host manipulation by parasites will be favoured by natural selection (Poulin, 1994). We therefore need to be cautious when interpreting observed changes in host behaviour induced by parasites.

The goal of this review is to situate parasite-induced alterations in insect behaviour within an evolutionary context. Here I use the word parasite in its broadest sense, encompassing pathogens and parasitoids as well as 'true' parasites. First, I will present a brief overview of the extent of host behavioural changes across the range of insect-parasite systems. I will then discuss the distinction

between side-effects and adaptations, and some of the problems associated with this difficult task. Finally, I will address the importance of looking at the phylogeny of host behavioural alterations to understand the evolution of manipulation, and illustrate this with selected case studies. Little is known about the evolutionary history of parasite-induced changes in host behaviour. This review is therefore not meant to be a thorough synopsis of the literature, but rather an overview of some of the challenges currently facing students of insect–parasite interactions.

## DIVERSITY OF INSECT–PARASITE INTERACTIONS

Insects form the most diverse group of living organisms on the planet, and have repeatedly been colonized by parasites during their evolutionary history. Many taxa of parasites are known to induce behavioural changes in their insect hosts; a representative, but not exhaustive, list of examples reported in the literature is given in Table 1. In this article I focus on eukaryotic parasites, although other parasites not covered here can also alter the behaviour of insects (e.g. viruses: Whitlock, 1974; Crawford & Kalmakoff, 1977). Behavioural alterations caused by parasites have been reported in only a small fraction of known insect taxa. This no doubt reflects more the uneven research effort among insect taxa than any true biological differences. More information is available for pest species, or insect species that affect human health such as disease vectors, than for other species (see Molyneux & Jefferies, 1986; Horton & Moore, 1993; Moore, 1993).

Typically, changes in the behaviour of parasitized insects first occur some time after infection, following a period of parasite development inside the host, and persist until the death of either the host or the parasite, or sometimes both. In some instances, parasites appear capable of manipulating host behaviour at a distance prior to infection (Evans *et al.* 1992; Pappas *et al.* 1995). In other cases, the parasite may keep exerting some influence on host behaviour after leaving the host (Brodeur & Vet, 1994).

The types of host behaviours influenced by parasite infection are varied. They include alterations in normal foraging, anti-predator, aggregation or reproductive behaviours. Two of the most commonly reported changes in insect behaviour, changes (usually reductions) in activity levels and changes in the preferred microhabitats, are highlighted in Table 1. A reduction in host activity is perhaps the most obvious behavioural change one would expect as a side-effect of pathology; its effect on parasite fitness may be merely coincidental. Changes in host microhabitat preferences, on the other hand, can be tested against *a priori* predictions based on a knowledge of

the parasite's life cycle, and they make easier the distinction between adaptation and side-effect. These two common types of alterations will be discussed in the next sections, because of their relevance to the issue of adaptiveness.

## AND THE WINNER IS...

In host–parasite interactions, there is no good reason to expect either antagonist to consistently benefit from changes in host behaviour and not the other: either one can be the winner in the struggle for control of host behaviour. Adaptive behavioural changes that help the host to eliminate the parasite or compensate for its effects are just as likely to evolve as adaptive changes in host behaviour that help the parasite to complete its life cycle. The problem is therefore not only one of determining whether the change in behaviour is an adaptation or not, but also of finding out whose adaptation it is.

Strict criteria and critical experimental tests are needed to distinguish between adaptations of hosts, adaptations of parasites, and mere pathological side-effects (Poulin, 1995). In particular there are two essential issues that must be addressed. First, fitness benefits for either host or parasite, derived from the change in host behaviour, must be demonstrated for that change to be an adaptation. The possibility exists that both host and parasite benefit from the change in host behaviour, which does not mean that it is a shared adaptation as it may be produced by only one of the two genotypes involved.

The second important question concerns the causal mechanism behind the change in host behaviour. In the absence of information on fitness benefits, showing that the behavioural change is caused, for instance, by a chemical secreted by the parasite would be a strong indication that the alteration of host behaviour is the product of an adaptation of the parasite. Indeed, many parasites interfere with the chemistry of their hosts, and the proximate cause of behavioural changes in parasitized insects often has a chemical basis (Hurd, 1990; Beckage, 1985, 1993). The mechanism needs not have a chemical basis, however: any specific action of the parasite having no function other than to alter host behaviour can suggest that the behavioural change is adaptive for the parasite. For most documented cases of behavioural changes in parasitized hosts, however, there is no information available on either who benefits or exactly what causes the changes. In these cases, interpreting host behavioural changes is problematic. Even sometimes when information is available the picture remains unclear. For instance, a switch in plant food preference by caterpillars harbouring larval tachinid fly parasitoids appears beneficial for both host and parasite following careful field experiments (Karban & English-Loeb, 1997). There is yet no simple

Table 1. *Some insect-parasite associations in which parasite-induced changes in insect behaviour have been observed*

| Parasite | Host | Change in microhabitat | Change in activity | Other changes | Source |
|---|---|---|---|---|---|
| **Protozoa** | | | | | |
| *Plasmodium yoelli* | Mosquito | – | Yes | – | Rowland & Boersma, 1988 |
| *P. cynomolgi* | Mosquito | – | Yes | – | Schiefer *et al.* 1977 |
| *P. gallinaceum* | Mosquito | – | – | Yes | Rossignol *et al.* 1984 |
| *Trypanosoma* sp. | Tsetse fly | – | – | Yes | Jenni *et al.* 1980 |
| *Leishmania mexicana* | Sand fly | – | – | Yes | Killick-Kendrick *et al.* 1977 |
| *L. major* | Sand fly | – | – | Yes | Beach *et al.* 1985 |
| *Nosema* sp. | Grasshopper | Yes | – | – | Boorstein & Ewald, 1987 |
| Gregarines | Cricket | – | – | Yes | Simmons, 1994 |
| **Fungi** | | | | | |
| *Alternaria tennis* | Ant | Yes | – | – | Marikovsky, 1962 |
| *Metarrhizium* sp. | Beetle | Yes | – | – | Nirula, 1957 |
| *Entomophthora* sp. | Moth | Yes | – | – | Yen, 1962 |
| *Entomophthora* sp. | Locust | Yes | – | – | Roffey, 1968 |
| *Entomophthora* sp. | Aphid | Yes | – | – | Harper, 1958 |
| *Entomophthora* sp. | Fly | – | – | Yes | Eilenberg, 1987 |
| *Entomophthora* sp. | Fly | – | – | Yes | Møller, 1993 |
| *Entomophthora* sp. | Fly | Yes | – | – | MacLeod *et al.* 1973 |
| *Entomophthora* sp. | Fly | Yes | – | – | Maitland, 1994 |
| *Empusa muscae* | Fly | Yes | – | – | Miller & McClanahan, 1959 |
| **Platyhelminthes** | | | | | |
| *Plagiorchis noblei* | Mosquito | Yes | Yes | – | Webber *et al.* 1987 |
| *Dicrocoelium* sp. | Ant | Yes | – | – | Carney, 1969 |
| *Dicrocoelium* spp. | Ant | Yes | – | – | Romig *et al.* 1980 |
| *Raillietina cesticillus* | Beetle | Yes | – | – | Graham, 1966 |
| *Hymenolepis diminuta* | Beetle | Yes | – | Yes | Hurd & Fogo, 1991 |
| *H. diminuta* | Beetle | Yes | Yes | Yes | Yan *et al.* 1994 |
| *H. diminuta* | Beetle | – | Yes | – | Robb & Reid, 1996 |
| **Acanthocephala** | | | | | |
| *Moniliformis moniliformis* | Cockroach | Yes | Yes | – | Gotelli & Moore, 1992 |
| *M. moniliformis* | Cockroach | – | – | Yes | Carmichael *et al.* 1993 |
| **Nematoda** | | | | | |
| *Brugia pahangi* | Mosquito | – | Yes | – | Townson, 1970 |
| *B. pahangi* | Mosquito | – | Yes | – | Rowland & Lindsay, 1986 |
| *B. malayi* | Mosquito | – | Yes | – | Husain & Kershaw, 1971 |
| *Dirofilaria immitis* | Mosquito | – | Yes | – | Berry *et al.* 1988 |
| Mermithids | Black fly | – | – | Yes | Colbo & Porter, 1980 |
| Mermithids | Mayfly | – | Yes | – | Benton & Pritchard, 1990 |
| *Gasteromermis* sp. | Mayfly | Yes | Yes | Yes | Vance, 1996 |
| *Mermis* sp. | Ant | Yes | – | Yes | Maeyama *et al.* 1994 |
| *Limnomermis* sp. | Midge | Yes | Yes | – | Wülker, 1985 |
| **Insecta** | | | | | |
| *Aphidius nigripes* | Aphid | Yes | – | – | Brodeur & McNeil, 1989 |
| *A. ervi* | Aphid | Yes | – | Yes | McAllister & Roitberg, 1987 |
| Braconids | Caterpillar | Yes | Yes | Yes | Shapiro, 1976 |
| Braconids | Caterpillar | Yes | Yes | Yes | Stamp, 1981 |
| *Cotesia glomerata* | Caterpillar | – | – | Yes | Brodeur & Vet, 1994 |
| Conopids | Bumblebee | Yes | – | Yes | Müller & Schmid-Hempel, 1993 |
| *Thelaira americana* | Caterpillar | – | – | Yes | Karban & English-Loeb, 1997 |
| Tachinids | Cricket | – | – | Yes | Cade, 1984 |
| Tachinids | Cricket | – | Yes | Yes | Adamo *et al.* 1995 |

answer to the question of whose adaptation this is. The following examples of insect–parasite interactions illustrate these problems further.

Male crickets sing to attract conspecific females. Often singing males also attract acoustically orienting tachinid flies which deposit larvae onto males (Cade, 1975). The ear of these flies shows a remarkable sensitivity to the dominant frequency of cricket songs (Robert, Amoroso & Hoy, 1992). Fly larvae burrow inside their cricket host where they grow for several days before emerging and pupating. The call duration of male crickets decreases following infection, and parasitized crickets are more likely to remain silent than non-parasitized ones

(Cade, 1984; Zuk, Simmons & Rotenberry, 1995). Is decreased singing activity a side-effect of infection, or is it an adaptation? The simplest explanation is that singing rates decline as a mere consequence of the internal tissue damage caused by the developing parasitoid. There is another possibility, however. The decline in call duration occurs hours after infection, when the fly larva is still small and before it causes substantial damage (Cade, 1984). If the fly could immediately reduce the singing ability of its host, it would prevent the host from attracting further parasitoids that could reduce the probability of survival of the initial parasitoid. Thus the reduction in host call duration must be advantageous to the parasite, whether it is a side-effect or the product of a manipulation. Only the discovery of either a substance released by the fly larva that has no purpose or effect other than reducing host singing, or of some similar specific mechanism, would allow a conclusion to be drawn on the evolutionary nature of this change in host behaviour following infection.

In other cases, the change in behaviour is more complex than a reduction in some activity, and therefore more likely to be the adaptive product of selection. The arguments centre instead around which organism benefits. For example, caterpillars of several butterfly species serve as hosts for braconid wasp parasitoids. Unlike non-parasitized individuals, parasitized caterpillars perch at the top of high branches. Shapiro (1976) suggested that this change in behaviour represents a host adaptation, whereby the host makes itself conspicuous to predators by moving to the top of plants. Since the host will be killed by the parasitoid anyway, it can increase its inclusive fitness by getting its wasp parasite eaten by a predator, thus protecting its nearby relatives from the parasite (Smith Trail, 1980). Suicidal behaviour could theoretically evolve in hosts through kin selection, if hosts live in groups of relatives. Other explanations for the upward migration of parasitized caterpillars are possible, however. Stamp (1981) proposed instead that the parasitoid benefits from the alteration, because other wasps are less likely to find and infect caterpillars perched at the top of plants. The change in behaviour would then be a manipulation of the host by the parasite to reduce the risk of hyperparasitism and increase the survival of the parasite. Until the proximate mechanism behind the change in behaviour is elucidated, or until precise measurements of host and parasite fitness are made with and without changes in host behaviour, the debate will remain open.

Similar confusion existed regarding a change in bumblebee behaviour induced by parasitic conopid flies. Parasitized bumblebee workers remain outside the nest longer than non-parasitized workers, and even abandon their nest altogether. Initially, this was thought to be an adaptive manipulation by the parasitoid: by ensuring that the host dies outside the nest, the parasitoid pupa should be less subject to bacterial and fungal infections and should survive better (Schmid-Hempel & Müller, 1991). Since bumblebee colonies consist of close kin, it is also possible that by abandoning its colony, a parasitized bumblebee could lower the risk of the parasitoid it carries emerging to infect its relatives (Poulin, 1992). Indeed, it has recently been demonstrated experimentally that by staying away from the nest, parasitized bumblebees experience colder temperatures that reduce the chances of their parasitoid developing successfully (Müller & Schmid-Hempel, 1993). A quantification of potential benefits for the host has allowed this example of behavioural change to be classified as a host adaptation.

The distinction between coincidental side-effects, parasite adaptations and host adaptations is not an easy one to make. Often several explanations are compatible with the observations, and only precise experiments can lead to a clear verdict. Frequently the change in host behaviour predicted to benefit the host is the same as that predicted to benefit the parasite. For instance, moving to high and exposed locations can be one way for a parasitized insect to increase its exposure to solar radiation and combat its parasite with a behavioural fever (see Boorstein & Ewald, 1987; Horton & Moore, 1993), while it may also be the best thing the host can do to facilitate the transmission of the parasite. Although difficult to perform, studies on mechanisms and fitness benefits are necessary. Very few have been done to date, and there are therefore very few cases in which we can be sure that parasite-induced behavioural changes are adaptations.

## PHYLOGENETIC APPROACHES

Like other traits, changes in host behaviour induced by parasites make more evolutionary sense when viewed in a phylogenetic context (Moore & Gotelli, 1990). For instance, the same change in host behaviour, observed in two distantly-related host species and caused by distantly-related parasite species having similar life cycles, is strong evidence that the behavioural change is either a host or parasite adaptation. The same trait, evolving more than once, independently in separate lineages under similar selective pressures, is most probably a case of convergent evolution (Poulin, 1995). My favourite example involves nematomorphs and some mermithid nematodes. The two taxa are not closely related, and have independently evolved similar life cycles, in which juveniles develop inside an insect host until they emerge as adults in freshwater. In both taxa, there are many anecdotal reports of identical changes in host behaviour caused by the parasites, in which parasitized hosts appear driven to find water bodies and throw themselves in water
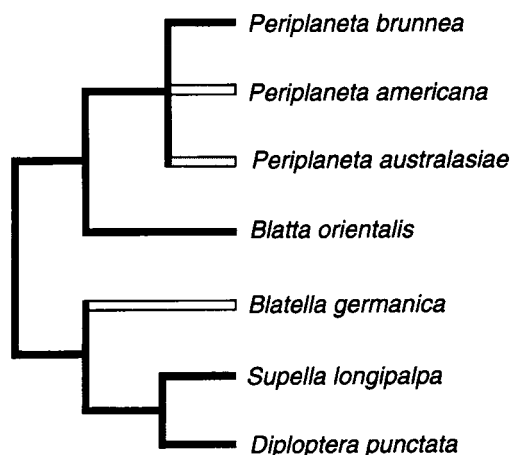
Fig. 1. Phylogenetic pattern of altered behaviour among seven species of cockroaches experimentally infected by the acanthocephalan *Moniliformis moniliformis* (adapted from Moore & Gotelli, 1996). The phylogeny has been independently derived from morphological data. Results are only shown for one of ten behavioural traits examined. Black branches indicate that host behaviour is unaltered by the parasite (the ancestral condition). White branches indicate that infection increases the time spent by the host on black surfaces in the test arena relative to uninfected individuals. The shaded branch indicates that infection decreases the use of black surfaces by hosts.

(Poinar, 1991; Maeyama, Terayama & Matsumoto, 1994). This complex behavioural modification is unlikely to have appeared independently twice by chance alone, and it would be interesting to know whether the two parasite lineages have also adopted the same mechanism to achieve the same host manipulation.

Other informative comparisons could involve the effect of one parasite species on the behaviour of several species of hosts, or the effect of several parasite species with similar cycles on the behaviour of a common host species. These comparisons would indicate whether behavioural changes are 'repeatable' rather than chance accidents, if we view different host–parasite systems as different evolutionary experiments. They could also serve to detect constraints acting on either hosts or parasites, constraints that may influence the types of behavioural change observed in particular host or parasite clades. A perfect concordance between the taxonomic distribution of a character such as parasite-induced behavioural change and host or parasite phylogeny can serve as a null model for evolutionary studies of that character (Moore & Gotelli, 1990). I will use two case studies to illustrate the power of the phylogenetic approach to understand the evolution of parasite-induced changes in host behaviour. In both examples, the behaviour changes are assumed to be cases of host manipulation by the parasite resulting in higher parasite transmission.

The first example comes from a study by Moore & Gotelli (1996), who examined the effects of the acanthocephalan parasite *Moniliformis moniliformis* on the behaviour of seven species of cockroaches, all suitable intermediate hosts. The parasite completes its life cycle in the rat, its definitive host, and is known to alter the behaviour of cockroaches in ways that may render them more susceptible to predation by rats. Under standard laboratory conditions, parasitized and control cockroaches of all seven species were tested for differences in ten behavioural traits (various measures of activity, substrate choice and photic response). The behaviours were scored as either unaltered, increased, or decreased by parasitic infection, and then mapped onto a cockroach phylogeny derived exclusively from morphological data (Fig. 1). Concordance between the effect of the parasite on host behaviour and the relationships among hosts would suggest that behavioural changes are constrained by phylogeny, and that their occurrence in a particular host-parasite system may simply be due to inheritance from an ancestral association. Moore & Gotelli (1996) found no evidence of strong concordance between alterations in any of the 10 behavioural traits and the cockroach phylogeny. In other words, the effect of the parasite on host behaviour is independent of phylogeny, and has evolved separately in different parasite-cockroach combinations. This finding supports the idea that changes in host behaviour are adaptive for host and/or parasite.

The second example is that of entomogenous fungi, i.e. fungi parasitic in insects. The distribution of the parasitic habit among different taxa of fungi suggests that parasitism of insects has evolved independently on more than one occasion (Madelin, 1966; Evans, 1988), just as fungal parasitism on plants has arisen many times over evolutionary time (Heath, 1987). Entomogenous fungi are transmitted by spores, which are either passed from host to host during contact or dispersed by the wind, or both. Behavioural changes in insects parasitized by fungi have been reported frequently, especially in the context of microhabitat choice (Evans, 1988; Samson, Evans & Latgé, 1988). Some parasitized insects climb to the top of high branches before dying, a behaviour known as 'summit disease' (Evans, 1982, 1988) and reminiscent of the behavioural changes induced by some parasitoids (Shapiro, 1976; Stamp, 1981) and trematodes (Romig, Lucius & Frank, 1980). This altered behaviour could be an adaptive response of the insect host (see Evans, 1989), but is generally thought to be a manipulation by the fungus, which benefits from it by releasing its spores from a high location. The exact perching position chosen by the parasitized insect with respect to the direction of the prevailing wind also suggests that the behaviour is a manipulation serving to facilitate spore dispersal
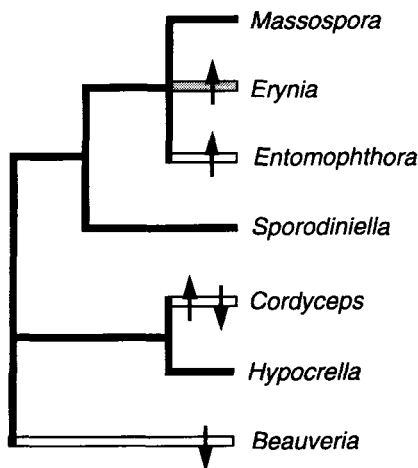
Fig. 2. Phylogenetic pattern of altered behaviour among seven genera of fungi parasitic in insects. The phylogenetic relationships among genera are inferred from the taxonomy in Samson *et al.* (1988). Black branches indicate that host behaviour, i.e. microhabitat choice, is unaltered by the parasite (assumed here to be the ancestral condition). White branches indicate that parasitized insects move to different microhabitats than uninfected conspecifics. The shaded branch indicates that only certain species within the genus induce a change in host behaviour. Arrows pointing upward indicate that parasitized hosts move to the top of plants, and those pointing downward indicate that parasitized insects move to the ground or below the leaf litter. Information on behavioural changes in parasitized insects is taken from Evans (1982, 1988) and Samson *et al.* (1988), and the figure includes only genera for which specific information on host behavioural changes was available.

(Maitland, 1994). Other insects parasitized by fungi tend to move downward rather than upward, dropping from trees or burying themselves in the leaf litter (Evans, 1988). Finally, in other cases, the behaviour of the parasitized insect does not appear to change with respect to microhabitat choice, spore transmission being achieved mostly by sexual contacts with uninfected hosts (Møller, 1993). Mapping these behavioural changes on a phylogeny of fungus genera indicates that parasite-induced behavioural changes have had multiple origins among fungi, and that they are not constrained by relationships among parasites (Fig. 2). Even within a genus, parasite species induce different alterations of host behaviour. As in the acanthocephalan–cockroach example, this pattern suggests that the manipulation can be an adaptation even in the absence of evidence of fitness benefits.

The above two examples demonstrate that a phylogenetic analysis can identify behavioural changes in parasitized hosts that are candidates for adaptations. Other insect–parasite systems also suggest that the taxonomic occurrence of behavioural changes is independent of phylogeny. For instance, a recent review of changes in susceptibility to pre-

dation in insects harbouring parasitoid wasps or flies indicates that closely-related parasite species can have widely different effects on their hosts (Brodeur, unpublished).

The different evolutionary directions that can be taken by different host–parasite systems is also apparent at the microevolutionary level, as illustrated in this further example. Larval stages of the cestode *Hymenolepis diminuta* are known to induce behavioural (Hurd & Fogo, 1991; Robb & Reid, 1996) and physiological (Blankespoor, Pappas & Eisner, 1997) changes in their intermediate host, which can be one of several beetle species such as *Tribolium* spp. or *Tenebrio* spp. The physiological changes lead to increased predation by the cestode's definitive host (Blankespoor *et al.* 1997). Although this remains to be tested, the behavioural changes are also believed to be due to adaptive manipulation by the parasite (Robb & Reid, 1996). There exists, however, variation among beetle strains in their susceptibility to behavioural manipulation, with some genetic strains showing no behavioural change whatsoever following infection (Yan, Stevens & Schall, 1994; Yan & Phillips, 1996). This variation suggests that caution is needed before making any generalization about host behavioural changes in a given host–parasite system. At the same time, it suggests that behavioural changes are not fixed or constrained traits but rather plastic phenomena that may reflect the current status of evolutionary arms races between hosts and parasites.

## CONCLUSION

Not many features are as difficult to classify from an adaptive viewpoint as parasite-induced changes in host behaviour. The reason is simple: unlike other traits, their expression is the result of interactions between the genotypes of two different organisms. It is one thing to determine if the behavioural change is derived from specific instructions in one of the two genotypes, and another thing to identify which genotype.

Nevertheless, this challenging problem can be tackled in several ways. Firstly, experiments on given host–parasite systems can provide clear evidence regarding the nature of host behavioural changes in that system. As emphasized here, behavioural changes must confer fitness advantages to either host or parasite to be labelled adaptive, and these can often be demonstrated at least qualitatively. Alternatively, identifying the precise mechanisms causing changes in host behaviour can also help to distinguish between adaptation and side-effect. Secondly, phylogenetic studies of the distribution of host behavioural changes among taxa of hosts or parasites are also very instructive, because they can establish how often specific behavioural changes

have evolved in different lineages. The above approaches have only been used in rare occasions in the study of insect-parasite interactions, as in the study of other host-parasite associations. As more experimental and phylogenetic studies are performed, our understanding of the evolution of parasite-induced changes in insect behaviour can only improve.

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