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Water-seeking behavior in insects harboring hairworms: should the host collaborate?

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We explored the idea that hosts infected with manipulative parasites might mitigate the costs of infection by collaborating with the parasite rather than resisting it. Nematomorphs are usually considered to be manipulative parasites of arthropods because they cause hosts to seek an aquatic environment, which is needed by the adult parasite. We placed infected cricket hosts in situations of forced noncompliance and compared some fitness parameters (life expectancy, gonad development, and reproductive behaviors) in noncompliant hosts and hosts allowed to express parasite-induced behavior. Compared to uninfected controls, reduced survival was observed in both males and females from the two categories of infected hosts, collaborative or not. A substantial proportion of collaborative females produced eggs or had developed ovaries while such phenomena were never observed among noncollaborative ones. Collaborative females retained a nymphal phenotype, but adult males nevertheless courted and produced spermatophores to such females. However, collaborative females had difficulties mounting males, taking spermatophores and/or ovipositing. In contrast to females, all males were entirely castrated by the parasite regardless of their behavior, collaborative or not. Thus, bringing the parasite into water does not effectively mitigate the costs of infection for the host. *Key words:* host collaboration, host manipulation, Nematomorpha, Orthoptera. *[Behav Ecol 16:656–660 (2005)]*

The study of the strategies used by parasites for their transmission is a central topic in parasitology. One strategy of transmission that is especially intriguing is that of host manipulation, which occurs when a parasite enhances its own transmission by altering host behavior (for reviews see Combes, 1991; Moore, 2002). Despite the increasing evidence of such parasite adaptations, the underlying reasons for why infected hosts "capitulate" and act in ways that benefit the parasite remain unexplored in most cases (Poulin, 1998; Thomas et al., 2005).

Hairworms (Nematomorpha: Gordiida) typically develop in arthropods (mainly terrestrial species) until they are ready to exit the host (Schmidt-Rhaesa, 1997, 2001). In accordance with several anecdotal reports, it has recently been shown that insects harboring mature hairworms display a behavior originally not present in the host's repertoire: seeking and jumping into water (Thomas et al., 2002). The adult worm then actively emerges from the host and starts searching for a sexual partner (Thomas et al., 2002). Because it is usually assumed that seeking and jumping into the water kills the insect host (through drowning or because of the parasite release itself) (Schmidt-Rhaesa, 1997, 2001), the water-seeking behavior of infected hosts has often been considered as an example of "true" host manipulation (i.e., an adaptive parasite-induced behavioral change) aimed at reaching a suitable place for reproduction (Combes, 1995; Moore, 2002; Poulin, 1995, 1998; Thomas et al., 2002, 2003).

Although the manipulation hypothesis appears to be a plausible scenario in this case, little attention has been devoted to explore other hypotheses. In particular, the idea that infected arthropods that are collaborative, bringing mature hairworms into water, achieve higher fitness than those that do not collaborate (or are unable to find water) has never been tested. Conditions for host collaboration rather than host manipulation could be met if the host (1) does not always die after emergence of the worm, (2) is able to reproduce when the worm has been released into water (i.e., the host has not been completely castrated by the parasite and/or it can recover from the damage caused by the parasite), and (3) has no reproductive potential (e.g., complete castration) if it fails to bring the worm into water.

The aim of this study was to explore whether or not such assumptions are realistic in the association between the cricket *Nemobius sylvestris*, Bosc (Orthoptera: Gryllidae), and its parasitic hairworm *Paragordius tricuspidatus*, Dufour (Nematomorpha: Gordiida). This cricket becomes infected by *P. tricuspidatus* when it ingests larvae, presumably through a paratenic host. During development, the parasite grows from a microscopic larva to a large worm (10–15 cm), which is ready to emerge in early summer (i.e., almost exclusively in July in southern France; Thomas et al., 2002). Both field and laboratory experiments confirmed that water-seeking behavior exists in *N. sylvestris* harboring mature *P. tricuspidatus* (Thomas et al., 2002). Under natural conditions, particularly in ponds, infected *N. sylvestris* have sometimes been seen to leave the water after the emergence of the parasite (Thomas, unpublished data), but it is not known what happens to these crickets thereafter.

In the present work, we studied life expectancy, gonad development, and reproductive behavior (courting and ovipositioning behaviors) in infected crickets allowed to release their parasite into water (i.e., collaborative behavior) and in those prevented from bringing the parasite into a suitable aquatic environment (i.e., noncollaborative behavior).

MATERIAL AND METHODS

Survival and gonad development

Sampling

As in Thomas et al. (2002), infected *N. sylvestris* were captured at night (between 10 p.m. and 1 a.m.) around a pool (15×10 m)

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located in Avènes les Bains (Southern France, 70 km north from Montpellier, 43° 45′ N, 3° 06′ E). This pool was located near a forest containing numerous small streams in which adult *P. tricuspidatus* were commonly found during the summer. Between this pool and the forest, a 5-m-wide concrete area allowed direct observation and capture of infected crickets moving from the forest in the direction of the pool. Previous observations (Thomas et al., 2002) revealed that crickets detected on the concrete area were always infected and, when not disturbed, systematically entered the pool within a few minutes to release their worm(s). We also captured uninfected individuals in the forest surrounding the pool. Collections were made between 2 July and 18 July (2003). During this time of the year, all individuals of *N. sylvestris* are nymphs. Adults begin to appear in August. We sampled 48 uninfected (26 males, 22 females) and 127 infected (69 females and 58 males) individuals in total.

Procedure

A first group of randomly chosen infected crickets ($n = 75$, 46 females and 29 males) were placed immediately after their capture in a tank containing freshwater, until the emergence of their worm(s). These crickets were then placed in a dry opaque plastic tank for 1 h, until they became active again. We called this category of hosts "collaborative crickets." Conversely, the second group of infected crickets ($n = 52$, 23 females, 29 males) was placed directly under experimental conditions (see below), thus being prevented from releasing their worm(s) into an aquatic environment. Because this situation is clearly unfavorable for parasites, we termed this category of hosts "noncollaborative." The 48 uninfected crickets were also placed immediately after their capture under experimental conditions (see below).

In the laboratory, we tracked the survival, the development, and the gonad state (at death) of uninfected, collaborative, and noncollaborative crickets. Under experimental conditions, each cricket was maintained individually in plastic tanks (8 × 8 cm, height 16 cm), at 25°C and provided with ad libitum food (in equal proportions: cereals, fish food Tetra Ani Min, dry gammarids, and dry tubifex) and humidified cotton (changed every week). In order to avoid positional biases, plastic tanks were placed randomly in the room and changed every day during the entire experiment. The photoperiod was 16:8 h light:dark, which is the natural photoperiod at capture time. Tanks were examined daily until the death of all crickets. When a cricket died, it was immediately preserved in alcohol (70%) and the time between its capture in the field and its death in the laboratory as well as its developmental stage (adult or nymph) were recorded. These crickets were also sexed and dissected to confirm their infection status (uninfected versus infected) and to examine their reproductive state (gonad development level, presence of unfertilized eggs in females).

Courtship and oviposition behavior

Subjects

A new collection of infected females was made during July 2004 following the same sampling method described previously. We also captured two large samples (more than 100) of uninfected males and uninfected females in the forest surrounding the pool. As before, all individuals were nymphs. In order to obtain collaborative females, all infected females were placed immediately after their capture into water until the emergence of their worm. Uninfected females and collaborative females were maintained individually until September, under the same experimental conditions as previously described (see above). Males were kept together in a terrarium (70 × 30 cm, height 30 cm) until September, with ad libitum food and water.

Procedure

In September, uninfected survivors (both males and females) were all adults while collaborative females typically retained a nymphal phenotype. With these individuals, we performed the following experiments. One uninfected male and one female (uninfected or collaborative) were placed in a plastic box (12 × 8 cm, height 5 cm) for a maximum of 3 h. For each trial, we recorded whether males performed courtship songs and produced spermatophores and whether females attempted to mount the male in order to achieve spermatophore uptake. In all cases where copulation did not occur, another trial was performed within the 4 following days with the same female and with another adult male chosen randomly. All tested females were returned to their plastic tank and oviposition was monitored every day for a maximum of 2 months by examining the humidified cotton (in the absence of soil, females usually oviposit in humidified cotton). Females that died during this period as well as those that were still alive after 2 months were preserved in alcohol (70%) and dissected to examine their reproductive state (degree of gonad development, number of eggs).

Survival data was analyzed using the SURVIVAL procedure (log-rank test) using JMP IN 3.2.1 (SAS Institute, 1996). All other statistical tests were performed following Sokal and Rohlf (1981) and Siegel and Castellan (1988). When the assumptions of parametric tests were not upheld, nonparametric statistical tests were used. All tests reported are two tailed.

RESULTS

Dissection revealed that 4% (two females and one male) of the individuals allocated to the group of collaborative crickets in fact still harbored a worm at the end of the experiment (they initially had two worms, and the one we saw emerging at capture time was probably the older one). These three individuals were excluded from the analysis. In the group of noncollaborative crickets, errors in the a priori determination of the infection status resulted in one female and five males being uninfected (they were probably captured just after they released their worm). These individuals were also excluded. One cricket (a male) allocated to the group of uninfected individuals in fact harbored a worm (the worm was immature when the host was captured). Finally, within the uninfected category, five individuals (one female and four males) had an ambiguous status because, although they harbored no worm, they never reached adulthood (they kept a nymphal phenotype and never produced gonads) as this is normally the case with uninfected crickets (see below). Because we suspect that these five ambiguous individuals corresponded to previously infected crickets that had already released their worm at capture, we mention them but did not include them in the analysis. The analyses were thus based on 72 collaborative crickets (44 females and 28 males), 46 noncollaborative crickets (22 females and 24 males), and 42 (21 males and 21 females) uninfected crickets.

Survival

Because the consequences of infection might be different between sexes, we analyzed males and females separately. Distinguishing between infection status, infected crickets of both categories (i.e., collaborative and noncollaborative) had significantly higher mortality than uninfected controls among both females (log rank $\chi^2 = 45.5$, df = 2, $p < .0001$,

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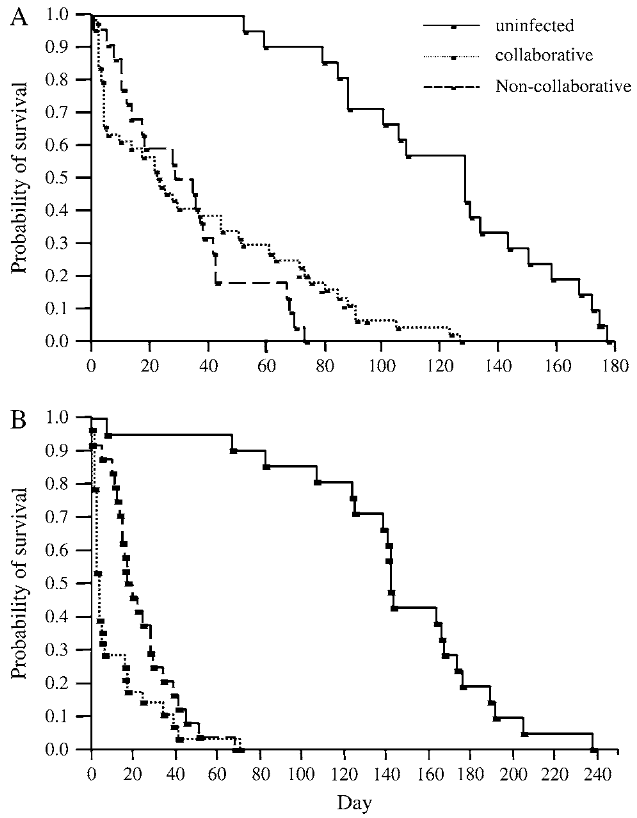

Figure 1
Survival curves (A: females; B: males), measured as the proportion of individuals remaining alive at each time for uninfected, collaborative, and noncollaborative crickets.

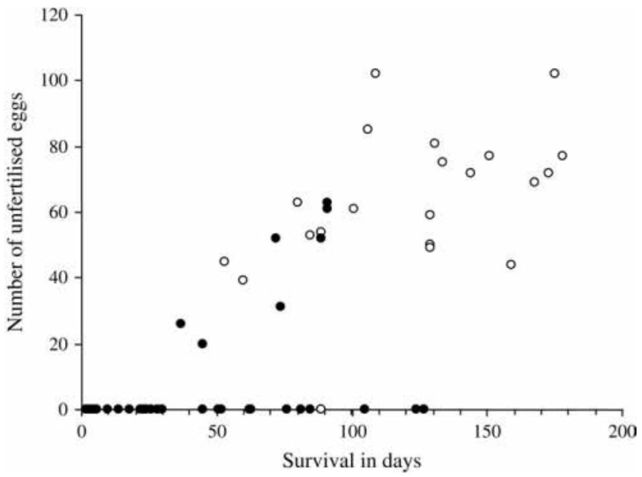

Figure 2
Number of (unfertilized) eggs produced by collaborative and uninfected females in relationship to their survival. Uninfected females are denoted by open circles and collaborative ones by filled circles.

Figure 1A) and males (log rank $\chi^2 = 61.7$, df = 2, $p < .0001$, Figure 1B). The mean survival in days (±SE) of uninfected crickets (females: 122.5 ± 8.2, $n = 21$, males: 144.9 ± 11, $n = 21$) was at least four times higher than that of individuals from infected categories (collaborative individuals, females: 37.5 ± 5.6, $n = 44$, males: 11.7 ± 3.1, $n = 28$; noncollaborative individuals, females: 32.5 ± 4.8, $n = 22$, males: 23.9 ± 3.4, $n = 24$).

The overall pattern of mortality was not significantly different between the two categories of infected females (log rank $\chi^2 = 1.11$, df = 1, $p = .29$, Figure 1A). However, a closer examination of the survival curves revealed that the mortality during the first week was significantly higher among females from the collaborative group (16/44, i.e., 47%) compared to those from the noncollaborative group (2/22, i.e., 9%) (Fisher's Exact test, $p = .038$), suggesting that the emergence of the parasite is associated with an increased risk of mortality after emergence. Conversely, among females which survived 1 week postemergence, survival (mean in days ± SE) was better among collaborative crickets (49.7 ± 6.4, $n = 28$) compared to noncollaborative ones (28.4 ± 4.7, $n = 20$) (log rank $\chi^2 = 8.26$, df = 1, $p = .004$).

As in females, the parasite emergence in collaborative males was associated with an increased mortality during the first week (71%, i.e., 20/28, among collaborative individuals versus only 12.5%, i.e., 3/24, among noncollaborative ones, Fisher's Exact test, $p = .00002$). As a result of this phenomenon, the global pattern of survival was significantly different between the two categories of infected males (log rank $\chi^2 = 4.42$, df = 1, $p = .035$, Figure 1B), with collaborative crickets having on average a survival rate less than half as high (mean survival ± SE, 11.7 ± 3.1, $n = 28$) than noncollaborative ones (mean survival ± SE, 23.9 ± 3.4, $n = 24$). The sex difference concerning the first week mortality rate in collaborative crickets (i.e., females 47% versus males 71%) was significant (Fisher's Exact test, $p = .007$), indicating that the consequences of parasite emergence are more severe in males than in females.

Gonad development

As specified before, one female considered as "uninfected" did not reach adulthood and did not develop ovaries. All the other uninfected females reached the adult stage and displayed normal gonad development by either producing eggs ($n = 20$ females), or by having well-developed ovaries ($n = 1$ female). The mean number of eggs (±SE) produced by these females was 66.4 ± 4.0 ($n = 20$). Although all collaborative females retained a nymphal phenotype, 10 out of the 28 crickets that survived through the first week (i.e., 36%) also displayed a normal reproductive development (seven females with eggs and three with well-developed ovaries). The mean number of eggs (±SE) of these 7 females was 43.6 ± 6.6, which is significantly lower than that observed among uninfected females (see above, unpaired t test, $t = 2.9$, df = 25, $P = .007$). The lower life expectancy of collaborative females compared to that of uninfected ones may partly explain this result as the number of eggs and survival were positively correlated ($r = .78$, $n = 65$, $p < .001$, Figure 2). However, survival-corrected fecundity (test for the normality of the residual's distribution, Shapiro-Wilk W test, W = 0.96, $p = .06$) still indicated that collaborative females produced fewer eggs (mean residual value ± SE, −5.4 ± 2.7, $n = 44$) than uninfected ones (mean residual value ± SE, 11.3 ± 4.6, $n = 21$) (t test, $t = 3.29$, df = 63, $p = .002$).

Noncollaborative females that survived after the first week postemergence ($n = 20$) also kept a nymphal phenotype but none contained either eggs or ovaries; instead the worm (sometimes obviously dead for several days) occupied the entire body cavity. Compared with collaborative females, this difference was significant (i.e., 36% versus 0%, Fisher's Exact test, $p = .003$). When considering the complete dataset (i.e., including all individuals), 10 out of the 44 collaborative females (23%) were found to display normal gonad development

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several weeks after the emergence, while such a phenomenon was absent among the 22 noncollaborative females (Fisher's Exact test, $p = .024$).

Twenty out of 21 males from the uninfected group reached the adult stage. All collaborative and noncollaborative males retained a nymphal phenotype. Among collaborative males, none (even the eight individuals that survived after the first week) had developed testes. Noncollaborative males also lacked testes, and, as in noncollaborative females, the worm occupied the entire body cavity. Conversely, the 20 uninfected males that survived until adulthood had well-developed testes.

Courtship behavior and ovipositioning

From the large sample of females collected in July 2004 and maintained in the laboratory during the summer, we could perform tests on 24 uninfected and 27 collaborative survivors. Dissections revealed that 100% (i.e., 24/24) of uninfected females versus 67%, (i.e., 18/27) of collaborative females had eggs inside the abdomen (Fisher's Exact test, $p = .002$). As before the mean number of eggs was significantly higher for uninfected females (mean ± SE, 73.3 ± 5.4, $n = 24$) than for collaborative females (mean ± SE, 51.3 ± 3.2, $n = 18$; t test, $t = 3.2$, df = 40, $p = .002$). Courtship behavior and spermatophore production (at least by one of the two males tested) were observed in 100% (24/24) of the trials involving uninfected females but only in 88% (21/27) of the trials involving collaborative females (Fisher's Exact test, $p = .02$). Among trials involving collaborative females ($n = 27$), the proportion of positive responses by males (i.e., courtship songs and spermatophore production) was not related to whether females had eggs or not (females with eggs: 15 positive responses out of 18, i.e., 83%; females without eggs: 6 positive responses out of 9, i.e., 67%, Fisher's Exact test, $p = .63$).

When considering trials in which males courted females (at least one of the two tested), the proportion of females that attempted to mount the male in order to take the spermatophore was not significantly different between uninfected (19/24, 79%) and collaborative females (15/21, 71%) (Fisher's Exact test, $p = .73$). However, among collaborative females, those with eggs ($n = 15$) were significantly more likely to mount the male than those without eggs ($n = 6$) (females with eggs, 13 positive answers out of 15; females without eggs, 2 positive answers out of 6, Fisher's Exact test, $p = .03$). While all uninfected females attempting to take the spermatophore were successful ($n = 19$), only 7 out of 15 collaborative females displaying the mounting behavior succeeded in obtaining a spermatophore (Fisher's Exact test, $p = .0003$).

Finally, there was a significant difference between uninfected and collaborative females in their oviposition behavior. Two out of 27 (7%) collaborative females laid eggs while 12 out of 24 (50%) uninfected females did so (Fisher's Exact test, $p = .001$). When considering only females that had eggs inside the abdomen, this difference remained significant (i.e., collaborative 2/18, uninfected 12/24, Fisher's Exact test, $p = .02$).

DISCUSSION

Hosts infected with debilitating parasites are under selection to evolve not only ways to eliminate them but also ways of compensating for their effects in the event they cannot eliminate them. Under some circumstances, hosts may reduce costs imposed by parasites by behaving in ways that benefit the parasite (Soler et al., 1998; Zahavi, 1979). From an evolutionary point of view these considerations are important as they suggest that phenotypic changes in infected hosts, even when they result in clear fitness benefits for the parasite, are not necessarily an illustration of the extended phenotype of the parasite (sensu Dawkins 1982, i.e., parasite genes expressed in host phenotypes). They may instead be the direct product of natural selection acting on the host genome (e.g., given that hosts can still reproduce and/or that its "suicide" prevents infection of kin).

In the present work, we first showed that hairworm emergence is not lethal per se for the host, instead crickets of both sexes can live several months after having released the parasite. Despite this finding there is, however, an important mortality during the first week after parasite emergence (47% for females and 71% for males). Causes of this phenomenon are potentially numerous ranging from irretrievable physical damage as a result of the emergence, dehydration and/or subsequent hyperinfection caused by the emergence hole. Presently, the reason why this mortality is significantly higher in males than in females remains obscure but could be due to the smaller size of males compared to females, making the relative consequence of hairworm development and emergence more detrimental for males than for females. Finally, the collaborative behavior is likely to come with several other costs not quantified in the present work. For instance, crickets jumping into a natural aquatic environment (e.g., a river) probably experience a substantial risk of dying through drowning or predation (fishes or frogs). More data are needed concerning the true proportion of individuals that, in natural conditions, are able to leave water after the emergence of the parasite.

Our experiments also revealed that a substantial proportion of the females (23%) that liberated the worm(s) into water produced eggs or had developed ovaries several weeks postemergence, while this did not occur among females prevented from releasing the parasite(s). The inability of noncollaborative females to produce eggs is observed even after the death of the parasite inside the host. Thus, it seems that for infected females, bringing the parasite into a suitable aquatic environment is a necessary condition before any gonad development becomes possible. The reason why not all collaborative females retain the ability to produce eggs is unclear. It is possible that hairworms, once mature, start manipulating the host and continue their development and growth until the host finds water. Because the time to achieve this task can vary, the degree of damage (from partial to complete castration) would simply reflect the length of the manipulative period. Further experiments are needed to address this point. Finally, even when collaborative females were not castrated, the mean number of eggs produced was significantly reduced compared to that of uninfected females. Complete castration and/or fecundity reduction are not mere consequences of the reduced survival of collaborative females compared to uninfected ones because controlling for this effect did not change the results. These findings may be indicative of other parasite-induced costs, by either the past infection being directly costly or by the parasite having prevented host resources being normally allocated into reproductive functions.

The second experiment revealed that collaborative females lacking eggs have a significant reduction in their response to courtship behaviors compared to collaborative females with eggs, making them less likely to mount the male and to take the spermatophore. Presently, the proximal nature of this phenomenon (e.g., behavior, pheromones) remains unclear. Moreover, when collaborative females display mounting behavior, the spermatophore transfer failed in about 50% of the cases versus 0% with uninfected females. Finally, from an evolutionary point of view, a last important result is the

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oviposition response. Indeed, collaborative females, even when they are able to produce eggs and to successfully take spermatophores from males, subsequently have difficulties in laying their eggs compared to uninfected females. When all these findings are cumulated (i.e., high postemergence mortality, reduced probability of egg production, altered mounting and oviposition behaviors), it seems that collaborating with the parasite would be a strategy that could only rescue a very small proportion indeed of the reproductive success enjoyed by uninfected individuals. It is therefore difficult to argue that infected females can effectively mitigate costs of infection by collaborating in this system.

The second experiment also revealed that despite the significantly higher rate of positive responses (courtship songs and spermatophore production) by males when presented with uninfected females compared to collaborative ones, the later proportion remains substantial (i.e., 88%) regardless of the presence/absence of eggs (although this last finding could also result from a lack of correlation between the number of eggs at test—and at death—time). It remains unclear why males produce and transfer spermatophores to collaborative females despite their functional sterility. One explanation would be that males of *N. sylvestris*, especially those in our experiment that remained for several weeks in a terrarium containing only males, subsequently produced and tried to transfer spermatophores to any female they contact (i.e., a laboratory-induced artifact). Alternatively, avoidance by males of collaborative females may not have evolved because such females are rare in nature. Unfortunately, at this moment, there is no information on the frequency of these females in natural populations during reproductive periods.

The results obtained for male crickets were substantially different. The most important difference is the complete castration of infected individuals, which is systematic regardless of male behavior (collaborative or not). Thus, as for females, it seems difficult to argue from the present dataset that males bringing the parasite into water would obtain fitness compensation for such collaborative acts.

This is the first study investigating life-history traits in arthropods harboring, or having harbored, hairworms. Although several aspects of this system need to be confirmed under natural conditions, our results suggest that the water-seeking behavior of crickets is more likely to represent true manipulation than collaboration. We suggest that placing infected hosts in situations of "disobedience" with regard to what benefits the parasite, and to then study the fitness consequences of this, is an empirical avenue that will help us distinguish between true manipulation (in which manipulated hosts obtain no fitness benefits) and collaboration (in which fitness compensations are associated with compliant behaviors).

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