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Letter to the Editor

Why do nematomorphs leave their hosts?

I am rarely surprised when something that can happen happens. But when I found *them* in my Australian shepherd's bowl (Fig. 1a), I could not help thinking this was too much of a coincidence. The Gordian worm (Nematomorpha) whirling in the water was one of the sparks that ignited my interest in parasitology, when I first learned about its creepy mind-twisting ability. And the day it appeared in the bowl, more than a decade later, I had just published a paper dealing with intangible, digital parasites living in artificial life simulations (Strona and Lafferty, 2016). Weird as it sounds, I was sure that the worm was telling me it was time to take a break from computer code, and see what a real parasite looks like. As much as I was sure that the suicidal grasshopper, floating above the worm, was asking for help.

The bowl was not the easiest target for a mind-controlled grasshopper looking for somewhere to drown itself. Although nematomorphs can make their hosts wander more than usual, hence increasing their chances of finding water, they do not give them water-divining abilities (Thomas et al., 2002). However, nematomorphs do promote positive phototaxis, which could help hosts locate streams and ponds reflecting the light from the night sky (Ponton et al., 2011). But the bowl was in the shade.

When I took it out of the water, the grasshopper was fine, and when I released it a few hours later, it jumped away as though nothing had happened (Fig. 1b; see also https://youtu.be/oWnZtlEfBzs). Although amazing, considering the worm's length, this was not an exceptional circumstance: if they release the parasite timely, hosts have high chances of not only surviving, but also of reproducing (Biron et al., 2005). That is, if they do not drown.

To balance the situation, I released the worm in the closest lake, about a kilometer from the bowl. In doing so, I wondered whether inducing a host to jump into the bowl of a merciful parasitologist's dog is a stable evolutionary strategy. At first I figured it had worked, this time at least, by giving the worm a chance to find a sexual mate. But observing it swimming away, I became less convinced. It looked like such an easy prey for a passing fish that I wondered: why leave the host? The odds of being eaten, combined with the challenges of finding a partner, make the once-in-a-lifetime journey extremely risky. Yet, a suicidal insect is easy prey for a fish, or for an amphibian, which gives the worm a valuable evolutionary possibility in waiting for its host to be ingested, and then using the predator as the final host, trading freedom for safety (Brown et al., 2001).

One of the greatest evolutionary barriers to a parasite increasing its life-cycle complexity is not to be digested by the potential new host. However, nematomorphs have already made some important steps in that direction: after surviving their hosts' ingestion, like Houdini, nematomorphs can sometimes find their way out of the predator (Ponton et al., 2006). Assuming that this ability had emerged from frequent predation events would also suggest that predation on nemathomorphs' hosts is common, as confirmed by studies that show how nematomorphs affect food webs by bringing food from terrestrial to aquatic habitats (Sato et al., 2012). This rules out a lack of predators from the possible reasons for leaving the invertebrate host.

Nevertheless, this strategy could be an advantage in permitting nematomorphs to colonize habitats free from fish or amphibians, such as small or temporary watersheds. However, the importance of this kind of habitats as reproduction sites for nematomorpha is unclear. Furthermore, the probability that a worm is released into a predator-free environment is not independent of its chances to find a mate. A watery habitat sustaining a stable nematomorph population would likely be inhabited (or visited) by several predators. Conversely, a bowl, or a temporary puddle, would probably be predator-free, but would not likely be inhabited by many worms, nor provide the new generation with access to definitive hosts. Because multiple infections are relatively rare (8–18% of hosts), and parthenogenesis is currently known only for one nematomorph species, left-isolated worms such as the bowl's visitor would have a hard time mating (Hanelt et al., 2012). Thus, since being released in a predator-free habitat can be either an advantage or a dead-end for a nematomorph depending on many unknown, possibly stochastic factors, it is difficult to identify it as a definitive constraint against increasing life cycle complexity.

Are nematomorphs so efficient in finding a mate and avoiding predation that increasing life-cycle complexity is unnecessary? Little is known about their mate finding ability, but chemical cues may enable nematomorphs to find a partner efficiently (Hanelt et al., 2005). Furthermore, unsuccessful attempts to find a mate could be compensated by nematomorphs' very high fecundity (Hanelt and Janovy, 2004; Hanelt, 2009).

Movements of the abandoned suicidal host can distract predators while the worm swims away, reducing its risk of being eaten. Yet, the worm may take several minutes to exit the host (Hanelt et al., 2005), which makes the release phase (which usually happens at night) critical, and raises doubts as to whether the distracting action of the drowning host compensates the high risk deriving from the lure of the host-parasite association splitting up. Moreover, a study found nematomorphs in fish stomachs only when insect hosts were also found (Sato, 2011). The author interpreted this observation as proof that free-living nematomorphs are not preyed upon. I wonder whether this could suggest, instead, that nematomorphs retain their Houdini ability even after having left their host, despite them being more at risk of mechanical and digestive enzyme damage. In any case, we may conclude that predation is a secondary concern for adult worms.

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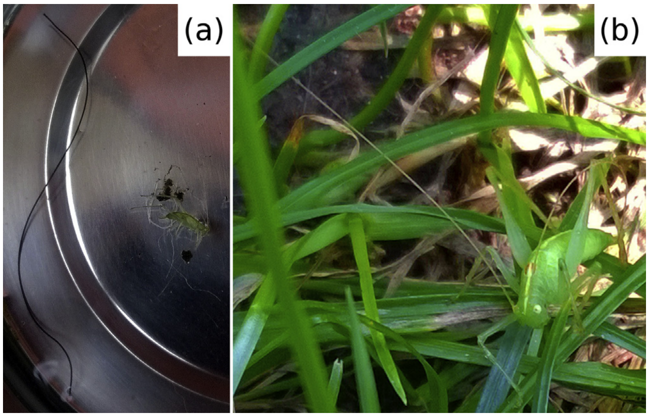

Fig. 1. The Gordian worm, the grasshopper and the dog-bowl. (a) The Gordian worm found in the bowl and its abandoned host, an immature grasshopper. (b) The immature grasshopper, fine and alive a few hours after having been 'rescued' from drowning. See also https://youtu.be/oWnZtlEfBzs.

Two more aspects, however, suggest that Gordian worms' life-cycle is indeed peculiar, regardless of their efficient mate-finding strategy, high fecundity, and ability to escape predation. First, by leaving their host's predator, nematomorphs limit their dispersal ability, in a fashion opposite to the strategy adopted, for example, by trematodes that use birds or fish as final hosts. Second, nematomorphs do not eat in their free-living stage (Hanelt et al., 2005), so their energetic resources are limited to those accumulated during their parasitic stage, making the search for a partner a race against time.

A potential solution to these issues may lie in some aspects of nematomorphs' life cycle that are still not completely clear. After hatching, nematomorphs' larvae can encyst into aquatic larvae of flying insects that serve as paratenic hosts (i.e. hosts where larvae survive without developing). The cysts can survive the insect's metamorphosis, and being then transported for some distances. When the insect dies, its corpse may be eaten by a scavenging orthopteran, that can become therefore infected, closing the cycle (Hanelt et al., 2005, Fig. 2). The presence of nematomorph cysts has been sometimes documented also in other organisms, including fish (see, for example, Torres et al., 2017), however, if and how cysts can be transmitted from those hosts to the final ones is unclear.

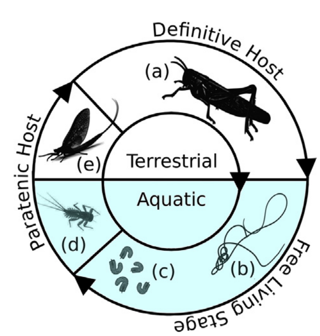

Fig. 2. Schematic representation of nematomorphs' life cycle in the wild: (a) infected invertebrates are manipulated by adult nematomorphs living in their hemocoel, which induce the hosts to jump into a watershed; (b) adult worms escape from drowning hosts, find a partner, and mate producing eggs; (c) over 7–14 days eggs develop into semi-sessile larvae; (d) larvae encyst into aquatic immature stages of insects such as mayflies; (e) cysts survive insect metamorphosis, and remain viable even when the insect dies; when the insect is eaten by a predator, or when its dead body is consumed by a scavenger, cysts are transmitted; in the right host, they eventually mature into adults, closing the cycle (a). Figure redrawn from Hanelt et al. (2005).

Paratenic hosts, can prolong nematomorphs' survival, concentrate worms in final hosts (hence increasing their future mating chances), and improve their dispersal potential (Hanelt and Janovy, 2004). However, the three aspects are not completely convincing. First, the extended survival of encysted larvae does not add to adults' limited energy. Second, most final hosts harbour only one worm (Hanelt and Janovy, 2004). Third, paratenic hosts most likely to deliver nematomorphs to the final host have often a reduced vagility (Hanelt et al., 2005). Good insect flyers such dragonflies and damselflies could make an exception, yet results from a recent study (Yamashita et al., 2017) identify feeding strategy as a major determinant of paratenic host suitability, and filter-feeding insect larvae, such as Ephemeroptera – that are far from being exceptional flyers - as the most common carriers for nematomorphs' cysts.

Could we simply be unaware of nematomorphs using fish or amphibians as final hosts? Fish parasitofauna has been investigated well enough that the lack of records about nemathomorphs using fish as *final* hosts rules out this possibility. Then again, *why leave the host*?

One may argue that nematomorph's life-cycle is not that surprising: many other parasites spend their adult phase as free living organisms. Yet, most of these, are *parasitoid* more than *parasites*, feeding on a host that is ultimately killed. Many wasps use this strategies, as well as flatworms of the family Fecampiidae (see, for example, Shinn and Christensen, 1985; Kuris et al., 2002). The host manipulation strategy of nematomorphs clearly sets them apart from this category, and looks seemingly indistinguishable from typical cases of "parasite increased trophic transmission (PITT)" (Lafferty, 1999), such as acanthocephalans of the genus *Polymorphus*, which increase the chances of their intermediate amphipod hosts to be eaten by waterfowls by making them swim closer to the surface than uninfected individuals (Cézilly et al., 2000); or the trematode *Dicroelium dendriticum*, which induces infected ants to move towards the top of vegetation, making them more likely to be ingested by the final host (e.g. a grazing sheep) (Carney, 1969). Similar to those examples, Gordian worms have evolved a manipulation strategy which increases the chances of their host to be eaten by an aquatic predator. But, remarkably, they have also evolved a strategy to escape from the predator as soon as possible.

In the long run, nematomorphs' simple life-cycle could protect them from co-extinction. Communities acquire complexity with consumers specializing on dependable resources (Strona and Lafferty, 2016). Could vertebrate predators have been a historically risky resource for nematomorphs? Certainly, insects are more equipped than vertebrates to face a dark future. Nevertheless, thinking of insects as indestructible entities capable of surviving mass extinctions is mostly a science fiction fantasy. But if we indulge in the vision of a post-human Earth dominated by arthropods, and we look more carefully, we will be surprised to discover that the real masters of that world will hide instead of crawl, manipulating their hosts' minds unseen, maneuvering them like lifeless machines.

Conflict of interest

I declare no conflict of interest.

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