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Author for correspondence:
Jean-François Doherty
e-mail: jeff-doherty@hotmail.com

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When fiction becomes fact: exaggerating host manipulation by parasites

Jean-François Doherty

Department of Zoology, University of Otago, Dunedin, New Zealand

J-FD, 0000-0003-4766-9417

In an era where some find fake news around every corner, the use of sensationalism has inevitably found its way into the scientific literature. This is especially the case for host manipulation by parasites, a phenomenon in which a parasite causes remarkable change in the appearance or behaviour of its host. This concept, which has deservedly garnered popular interest throughout the world in recent years, is nearly 50 years old. In the past two decades, the use of scientific metaphors, including anthropomorphisms and science fiction, to describe host manipulation has become more and more prevalent. It is possible that the repeated use of such catchy, yet misleading words in both the popular media and the scientific literature could unintentionally hamper our understanding of the complexity and extent of host manipulation, ultimately shaping its narrative in part or in full. In this commentary, the impacts of exaggerating host manipulation are brought to light by examining trends in the use of embellishing words. By looking at key examples of exaggerated claims from widely reported host–parasite systems found in the recent scientific literature, it would appear that some of the fiction surrounding host manipulation has since become fact.

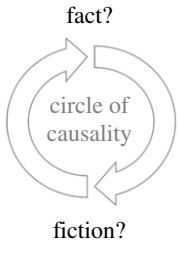
'But if thought corrupts language, language can also corrupt thought.'

—George Orwell

1. From harmless to harmful

A parasite, etymologically speaking, is a person that eats at the table of another. In biological terms, it is an organism that acquires nutrients at the expense of a host [1]. Harmless though the origin of the word is, the mere thought it evokes today of an unwelcomed creature invading the body can trigger feelings of disgust and even paranoia [2,3]. Arguably, the pervasive nature of parasitic infection and disease throughout human history has inspired numerous works of fiction [4], from the amoeboid aliens in the 1935 short story 'Brain leeches' [5] to the covetous characters in the award-winning 2019 film *Parasite* [6]. But if parasitic invasion does not sound gruesome enough, it would seem that science fiction has in turn inspired parasites. Remarkably, certain parasite species have evolved the ability to alter the phenotype of their hosts in ways that favour the transmission to another host or to an environment suitable for reproduction [7,8]. This phenomenon, known as host manipulation, ranges from striking changes in host appearance (e.g. limb malformation in amphibians infected with the trematode *Ribeiroia ondatrae* [9]) to conspicuous alterations of host behaviour (e.g. the 'death grip' in ants infected with the fungus *Ophiocordyceps unilateralis* [10]). Such parasite-driven modifications can have harmful, even lethal impacts on the host. Whether the phenotypic alterations in infected hosts are the result of adaptive parasitic manipulation or the by-products of infection has been debated for decades [11–15]. As a concept, host manipulation is inherently complex and includes a plethora of biochemical interactions between hosts and parasites [16], making it difficult to understand and communicate to a wider audience. Such complexity may have encouraged researchers to introduce scientific metaphors about host manipulation into the literature. In this regard, the current study strives to shine a light on what may yet be another contentious aspect of the phenomenon

(*a*) sensationalism in the popular media



(*b*) sensationalism in the scientific literature

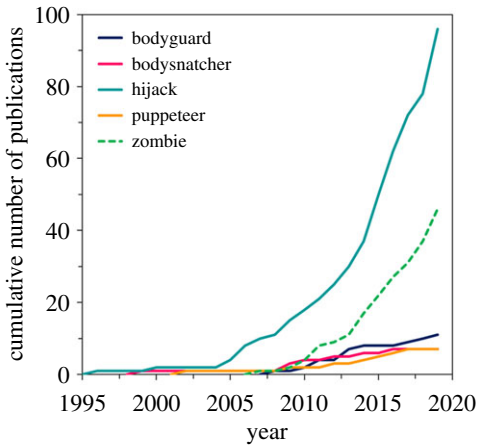


Figure 1. Trends in the use of catchy, yet misleading words describing host manipulation by parasites. The circle of causality in the centre highlights the ambiguous origin of the increasing popularity to portray host manipulation with exaggerated claims. (*a*) Word cloud of titles and headlines from randomly selected online newspaper and magazine articles ($n = 25$) covering host manipulation worldwide in the 2000s and 2010s (for methods, see electronic supplementary material, Part A). The more frequently a word is used, the larger it appears in the word cloud. (*b*) Cumulative number of scientific articles and review papers searched in Web of Science ($n = 167$) that include at least one of a selection of catchy words depicting host manipulation (see legend) used either in the title or abstract (electronic supplementary material, part B). Bacteria and viruses were excluded from the search. (Online version in colour.)

of host manipulation by parasites, which involves its very depiction in the popular media and the scientific literature.

2. How have the popular media and the scientific literature portrayed host manipulation?

Many online newspapers and magazines (referred to as popular media throughout the text) struggle to maintain readership in the age of digital journalism [17,18]. The competition resulting from this is a known factor promoting sensationalism, which is a writing style that provokes interest at the expense of accuracy [19]. This type of journalism typically includes exciting headlines and covers not only crime stories and scandals but also 'hard' news like science and technology [20]. Therefore, unsurprisingly, the popular media outlets that have reported on host manipulation tend to focus on parasites that cause spectacular changes in the host (e.g. the 'caterpillar tentacles' of snails infected with *Leucochloridium paradoxum* [21]) or ones that infect humans (e.g. *Toxoplasma gondii*) (electronic supplementary material, part A). Understandably, these stories typically include captivating words such as 'mind control', 'zombie' or 'hijack' in their title and main text, along with catchy headlines that may attract readers (figure 1*a*). While the use of such wording, which appears to be either anthropomorphic in nature (i.e. words that give humanlike characteristics, emotions, or intentions to non-human agents [22]) or directly borrowed from science fiction, may increase readership and result in profit for media corporations, the words themselves are inherently vague and misleading. Obviously, parasites do not literally hijack the body of their hosts (i.e. there is no unlawful seizure of the host at play). Nor do they cause the resurrection of dead hosts with an insatiable appetite for brains. But if popular media have widely adopted the use of such captivating, yet ambiguous words to describe host manipulation, how has the subject been represented in the scientific literature?

A quick search in Web of Science for articles and review papers that include eye-catching words describing host manipulation in their title or abstract shows some revealing trends (eye-catching words refer to metaphors, including the anthropomorphisms and terms appropriated from science fiction that are widely used in popular media; figure 1*a*). First, the usage of such words tends to appear in the scientific literature during the late 1990s and the 2000s, a period that coincides with the biological significance of host manipulation being put under scrutiny [12] and a renewed interest around host manipulation in the mid-2000s (fig. 1 in [15]). Second, while some words such as 'puppeteer' or 'bodyguard' appear only to be used in a small number of papers per year, other words like 'zombie' and 'hijack' occur more often and are used as frequently or more every year (figure 1*b*). Third, the popular media appear to focus on a slightly different set of catchy words than what can be found in the scientific literature (figure 1). Interestingly, most of the popular media articles covering host manipulation, containing the catchy vocabulary described earlier, started to appear during the mid-2010s onwards (electronic supplementary material, part A). Thus, one could advance that the usage of catchy, yet misleading words to describe host manipulation in the scientific literature pre-dates its adoption in popular media. This in itself does not indicate that the exaggerated claims and sensationalism surrounding host manipulation in the popular media are a direct consequence of what is published in the scientific literature. Perhaps the increased usage of a word like 'zombie' in the scientific literature is fuelled by popular media, or vice versa, thus creating a circular chain of causality (figure 1) [23]. Regardless, it does suggest that both researchers and reporters, at the risk of being inaccurate, employ sensationalism or hype to perhaps attract more readers [24]. Interestingly, hype is not uncommon in scientific writing; researchers regularly exaggerate their study systems in areas such as grant applications and institutional press releases [25]. While this strategy may appear harmless at first glance, the misleading vocabulary that represents host manipulation in both the popular media and the scientific

literature could unintentionally impact its narrative and our general perception of the topic.

3. Does the repeated use of catchy words impact the general narrative of host manipulation?

As previously mentioned, the vocabulary of host manipulation is rife with anthropomorphisms. Even the word 'manipulation' strongly implies the humanlike ability to influence someone in a cunning and deceitful manner. Other words used to describe parasitic manipulation, such as 'control', 'usurp', 'brainwash' or 'bodysnatcher', are all anthropomorphic by definition. The use of humanlike descriptors is common across many disciplines [22,26]; it helps readers to connect with a certain topic and perhaps better understand it, all while improving the capacity to retain information on said topic [27]. Anthropomorphisms can even impact how people view nature, going as far as shaping their opinions on environmental protection [28]. However, the general consensus drawn from research on science education strongly suggests that attributing humanlike qualities like intention to non-human subjects impedes the understanding of complex phenomena such as natural selection and climate change. People tend to use their generic background knowledge to integrate novel concepts, which can result in deep-rooted misconceptions about complex phenomena [29,30]. Given that host manipulation is an intrinsically complex subject covering many biological interactions between two co-evolving species [31], the abundant anthropomorphisms used to simplify and explain it may very well hinder its understanding by non-specialists and specialists alike. However, attributing humanlike descriptors to parasites may be just one of the factors impeding the factual interpretation of host manipulation.

All the anthropomorphisms and words borrowed from science fiction that are used to describe host manipulation form the essence of scientific metaphors (figure 1), which basically means that they do not literally apply to biological systems [32]. The power of such words becomes ever clearer when they are recognized as metaphors. Determining if a word such as 'manipulation' is metaphorical can be done with three diagnostic criteria [33]: expressiveness, paraphrasability and silliness. First, the expressiveness of a metaphor refers to its ability to evoke analogies that can be interpreted as predictions. For example, by assuming that a certain parasite manipulates its host, one can imagine that it is doing so to gain an increase in fitness. Predictions could thus be made regarding the changes in the host phenotype that increase parasite fitness, which of course depends on the nature of the host–parasite association. Second, paraphrasability highlights the imprecise nature of a metaphor. For instance, a 'trematode that manipulates its fish host' is not as precise as 'fish infected with trematodes are more conspicuous to predators'. Third, the silliness of a metaphor is usually accentuated when it is applied literally. As stated earlier, it is highly unlikely that any parasite is literally capable of cunning or deceit, two defining characteristics of manipulation.

Recognizing that host manipulation and its associated terms are metaphors is an important step in understanding the impact they have on our perception of the phenomenon. As defined by their expressiveness, metaphors are tools that help researchers think about their systems, which in turn helps generate novel predictions and explanations [33]. Moreover, metaphors can help bring scientists from different perspectives together to think about the same phenomenon, simply because metaphors can be interpreted in many ways [32]. However, researchers must be aware that when they use metaphors such as host manipulation and its many spinoffs, they may be highlighting certain aspects of their study systems while hiding other important ones [34]. As mentioned earlier, metaphors are vague, which could result in numerous contradictory interpretations. In practice, anyone can decide what 'hijack' or 'control' mean if they are used metaphorically. Because of their vagueness, metaphors are also difficult to quantify or measure. For example, it would be impossible to quantify the 'zombification' of ants infected with *Ophiocordyceps*. However, the real danger of metaphors lies in their reification, which occurs when they are treated as a real part of nature [35]. Researchers must be cognizant of the potential dangers of scientific metaphors and understand that they can mask important information and dilute truth. Host manipulation as a metaphor may help predict how a certain parasite changes host phenotype. However, this metaphor may hide other aspects of host–parasite associations, such as the extent to which parasites actually cause phenotypic changes in their hosts. Ultimately, not recognizing host manipulation and its associated terms as metaphors could lead to wrongful interpretations and generate misconceptions of the phenomenon.

Metaphor or not, whatever is published in the popular media and the scientific literature may have long-lasting impacts on human memory and belief systems. Known as the illusory truth effect [36], humans tend to remember erroneous statements if they are repeated enough and can even create false memories about them [37]. This tendency is stronger when the statement is presented using an official format such as a news article or a publicity slogan [38]. People are also known to incorporate information from works of fiction (e.g. novels and movies) into their general knowledge of the real world [39]. When presented with contradicting new information on a certain topic, people tend to accept the older repeated statements as truer, even when they are false [40,41]. Therefore, repeated statements, be they true or false, can form the foundations of false memories that are gradually accepted as a fact. For example, the recurrent sensationalism in news media is a known factor affecting the general perception of climate change in humans [42]. So, could the illusory truth effect impact the perception and understanding of host manipulation of both specialist and non-specialist readers? Well, combined with the dangers of using metaphors and the impact of anthropomorphisms on generating misconceptions about complex phenomena and hindering the ability for people to understand and interpret them, the abundant repetition of exaggerated and misleading claims about host manipulation in both the popular media and the scientific literature may be hampering the ability to properly communicate fact over fiction (figure 1). As such metaphors are vague and can hide certain truths, not only could this be steering the popular perception of host manipulation away from fact-based territory, it could very well have shaped the general scientific narrative of recent years.

4. Has the fictional narrative of host manipulation become fact?

If the hypothesis 'the use of science fiction, anthropomorphisms and catchy words to describe host manipulation by

parasites in both the scientific literature and the popular media impacts its general narrative and popular perception' were true, one could make the following prediction: it should be possible to find claims in the popular media and the scientific literature that are either fully or partially unsubstantiated or that negate the empirical evidence or lack thereof. Such claims could be made regardless of relative research effort, i.e. highly studied parasites versus ones that receive little attention. For example, the heavily studied *T. gondii* [43], a protist known for its negative health effects on humans and its wide-ranging behavioural impacts on warm-blooded animals [44–46], supposedly manipulates small rodents to increase their chances of getting eaten by felids. In the life cycle of *T. gondii*, small rodents and felids represent the intermediate and final hosts, respectively [47]. To achieve transmission between hosts, *T. gondii* has been said to cause a 'fatal feline attraction' in rodents by removing their aversion to cat urine through the expression of the disruptive dopamine-signalling *AaaH2* gene [48,49]. This catchy narrative has been widely reported in the popular media (electronic supplementary material, part A) and in the scientific literature, even within recent years (e.g. [50–52]).

However, it was shown that experimental strains of *T. gondii* without the *AaaH2* gene cause the same behavioural patterns in rodents as did the wild strains [53]. More recently, it was shown that *T. gondii* cyst load in the brains of infected mice correlates with neuroinflammation, which could result in behaviours related to lower anxiety and an aspecific aversion to predators [54]. This evidence supports the idea that the complex physiological impacts of *T. gondii* in warm-blooded animals are more than one dimensional; they are unlikely to result in a simple dopamine-related attraction towards cat urine. Moreover, *T. gondii* may have experienced little to no selective pressures to adaptively manipulate small rodent hosts. In fact, there is no sound evidence that the behavioural changes in infected rodents increase the transmission of *T. gondii* to felids [55]. The evidence surrounding the 'fatal feline attraction' is inconsistent and contradictory at best (as it is for all the impacts of *T. gondii* on human and non-human behaviours [56]). The fatal attraction of infected rodents would appear to be a reasonable explanation because it fits with the narrative that *T. gondii* must change hosts to complete its life cycle. However, the predominant lineages throughout Europe and North America are essentially clonal and do not need to reproduce sexually in felid hosts [57,58]. This raises the question: since its conception, has the anthropomorphic concept of fatal attraction in infected rodents driven the scientific narrative and impacted the general perception of the extent of host manipulation by *T. gondii*? Arguably, it has, because despite all the contradictory evidence challenging the claims of *T. gondii* host manipulation [55,56], it is possible to still find such misleading claims in recent works from both the popular media and the scientific literature cited earlier. Unless a complete scope of the literature is done to fully understand the extent of *T. gondii* host manipulation, it may be less exacting to adopt the popular narrative of the 'fatal feline attraction' at face value. Although this metaphor is relatively simple to understand, its current usage may mask the true complexity of *T. gondii* host manipulation. It would appear that, despite evidence to the contrary, the 'attractive' narrative of *T. gondii* host manipulation still holds a firm place in the scientific narrative.

5. The legend of the hairworm

With a parasite like *T. gondii*, which has been intensely researched around the world for decades [43], it is admittedly difficult to assess the full impact of a few catchy words on the entire scientific and popular narrative of *T. gondii* host manipulation. However, the effects of sensationalism become ever clearer when looking at examples of host manipulation by parasites that have received far less scientific scrutiny. Take, for example, gordiid hairworms (phylum Nematomorpha), which are parasites with a complex life cycle that live as dormant cysts within aquatic insect larvae and mature into long, slender worms typically within terrestrial scavenger-type insects [59,60]. Hairworms have a peculiar life cycle: the aquatic insect larvae that harbour cysts serve as intermediate transport hosts when they mature, reproduce, and die on land [61,62]; the final hosts become infected by consuming dead intermediate hosts with cysts. Most hairworm species must exit the final host to mate and lay their eggs in freshwater; however, there are some exceptions to this [63,64]. Therefore, as they develop and mature within terrestrial insects, hairworms must somehow return to water to complete their life cycle. The hairworm could rely on chance and escape from the host when close to water (hairworms are prone to desiccation), but observations on infected hosts, dating back to the nineteenth century [65], suggest that the host brings the hairworm to water [66]. Whether this unusual behaviour is the result of cooperation from the host or of host manipulation by hairworms, or a combination of both, is a question that still stands. Nonetheless, the popular media and the scientific literature have strung a far more sinister and fictitious narrative around hairworms.

According to popular media, hairworms have nearly absolute control over their insect hosts (electronic supplementary material, part A). They are apparently capable of coercing the host to commit suicide, forcing it to seek water at all costs. The host then supposedly drowns itself in a kamikaze-style death dive, unable to leave water under the mind-controlling powers of the hairworm (figure 2*a*). Fantastical though this narrative is, not one of these extraordinary claims is currently supported by any data. Currently, there is no empirical evidence supporting the hypothesis that infected hosts actively seek water or that hosts voluntarily jump into water when close to it [67]. Even though these ideas are testable, the sheer lack of evidence would make them appear like adaptationist just-so stories [68]. In fact, the few studies that have compared infected to uninfected hosts [67,69–75] have found perhaps a more subtle behavioural alteration possibly induced by hairworms. What has been suggested is that infected hosts tend to move around more, perhaps erratically, than uninfected hosts [74], which has received some empirical support [75] (figure 2*b*). Also, the behavioural changes in infected hosts appear to be circadian in nature and only mature hairworms are capable of inducing behavioural change [67,70,73]. Histological and biochemical studies have shown differences in neurogenesis and in levels of polyamines, monoamines and amino acids between infected and uninfected hosts, which may impact host behaviour [69]. Proteomic studies also showed differential expression of proteins between infected and uninfected hosts that relate to neurogenesis, the circadian rhythm and neurotransmitter activities in insects [70,73]. However,

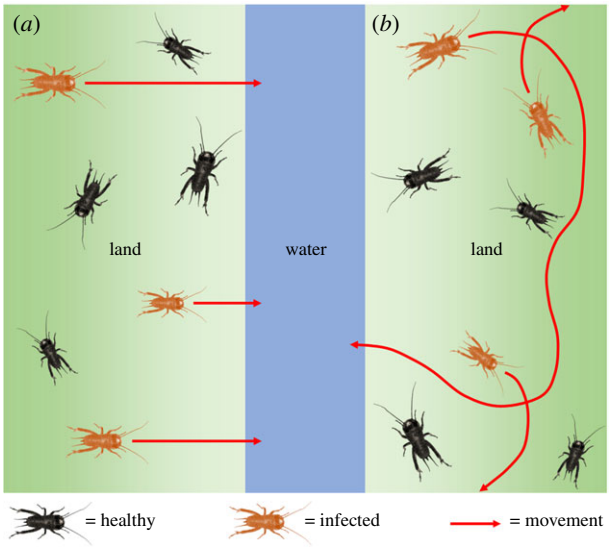


Figure 2. Behavioural depictions of terrestrial insects infected with hairworms (Nematomorpha). (*a*) Behaviour of infected insects depicted in the popular media (online newspaper and magazine articles) and the scientific literature. According to this narrative, hairworms coerce their hosts to seek water and then force them to commit suicide by jumping into water and drowning. (*b*) Based on the available evidence, infected insects appear to be more active and to move around erratically, which may or may not lead them to water. Very little is currently known on the proximate mechanisms of hairworm host manipulation that are behind this more subtle change in behaviour. (Online version in colour.)

despite these promising indications, all the aforementioned studies compared only field-caught individuals; no observations were performed on experimentally infected hosts. While this correlative and circumstantial evidence does offer some insight on the more subtle nature of behavioural changes in hosts infected with hairworms, it is impossible to draw sound conclusions of causation from naturally infected hosts that come with their own set of confounding and uncontrolled variables [11,15,76]. Moreover, some of the physiological differences between infected and uninfected hosts may simply result from the fortuitous side effects of infection or from the competition for nutrients between the hairworm and the host [59]. Thus, if hairworms adaptively manipulate their hosts to increase the likelihood of entering water, the evidence for a proximate mechanism remains very weak. To date, the observations simply do not support the claims in the popular media that hairworms coerce their hosts to seek water and commit suicide by drowning in it.

This extraordinary narrative is not only found in the popular media. The anthropomorphic suicide of hosts infected with hairworms is a concept as old as the question of whether hairworms adaptively manipulate their terrestrial hosts [67]. In fact, the scientific narrative closely mirrors that of the phenomenal manipulative capabilities of hairworms depicted in popular media [8,50,73–75,77–79] (figure 2*a*). While the use of such metaphors may seem quirky and harmless, and may be intended to help readers better connect with the subject, the repeated use of these anthropomorphisms and other misleading statements could ultimately impact the general understanding of the complex phenomenon that is host manipulation. Of course, it should seem obvious that infected insects do not literally commit suicide (see [80]) nor do hairworms come close to coercing their hosts to seek water. The case of misleading readers could also be made for other parasites that seemingly manipulate their host and have been researched even less (e.g. the nematode *Myrmeconema neotropicum* that appears to induce fruit mimicry in ants [81]). However, the use of such false narratives as hallmarks of host manipulation is still found throughout review articles and articles of the past few years. Non-specialist and specialist readers, who may not verify these exaggerated claims at the source, could build a fictional representation of the extent of host manipulation. One could thus argue that, over time, the metaphorical nature of host manipulation and its many spinoffs, repeated in popular media and endorsed by the scientific literature, may very well become indisputable fact.

6. Concluding remarks and future perspectives

Adaptive host manipulation is inherently difficult to study because separating accidental by-products of infection from trait-mediated manipulation, which occurs between a parasite and a host that may have co-evolved for millions of years, is intricately complex [8,82,83]. Consequentially, there has been a strong focus on the same old model organisms [15]. Despite these challenges, this opinion piece is in no way a critique of the quality of research on host manipulation developed in the past few decades. However, for the sake of argument, if the scientific literature continues to exaggerate the claims of host manipulation by parasites without check, it is possible that, for example, specialists and non-specialists alike will start to unequivocally believe that hairworms are capable of creating suicidal insect hosts or that *T. gondii* causes rodents to be attracted to cat urine. The fact is that these complex host–parasite systems need far more research effort to arrive at any sound conclusion on the nature of host manipulation. A holistic undertaking, incorporating many different scientific viewpoints, from the proximate (e.g. transcriptomics and genomics) to the ultimate (e.g. behavioural and evolutionary studies), would greatly enhance our ability to tease apart the intricate molecular interactions between host and parasite and better understand the true adaptive nature of host manipulation [68,84,85]. But all things considered, no piece of scientific writing, from peer-reviewed publications to grant applications and institutional press releases, is completely free from certain embellishment (including the current commentary). Metaphors have merit, and researchers should use them to better understand complex phenomena and make insightful predictions. However, it is imperative that researchers understand the potential dangers associated with metaphors and strive to use objective descriptions to communicate their findings as accurately as possible. If not, the use of anthropomorphisms and science fiction, fuelled by sensationalism and repeated abundantly by the popular media, could ultimately hamper our ability to convey a factual narrative and to correctly interpret and understand the complexities and scope of host manipulation by parasites.

Data accessibility. The data are provided as electronic supplementary material.

Competing interests. I declare that I have no competing interests.

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