



Investment in multiple defences protects a nematode–bacterium symbiosis from predation



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The act of predation often comprises multiple sequential steps whereby prey can employ defences at all or some of these stages to deter predation. However, investment in defences is costly unless they are outweighed by conferring some benefit to the bearer. One system that employs multiple defences is that of the entomopathogenic nematode *Heterorhabditis bacteriophora* and its symbiotic bacterium *Photobacterium luminescens*. This nematode–bacterium complex infects and kills soil-dwelling insect larvae, in which they then reproduce and juveniles emerge 2 weeks later. Predation of the infected host cadaver at any point during infection is fatal for the parasitic colony inside. Infected individuals, however, turn red, produce a chemical defence, bioluminesce and smell strongly at various stages of the infection process. We tested whether these colour and scent cues conferred a benefit to the infecting nematode–bacterium complex, utilizing feeding trials of nematode-infected waxworms, *Galleria mellonella*, with wild-caught great tits, *Parus major*. We tested for multimodality, as the cues are in different sensory modalities, and found no overall benefit in terms of initial attack on the first prey item, although this does not rule out the possibility of multimodality within this system. We then examined the first five prey attacked and found that scent overshadowed colour at various stages of infection, in terms of reducing levels of attack, but not when both signals were in concert in terms of consumption of infected individuals.

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Predation is virtually ubiquitous in the natural world with many animals experiencing the risk of predation at some part of their life history. This has driven the evolution of a wide variety of anti-predator defences employed between species (Caro, 2005) and within species (van Buskirk, 2001). One reason for this is that individuals face attack from many predatory species; for example, plants face attack from multiple predators in the form of insects and pathogens (Maleck & Dietrich, 1999). However, this is not the sole reason for within-individual variation in defences as a single individual can also utilize different defences against different predators in different attacks (Caro, 2005).

The predation process is often broken down into sequential steps with the most frequently cited being those described by Endler (1986, 1991). He proposed that predation can be split into discrete stages consisting of detection, identification, approach, subjugation and consumption (Endler, 1986). Prey are able to

counteract this through multiple defences which can act at one or more stages, meaning that prey can employ defences at each stage of attack to deter predation. However, defences are usually costly and each additional defence adds an associated cost (Caro, 2005). Different costs of various defences have been considered in depth in Ruxton, Sherratt, and Speed (2004). Endler (1991) argued that investment in a defence at a given stage of predation would reduce the benefit of investment in later stages, suggesting investment should be biased towards earlier defences. However, there are plenty of examples where individuals do invest in defences in later stages of predation (Edmunds, 1974; Eisner, Eisner, & Siegler, 2005 and references within).

A growing body of literature aims to examine this phenomenon whereby individuals invest in later defences and how prey invest across different defences. Broom, Higginson, and Ruxton (2010) utilized a simple model to explore when prey should invest in a single or multiple defences. When the ratio of the constitutive cost to the benefit of defences is low and similar, Broom et al. (2010) predicted investment across both defences. Furthermore, investment in multiple defences at different stages of predation are predicted when defences are relatively cheap or the individual has

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more resources available for investment in defence (Wang, Ruxton, Speed, & Broom, 2017). Additionally, investment in multiple defences has implications for the evolution of both predator and prey, as successful attack of a predator on prey depends on the number of defences for each species (Gilman, Nuismier, & Jhwueng, 2012).

Although a number of studies have examined multiple defences (van Buskirk, 2001; Jongepier, Kleeberg, Job, & Foitzik, 2014), these are normally considered in the context of multiple predators (Maleck & Dietrich, 1999; Poitrineau, Brown, & Hochberg, 2003; Rigby & Jokela, 2000; Sih, Englund, & Wooster, 1998; War et al., 2012). Individuals are normally attacked by multiple species of predator at some stage of their life cycle and so having multiple barriers, or barriers acting at different stages of predation, would be beneficial. This is supported by the literature on multimodality where it is suggested that the evolution of multimodal signals may have arisen to target predators with different perceptual capabilities (Rowe & Halpin, 2013). However, what seems to be lacking in this area is the view of multiple defences in a multimodal context. It seems logical that having multiple defences in a sequential fashion is beneficial against a single predator (Chen, 2008 and references within) but they can also be beneficial against a range of predators or parasites (Gilman et al., 2012; Poitrineau et al., 2003; War et al., 2012).

One such system that incorporates both these ideas is that of the entomopathogenic nematode *Heterorhabditis bacteriophora* and its symbiotic bacterium *Photorhabdus luminescens*. The nematode infects and kills soil-dwelling larval insect hosts within 48 h, although, rather than decaying (Milstead, 1979), they undergo a number of changes. The symbiotic bacteria must then provide defences to replace those of the now-dead host (Jones, Fenton, & Speed, 2016). Infected hosts bioluminesce (transiently), turn permanently red, become unpalatable (Ffrench-Constant & Bowen, 2000) and produce a strong-smelling odour. A key point here is that the infected carcass does not decay during the infection; rather it is preserved by antimicrobials synthesized by *P. luminescens* (Clarke, 2008). Hence the repellent odour is not that of a decaying corpse but something conferred by the nematode and/or its symbiont. Nematodes reproduce within this changing host and emerge 10–14 days postinfection before repeating the cycle of infecting a new host by cruising through the soil (Johnigk & Ehlers, 1999). Hence, predation at any stage will kill both the nematode and the symbiotic bacterium. Although each of these defences is a constitutive rather than an induced defence, they occur at different points of infection and at different stages of predation. Following Endler's (1991) framework these various defences mostly fall into the identification stage of predation, with noxiousness in the subjugation stage.

Previous work examining this system has shown an adaptive value to these host changes as chemicals produced by *P. luminescens* deterred ants from feeding on waxworms infected with this bacterium (Baur, Kaya, & Strong, 1998; Gulcu, Hazir, & Kaya, 2012; Zhou, Kaya, & Goodrich-Blair, 2002). Furthermore, avian predators also showed an aversion to *H. bacteriophora*-infected waxworms (Fenton, Magoolagan, Kennedy, & Spencer, 2011). This aversion was primarily attributed to the visual appearance of the infected waxworms. However, this experiment did not explicitly test the olfactory component of this avoidance but, if handled, infected prey tended to be rejected more frequently than uninfected ones (Fenton et al., 2011). This effect was only seen in prey 5 or 7 days postinfection whereas at day 3 postinfection avian predators were equally likely to select an infected or uninfected waxworm. Furthermore, Foltan and Puza (2009) found that a related nematode species, *Steinernema affine*, deterred beetles from eating infected waxworms. Jones, Fenton, & Speed (2016) have recently reported an olfactory deterrent towards carabid predators

whereby ground beetles avoided the scent of *H. bacteriophora*-infected waxworms across a range of infection stages. However, ground beetles fed on infected and uninfected waxworms to a similar extent during early infection stages, before avoiding infected individuals as infection progressed. Recently, Jones, Clarke, Fenton, Speed, and Hurst (2017) have found that bioluminescence acts as a deterrent early on during infection, with house mice, *Mus musculus domesticus*, avoiding bioluminescent over non-bioluminescent prey.

Although deterrent effects have been found for the defences individually (Baur et al., 1998; Fenton et al., 2011; Gulcu et al., 2012; Jones et al., 2016) there have been no studies explicitly testing combinations of these defences to determine why so many barriers to predation exist in this system. Our aim was to test a combination of the olfactory and visual deterrents (both deterrents considered at the identification stage of predation) to determine whether there is an advantage of having either of these defences singly or in concert. To do this we conducted three experiments; the first two to examine the effect of scent and colour in isolation and the third to examine colour and scent in concert.

METHODS

Experiments were run at the Konnevesi Research Station, University of Jyväskylä, Central Finland from January to March 2014. Permits for experiments with wild birds were issued by the Central Finland Centre for Economic Development, Transport and Environment (KESELY/1017/07.01/2010) and the National Animal Experiment Board (ESAVI-2010-087517Ym-23). We examined multimodality first by examining the first attack in each experiment and then carried out a broader analysis to see whether it was consistent, even when subsequent behaviours were different.

Nematode Culturing

Waxworm larvae (Livefoods Direct, Sheffield, U.K.) were infected with the nematode strain *H. bacteriophora* TT01 (supplied by D. Clarke & S. Joyce, University College Cork, Ireland) by infecting 10 waxworms per petri dish containing 90 mm filter paper with 1000 infective juveniles/ml stock nematode solution. These were then frozen or utilized fresh depending on each of the three experiments.

Bird Housing

Ninety wild great tits were trapped at feeding sites at Konnevesi Research Station and ringed. Birds were kept in individually illuminated, ventilated plywood cages (64 × 46 cm and 77 cm high) indoors in a daily light period of 11.5 h. Sunflower seeds, feed balls (lard and seeds) and fresh water were available ad libitum except for 2 h prior to trials when birds were food deprived to ensure motivation to forage during experimentation. All birds were released at their capture sites at the end of the experiment.

Experimental Arena

The experiments were run in illuminated, ventilated plywood cages (50 × 50 cm and 57 cm high) that contained a perch and fresh water bowl. Birds were allowed to habituate to the experimental cage for at least 1 h during which they had to consume two sunflower seeds before the experiments took place. The birds were observed through a one-way plastic front and in a dark room so they were less aware of an observer. Owing to a lack of birds towards the end of the season, some birds ($N = 7$) participated in multiple trials but only across the colour only and scent only trials.

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