

Introduction



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[†]This special issue emerges from a Royal Society meeting organized at the Kavli Centre at Chicheley Hall in Buckinghamshire on 12–13 June 2017. The meeting gathered scientists from different disciplines working on pathogen/parasite avoidance across taxa from invertebrates to vertebrates including humans, to discuss the evolution of parasite avoidance behaviour and its consequences. Audio recordings of the talks can be accessed at <https://royalsociety.org/science-events-and-lectures/2017/06/evolution-pathogen-parasite/>.

Evolution of pathogen and parasite avoidance behaviours[†]

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All free-living animals are subject to intense selection pressure from parasites and pathogens resulting in behavioural adaptations that can help potential hosts to avoid falling prey to parasites. This special issue on the evolution of parasite avoidance behaviour was compiled following a Royal Society meeting in 2017. Here we have assembled contributions from a wide range of disciplines including genetics, ecology, parasitology, behavioural science, ecology, psychology and epidemiology on the disease avoidance behaviour of a wide range of species. Taking an interdisciplinary and cross-species perspective allows us to sketch out the strategies, mechanisms and consequences of parasite avoidance and to identify gaps and further questions. Parasite avoidance strategies must include avoiding parasites themselves and cues to their presence in conspecifics, heterospecifics, foods and habitat. Further, parasite avoidance behaviour can be directed at constructing parasite-retardant niches. Mechanisms of parasite avoidance behaviour are generally less well characterized, though nematodes, rodents and human studies are beginning to elucidate the genetic, hormonal and neural architecture that allows animals to recognize and respond to cues of parasite threat. While the consequences of infection are well characterized in humans, we still have much to learn about the epidemiology of parasites of other species, as well as the trade-offs that hosts make in parasite defence versus other beneficial investments like mating and foraging. Finally, in this overview we conclude that it is legitimate to use the word 'disgust' to describe parasite avoidance systems, in the same way that 'fear' is used to describe animal predator avoidance systems. Understanding disgust across species offers an excellent system for investigating the strategies, mechanisms and consequences of behaviour and could be a vital contribution towards the understanding and conservation of our planet's ecosystems.

This article is part of the Theo Murphy meeting issue 'Evolution of pathogen and parasite avoidance behaviours'.

1. Introduction

While every child learns about predator–prey relationships, and identifies with the fears that drive the avoidance of predators, from an early age, the same is not true for parasite–host relations. Parasites are more common than predators, are more diverse [1], contain greater total biomass [2], may have a greater ecological footprint [3] and may exert a stronger selective force on their hosts than predators [4]. However, parasites (which include viruses, bacteria, fungi, protozoa, helminth worms, arthropods and social parasites) take myriad forms, are often invisible, use complex and devious strategies, and they also occasion an emotion: disgust, which may be one reason for their relative neglect by scientists [5]. This special issue of *Philosophical Transactions of the Royal Society* takes up the challenge of bridging this gap (building on the work of Benjamin Hart and colleagues [6–11], Val Curtis and colleagues [12–15], and the special issue 'Disease avoidance: from animals to culture' from Stevenson *et al.* [16]). It reviews the strategies, mechanisms and consequences of parasite avoidance

behaviour across Animalia, from the nematode to social insects, in the aquatic habitat, through avian species to terrestrial mammals including rodents, ruminants, primates and humans.

By taking this cross-species perspective on parasite avoidance behaviour, it quickly becomes apparent that there are multiple overlaps, but also that there are multiple gaps in our knowledge. Figure 1 depicts the state of our knowledge. In invertebrates, we are beginning to understand the molecular and cellular mechanisms of infection avoidance behaviour, as well as the strategies employed to evade parasites. In vertebrates, however, while understanding of the mechanisms of behaviour is much poorer, disease avoidance strategies are better described, and our knowledge of the epidemiological consequences of parasite infection is well developed, particularly in humans.

By bringing together contributions from specialists in parasite avoidance behaviour across species, a number of patterns begin to emerge. In the host–pathogen evolutionary arms race hosts have had to adapt to the infective strategies of parasites which track, evade detection, infiltrate, establish in, and on, and exploit hosts [17]. Host counter-strategies include hiding from, or fleeing from, parasites and their propagules, avoiding the conspecifics and the intermediate hosts that may contain them, and avoiding foods and habitat where parasite encounter is likely. Hosts can also remove parasites directly, or engineer their own niches so as to make their environments un conducive to parasites. These strategies can be found across taxa [14]. To accomplish such behaviour, hosts respond to cues that may be chemosensory, mechanosensory or visual, they may learn from episodes of sickness or from conspecifics, or they may carry out pre-programmed routines independent of any cue to parasite presence [17–20].

A further pattern emerging from this special issue is a general shift in the field from anecdotal reports of observed behaviour to the experimental testing of hypotheses, which has proven possible in captive species as diverse as bees [21] and bonobos [20], and, in some cases, in the wild as well [22,23]. It is also exciting to see how cross-disciplinary collaboration is bearing fruit, for example, where geneticists, cell biologists and behavioural scientists are collaborating to provide a complete picture of nematode infection avoidance behaviour [18]. A further promising interdisciplinary development is the engagement of psychologists who recognize the evolutionary continuity between disease avoidance behaviour across species and ask how this relates to the emotion of disgust in humans [24–27].

2. An evolutionary approach to understanding pathogen and parasite avoidance

In this introductory article to ‘Evolution of pathogen and parasite avoidance behaviours’, we discuss how the research presented in this special issue contributes to our understanding of the strategies, mechanisms and consequences of pathogen/parasite avoidance.

(a) Strategies

Our opening paper by Hart & Hart [28] explores the range of behavioural strategies employed by mammals to avoid and

remove various forms of parasites and pathogens, from ectoparasites such as flies and ticks to external pathogens like pathogenic bacteria potentially present on the skin surface, to internal parasites such as gastro-intestinal nematodes. As pointed out in their review, these strategies are species-specific and reflect the environment that the animal inhabits. For example, Asian elephants (*Elephas maximus*) use branches to repel biting flies from regions of their body where the skin is thinner and vulnerable to such blood-sucking ectoparasites. Rats, on the other hand, lick their penis after copulation and their saliva has proven bactericidal properties against genital pathogens. This latter behaviour may protect males from potential venereal diseases harboured by a female they just mated with, and may also protect females they might subsequently mate and have offspring with, which ultimately could enhance that male’s fitness. Another example of behavioural strategy against orofaecally transmitted parasites this time concerns denning canids which defecate and urinate away from the den and rest areas. Newborns, however, have no mobility, hence mothers keep the den clean by consuming the fresh excreta. Mothers avoid infection because parasite ova take several days to hatch into infective larvae.

One widespread strategy against ectoparasites in mammals—grooming [28], is also characteristic of bird hygiene—preening and scratching [17]. In addition, birds present a large panel of ectoparasite avoidance behaviours such as anointing, sunning and nest fumigation [29]. In this special issue, Bush & Clayton [17] review some of the most up to date findings regarding anti-parasite behaviours in birds. They classify these into five categories: body maintenance, nest maintenance, avoidance of parasitized prey, migration and tolerance. The authors acknowledge that most research into avian behaviour remains observational in nature and needs to become more experimental. They suggest future research directions such as investigating interactions between immunological and behavioural defences, the energetics of anti-parasite behaviours, and the necessity of early exposure to parasites to develop efficient behavioural defences. The theme of ectoparasite avoidance is further explored in this issue by Kupfer & Fessler [25] who review the evidence for ectoparasite defences in animals and humans (see below).

Some of the best experimental models of parasite avoidance behaviour may be the social insects, which are also some of the most strategic fighters when it comes to combatting social parasites. In their review, Grüter *et al.* [30] show the different defence traits that social insects such as ants, termites, social wasps and bees have evolved to interrupt the entry and establishment of parasites into the colony. These strategies involve several steps; firstly, the avoidance of contacting parasites or being detected by them (e.g. nesting near parasite deterrents, having several queens, or building a nest with architectural features preventing invasion); secondly, the recognition of parasites and their rejection once avoidance has failed (relying on chemical cues); and finally, the avoidance of exploitation by social parasites (e.g. coordinated defence, resistance to parasite manipulation). However, if the parasites are successful in establishing themselves, then hosts must kill the parasitized brood or find ways to reproduce in the parasite’s presence, which can lead to the coevolution of host defensive traits and parasite invasive adaptations. One of these strategies of last resort is bee hygienic behaviour—a group defence against diseases in which

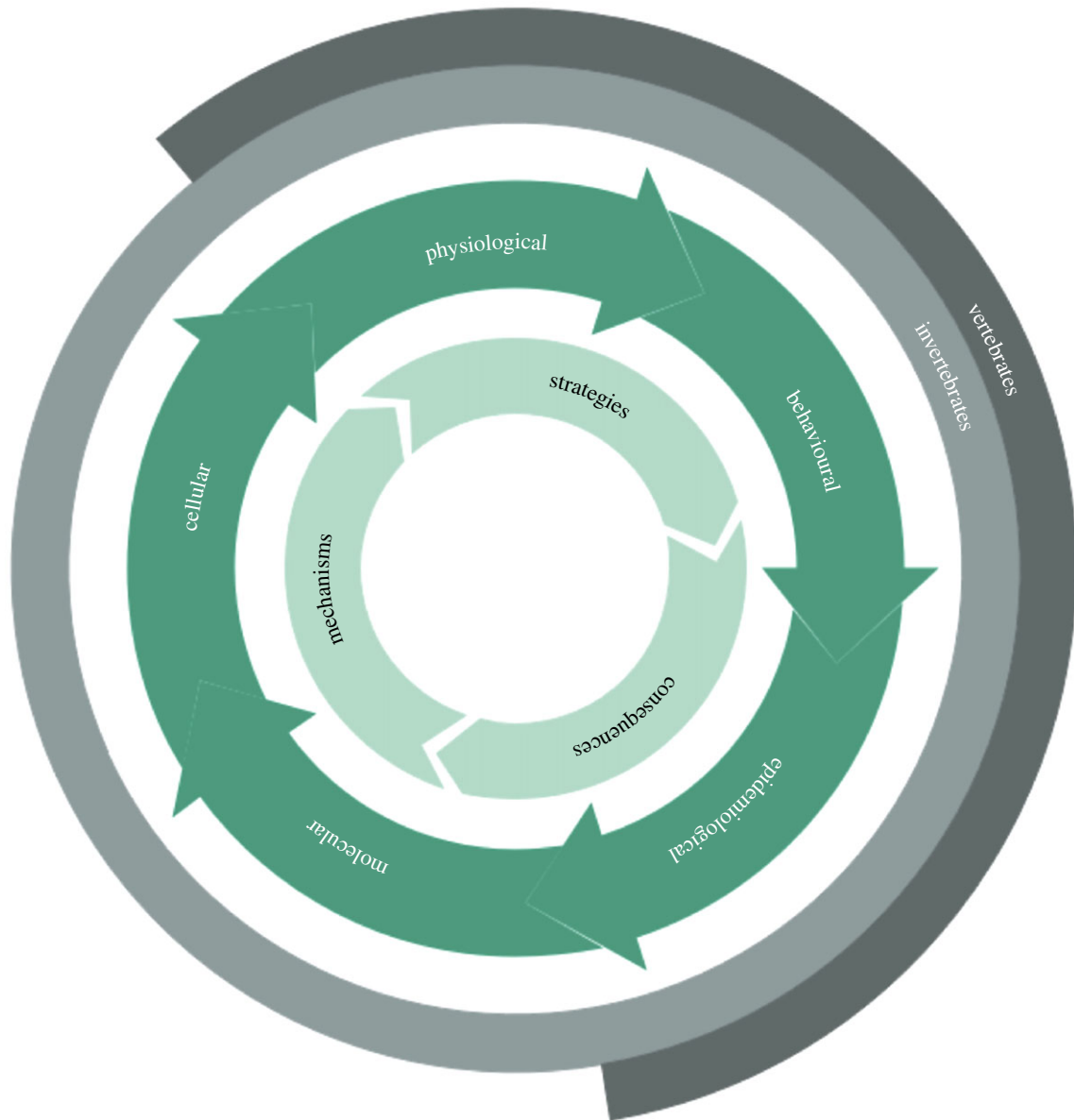


Figure 1. Towards a complete understanding of pathogen/parasite avoidance behaviour. As illustrated by the papers in this special issue the evolution of parasite avoidance behaviours provides an opportunity to take an interdisciplinary approach in order to fully understand the strategies, mechanisms and consequences of parasite avoidance behaviour.

workers remove dead, dying and diseased individuals from the nest. In honeybees (*Apis mellifera*), hygienic behaviour specifically refers to the uncapping and removal of dead larvae and pupae in sealed cells. Here, Al Toufaïlia *et al.* [21] provide an explanation for why this hygienic behaviour is uncommon in honeybees by demonstrating that even colonies of honeybees with low hygienic behaviour against sealed cells are highly hygienic against dead larvae in open cells.

All the examples of behavioural strategies mentioned above occur on land but what about pathogen/parasite avoidance in water? In their review, Behringer *et al.* [22] address some of the fundamental differences and similarities between parasite avoidance behaviours in terrestrial versus aquatic (marine and freshwater) environments. In the latter, parasites and pathogens are suspended in the water column which may increase the occurrence of contact. Thus, spatial avoidance of parasitism is one widespread strategy among aquatic invertebrates and vertebrates. Tadpoles (*Rana clamitans* and *R. sylvatica*), for example, avoid areas of the water column with high densities of parasitic flukes and this

behaviour was associated with lower levels of parasitism [31]. In addition, aquatic animals reduce infection risk by increasing or lowering activity levels, avoiding infected prey, avoiding infected mates, migrating, grouping and avoidance learning. Behinger *et al.* [22] discuss the mechanisms and cues that engender these avoidance strategies, as well as how anthropogenic activities may affect such behaviours.

(b) Mechanisms

Our current understanding of the mechanisms of parasite avoidance behaviours largely comes from research on invertebrates, amphibians and rodents, and focuses on only a few pathogens and parasites.

One way in which animals can minimize their risk of infection is to reduce contact with contaminated food. In this issue, Anderson & McMullan [18] show that the nematode worm *Caenorhabditis elegans* avoids lawns contaminated with the pathogenic bacteria *Microbacterium nematophilum* and by doing so, protects itself from the deleterious effects,

that is, slowed growth. Similarly, Sarabian *et al.* [20] show that bonobos (*Pan paniscus*), when exposed to food contaminated with conspecific faeces which may harbour pathogenic bacteria, viruses and parasites (e.g. *Salmonella typhi*, *Rotavirus* or *Giardia* spp.), balance their feeding decisions to minimize infection risk. The benefits of avoiding contaminated food shown in *C. elegans* have also been found in primates, as individuals that kept away from food contaminated with faeces and soil had lower levels of gastro-intestinal parasite infection [32].

Detecting pathogen threats can rely on different sensory modalities. *Caenorhabditis elegans* uses mainly its olfactory system for pathogen avoidance [33] and learns to avoid odours associated with infection by pathogenic bacteria [34], a behaviour analogous to conditioned-taste aversion found in mammals, snails, cuttlefish, fish and lizards [35–38]. Similarly, *Drosophila melanogaster* and the ball-rolling dung beetle *Scarabaeus (Kheper) lamarcki* avoid faeces enriched in phenol, suggesting that phenol is a widespread avoidance signal because of its association with pathogenic bacteria [39]. The detection of sick conspecifics in amphibians and crustaceans may also rely on chemical cues [40,41] and in mice the vomeronasal organ (involved in pheromone sensing [42]) mediates the avoidance of sick conspecifics via the detection of aversive cues contained in the urine of infected mice [43]. Supporting the role of its olfactory system in pathogen avoidance, Anderson and McMullan demonstrate that, in the case of avoidance of food contaminated with *M. nematophilum*, the avoidance mechanism predominantly requires signalling in multiple sensory neurons, although attachment of the pathogen (i.e. *M. nematophilum*) to non-neuronal cells in *C. elegans* tail, which activates the cellular immune response, is also required [18]. Bonobos, on the other hand, seem to use multisensorial cues to inform their feeding decisions [20]. For example, when all cues from the contaminant (i.e. faeces or soil) were present and associated with food items, bonobos clearly preferred the control items. Their sensitivity to contamination risk increases along a probability gradient as they prefer food farthest from the contaminant (i.e. faeces). In addition, bonobos exhibit reduced tactile, gustatory and tool use activities when exposed to contaminant (i.e. faeces, rotten fruit and rotten meat) versus control odours in a challenging foraging context. These results build on previous work showing the importance of visual [32,44,45], tactile [46] and olfactory [19,20] cues in food aversion in primates. While these experiments in bonobos aim at a better understanding of the ways in which the parasite avoidance system operates in primates, models such as *C. elegans* can be used to genetically dissect the molecular and cellular basis of feeding decisions under contamination risk.

Certain infection avoidance responses incorporate social cognition, such as social partner and mate choice, recognition and avoidance of strangers, or the process of individual and social learning of parasite avoidance itself [19]. Social insects like ants protect their colonies through collective defences that result in social immunity. In ants, workers first try to prevent infection of colony members. However, if this fails and a pathogen establishes an infection, unicolonial invasive garden ants (*Lasius neglectus*) perform a ‘destructive disinfection’ by specifically targeting infected pupae during the non-contagious incubation period of the pathogen, relying on chemical ‘sickness cues’ emitted by pupae. They remove the pupal cocoon, perforate its cuticle and administer

antimicrobial poison, which enters the body and prevents pathogen replication from the inside out, thus protecting the rest of the colony [47].

These social avoidance strategies involve multimodal sensory information and particularly olfactory cues as demonstrated in mice [43] and mandrills [48]. In their review, Kavaliers & Choleris [19] discuss the neurobiological aspects of these responses and the role that oxytocin, arginine-vasopressin and oestrogens play in social cognition and parasite avoidance. For example, oxytocin mediates the social avoidance of infected individuals via olfactory cues in female deer mice [49] and facilitates negative responses to out-group members in humans [50]. Similarly, previous research in mice has shown that oestrogen-receptors are necessary to discriminate between odours of infected and uninfected conspecifics, and call for further research investigating sex differences in social cognition and their neuroendocrine substrates, which mediate pathogen recognition and avoidance.

In humans, the emotion of disgust is suggested to be an adaptive system based in neural tissue that evolved to keep us away from sources of infection: the so-called Parasite Avoidance Theory of Disgust [5,12], supported by the strong correlation that exists between disgust elicitors and infectious agents [12,51,52]. In their research paper, Curtis & de Barra [27] test whether the factor structure of the disgust response in humans reflects the main transmission routes of infection: direct interpersonal contact; interpersonal contact through aerosolized droplets; interpersonal sexual contact; contact with a secondary host or vector; ingestion of contaminated food or water; and contact with a fomite. To do this, they generated a set of stimuli based on cues derived from the epidemiology of disease transmission. Using a factorial analysis approach, they identified patterns of covariation across these descriptions of infection threats presented to a large sample of people. Six domains emerged from this factorial analysis: atypical appearance, lesions, sex, poor hygiene, off foods and animals. These factors did not exactly mirror the transmission routes of infection but, instead, reflected different kinds of behavioural tasks involved in parasite avoidance. These six strategies for parasite avoidance may be universal, and examples in many other species can be found throughout this special edition, for example, fish avoid conspecifics of atypical appearance or with lesions [22], nematodes and primates avoid contaminated foods [18,20], mice avoid sex with infected conspecifics [19], bees are hygienic [21] and birds and ruminants avoid unhygienic environments [17,23]. Heterospecific avoidance behaviour has been rarely reported in the animal literature but could be expected to occur when other species serve as vectors or intermediate hosts of specific parasites.

(c) Consequences of parasite infection and parasite avoidance

When animals fail to behave in ways that minimize their disease risk, because avoidance is too difficult or too costly, then they must bear the consequences in terms of morbidity and mortality. Owing to the impact that parasites can have on livestock production, research on faecal–oral parasite avoidance has been focused on domestic ruminants. Much less is known about the dynamics of parasite avoidance in the wild. In their paper, Coulson *et al.* [23] review trade-offs between parasitism and foraging in mammalian herbivores.

Mammalian herbivores are infected by parasites such as gastro-intestinal bacteria and nematodes which are acquired via faecal–oral transmission from conspecific or heterospecific faeces during feeding. Studies assessing the fitness costs of such parasites have been difficult to carry out in the wild, however experimental studies manipulating host's parasite load with anthelmintic treatments have been possible in multiple species, with equivocal effects on host foraging behaviour. Coulson *et al.* [23] discuss the limited evidence that exists for herbivores to prioritize faecal avoidance over forage intake in mammalian herbivores, citing for example that eastern grey kangaroos' (*Macropus giganteus*) foraging preference for tall grass is not maintained if patches are faecally contaminated [53]. The authors suggest the use of new technology including motion-sensitive camera traps at latrines and animal-borne video cameras to further investigate the parasite avoidance behaviour of wild herbivores.

In view of the considerable selection pressures that ectoparasites exert on both animals and humans, Kupfer & Fessler [25] extend the discussion of ectoparasite avoidance behaviour into the human domain. They argue that human ectoparasite defence psychology may have important social and clinical implications regarding compulsive skin picking and related skin damaging syndromes, as well as trypanophobia (fear of patterns of holes that resemble ectoparasite skin damage) and delusional parasitosis.

Lieberman *et al.* [26] situate the human emotion of disgust within an information processing model that, they propose, has to solve three major adaptive problems: what to eat, who to contact and with whom to have sex. A compiler computes the likely value versus the costs of consumption, contact and copulation, and when the expected value is negative, whether because of pathogen risk, food toxicity or a suboptimal mating threat to genetic fitness of possible offspring, disgust results.

(d) Variation in avoidance responses

If disgust has such an important adaptive function, one may ask why do we then vary in disgust sensitivity? In our closing paper, this is the question Tybur *et al.* [24] investigate, evaluating three hypotheses: (i) disgust-sensitivity varies with emotionality, (ii) parental modelling, and (iii) exposure to pathogens. They conclude that empirical evidence does not support any of these hypotheses and they put forward alternative proposals such as disgust sensitivity varies with people's sexual, nutritional and social requirements or strategies.

3. New avenues of exploration: towards consilience

Parasite avoidance is a task that has to be accomplished by all living things. Hence, inevitably, there will be commonalities in the mechanisms, strategies and consequences of parasite avoidance behaviour across Animalia. In our Royal Society meeting on disease avoidance behaviour it was striking how much students of different host-parasite systems had in common, and it was exciting to see specialists in areas as diverse as parasitology and psychology, molecular biology, immunology and behavioural ecology, cognitive ecology and public health, and terrestrial and marine disease ecology share insights and begin to form new collaborations. One

product of the meeting is this special edition where we have compiled research, reflections and reviews from scientists working with invertebrates, vertebrates and humans investigating pathogen and parasite avoidance behaviours from strategic, mechanistic and consequential perspectives. We hope that this theme issue will provide a starting point for establishing a parasite avoidance network, and that it will inspire much further investigation.

Areas for future investigation are multiple. While this edition covers a huge array of strategies employed by hosts to avoid becoming prey to pathogens, there is still no overarching theory or common consensus as to what the basic strategies are. Above, we have suggested that behavioural strategies must include avoiding parasites themselves and cues to their presence in conspecifics, heterospecifics, foods and habitat. Further, parasite avoidance behaviour can also be directed at constructing parasite-retardant niches—which include the skin and the nest.

The mechanisms of parasite avoidance behaviour, including its genetic, hormonal and neurological underpinnings remain largely to be understood. Taking a cross-species perspective is likely to be especially helpful as we unpick the architecture of sensorial response to cues, recognition and categorization, learning, information processing in brains and neural tissue and the selection of behavioural responses in the face of the numerous trade-offs between parasite avoidance and alternative investments of time and effort. Indeed parasite avoidance behaviour may provide an ideal model system for uncovering the mechanics of behaviour in general.

One aspect of the infection avoidance system is the conscious experience of feelings of disgust in humans. Debates have raged long and hard about whether the parasite avoidance system should be regarded as contiguous with the disgust response (e.g. [13,54]), in the same way that the predation avoidance system is labelled a fear response across species. Given the many parallels, we argue that it is reasonable and useful to use the disgust term for animal disease avoidance behaviour, and are glad to see this is beginning to catch on [3].

In terms of the consequences of disease avoidance, much work remains to be done. While most investment has, understandably, gone into investigating the epidemiology of human infectious disease, and of those species which are of economic or companion importance to us, the range of parasites and their disease consequences is much less well characterized in wild species. It is vital that we better understand the full range of viral, bacterial, protozoal, fungal, helminthic, arthropod and other endo- and ectoparasites that attack free-living animals. Parasite ecologists have tended to concentrate on the more easily detectable parasites, for example, ticks and gastro-intestinal nematodes, when the causes, consequences and defences against viral and bacterial pathogens may be just as important for species' and for ecosystem health, and go less well studied.

Other major gaps that remain to be addressed include the parasite avoidance behaviour of unicellular organisms and reptiles, the importance of parasite-driven selection in the evolution of sex and sociality, and many other trade-offs in fitness investment and reproductive opportunity that animals have to make to avoid paying the cost of not avoiding parasites.

In the longer term, understanding the working of the disgust system across species offers an excellent model for investigating the strategies, mechanisms and consequences of behaviour and could provide a vital contribution towards

the understanding and conservation of the ecosystems of our planet.

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Val Curtis is Professor of Hygiene at the London School of Hygiene and Tropical Medicine. Trained in engineering, epidemiology and anthropology, she leads the multi-disciplinary Environmental Health Group at LSHTM. Her research into human hygiene-related behaviour led her to propose the Parasite Avoidance Theory of Disgust in 2001. Her current work involves applying evolutionary theory to the problem of behaviour change; researching and advising governments, international agencies and industry on improving sanitation, water, hygiene and nutrition-related behaviour. She is author of *Don't look, don't touch! The science behind revulsion* (Oxford University Press, 2014) and is co-author of *Gaining control: how human behaviour evolved* (Oxford University Press, 2015).



Rachel McMullan is a lecturer in the School of Life, Health and Chemical Sciences at The Open University. Following a postdoc at the MRC Laboratory for Molecular Cellular Biology, University College London, during which Rachel studied the function of small GTPases in *Caenorhabditis elegans* in neurotransmission, she received a Wellcome Trust Research Career Development Fellowship to study behavioural and cellular responses to pathogen infection in *C. elegans*. In 2015, she moved to her current post where she continues to use *C. elegans* as a model to understand the evolution of pathogen avoidance behaviours and their role in protecting hosts.

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