

Evolution of pathogen and parasite avoidance behaviours

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Abstract

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

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1. Introduction

Whilst 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, Case and Oaten [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, whilst 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.

Figure 1 inserted around here

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

64 encounter is likely. Hosts can also remove parasites directly, or engineer their own niches
65 so as to make their environments unconducive to parasites. These strategies can be found
66 across taxa [14]. To accomplish such behaviour, hosts respond to cues that may be
67 chemosensory, mechanosensory or visual, they may learn from episodes of sickness or
68 from conspecifics, or they may carry out pre-programmed routines independent of any cue
69 to parasite presence [17-20]

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71 A further pattern emerging from this special issue is a general shift in the field from
72 anecdotal reports of observed behaviour to the experimental testing of hypotheses, which
73 has proven possible in captive species as diverse as bees [21] and bonobos [20], and, in
74 some cases, in the wild as well [22,23]. It is also exciting to see how cross-disciplinary
75 collaboration is bearing fruit, for example, where geneticists, cell biologists and behavioural
76 scientists are collaborating to provide a complete picture of nematode infection avoidance
77 behaviour [18]. A further promising inter-disciplinary development is the engagement of
78 psychologists who recognise the evolutionary continuity between disease avoidance
79 behaviour across species and ask how this relates to the emotion of disgust in humans [24-
80 27].

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82

83 **2. An evolutionary approach to understanding pathogen and parasite avoidance**

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

87

88 **(a) Strategies**

89

90 Our opening paper by Hart & Hart [28] explores the range of behavioural strategies
91 employed by mammals to avoid and remove various forms of parasites and pathogens,
92 from ectoparasites such as flies and ticks to external pathogens like pathogenic bacteria
93 potentially present on the skin surface, to internal parasites such as gastrointestinal
94 nematodes. As pointed out in their review, these strategies are species-specific and reflect
95 the environment that the animal inhabits. For example, Asian elephants (*Elephas maximus*)
96 use branches to repel biting flies from regions of their body where the skin is thinner and
97 vulnerable to such blood-sucking ectoparasites. Rats, on the other hand, lick their penis
98 after copulation and their saliva has proven bactericidal properties against genital

99 pathogens. This latter behaviour may protect males from potential venereal diseases
100 harboured by a female they just mated with, and may also protect females they might
101 subsequently mate and have offspring with, which ultimately could enhance that male's
102 fitness. Another example of behavioural strategy against orofaecally-transmitted parasites
103 this time concerns denning canids which defecate and urinate away from the den and rest
104 areas. Newborns, however, have no mobility, hence mothers keep the den clean by
105 consuming the fresh excreta. Mothers avoid infection because parasite ova take several
106 days to hatch into infective larvae.

107

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

121

122 Some of the best experimental models of parasite avoidance behaviour may be the social
123 insects, which are also some of the most strategic fighters when it comes to combatting
124 social parasites. In their review, Grüter et al [30] show the different defence traits that social
125 insects such as ants, termites, social wasps and bees have evolved to interrupt the entry
126 and establishment of parasites into the colony. These strategies involve several steps;
127 firstly, the avoidance of contacting parasites or being detected by them (e.g. nesting near
128 parasite deterrents, having several queens, or building a nest with architectural features
129 preventing invasion); secondly, the recognition of parasites and their rejection once
130 avoidance has failed (relying on chemical cues); and finally, the avoidance of exploitation by
131 social parasites (e.g. coordinated defence, resistance to parasite manipulation). However, if
132 the parasites are successful in establishing themselves, then hosts must to kill the
133 parasitized brood or find ways to reproduce in the parasite's presence, which can lead to

134 the coevolution of host defensive traits and parasite invasive adaptations. One of these
135 strategies of last resort is bee hygienic behaviour –a group defence against diseases in
136 which workers remove dead, dying and diseased individuals from the nest. In honey bees
137 (*Apis mellifera*), hygienic behaviour specifically refers to the uncapping and removal of dead
138 larvae and pupae in sealed cells. Here, Al Toufailia et al [21] provide an explanation for why
139 this hygienic behaviour is uncommon in honey bees by demonstrating that even colonies of
140 honey bees with low hygienic behaviour against sealed cells are highly hygienic against
141 dead larvae in open cells.

142
143 All the examples of behavioural strategies mentioned above occur on land but what about
144 pathogen/parasite avoidance in water? In their review, Behringer et al [22] address some of
145 the fundamental differences and similarities between pathogen/parasite avoidance
146 behaviours in terrestrial versus aquatic (marine and freshwater) environments. In the latter,
147 parasites and pathogens are suspended in the water column which may increase the
148 occurrence of contact. Thus, spatial avoidance of parasitism is one widespread strategy
149 among aquatic invertebrates and vertebrates. Tadpoles (*Rana clamitans* and *R. sylvatica*),
150 for example, avoid areas of the water column with high densities of parasitic flukes and this
151 behaviour was associated with lower levels of parasitism [31]. In addition, aquatic animals
152 reduce infection risk by increasing or lowering activity levels, avoiding infected prey,
153 avoiding infected mates, migrating, grouping, and avoidance learning. Behinger et al [22]
154 discuss the mechanisms and cues that engender these avoidance strategies, as well as
155 how anthropogenic activities may affect such behaviours.

156 157 **(b) Mechanisms**

158
159 Our current understanding of the mechanisms of pathogen/parasite avoidance behaviours
160 largely comes from research on invertebrates, amphibians and rodents, and focuses on only
161 a few pathogens and parasites.

162
163 One way in which animals can minimize their risk of infection is to reduce contact with
164 contaminated food. In this issue, Anderson & McMullan [18] show that the nematode worm
165 *Caenorhabditis elegans* (*C. elegans*) avoids lawns contaminated with the pathogenic
166 bacteria *Microbacterium nematophilum* (*M. nematophilum*) and by doing so, protects itself
167 from the deleterious effects, i.e. slowed growth. Similarly, Sarabian et al [20] show that
168 bonobos (*Pan paniscus*) when exposed to food contaminated with conspecific faeces, which
169 may harbour pathogenic bacteria, viruses and parasites (e.g. *Salmonella typhi*, Rotavirus, or

170 *Giardia* spp.), balance their feeding decisions to minimize infection risk. The benefits of
171 avoiding contaminated food shown in *C. elegans* have also been found in primates, as
172 individuals that kept away from food contaminated with faeces and soil had lower levels of
173 gastrointestinal parasite infection [32].

174

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

202

203 Certain infection avoidance responses incorporate social cognition, such as social partner
204 and mate choice, recognition and avoidance of strangers, or the process of individual and

205 social learning of pathogen/parasite avoidance itself [19]. Social insects like ants protect
206 their colonies through collective defences that result in social immunity. In ants, workers first
207 try to prevent infection of colony members. However, if this fails and a pathogen establishes
208 an infection, unicolonial invasive garden ants (*Lasius neglectus*) perform a “destructive
209 disinfection” by specifically targeting infected pupae during the non-contagious incubation
210 period of the pathogen, relying on chemical ‘sickness cues’ emitted by pupae. They remove
211 the pupal cocoon, perforate its cuticle and administer antimicrobial poison, which enters the
212 body and prevents pathogen replication from the inside out, thus protecting the rest of the
213 colony [47].

214

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

225

226 In humans, the emotion of disgust is suggested to be an adaptive system based in neural
227 tissue that evolved to keep us away from sources of infection; the so-called Parasite
228 Avoidance Theory of Disgust [5,12], supported by the strong correlation that exists between
229 disgust elicitors and infectious agents [12,51,52]. In their research paper, Curtis & de Barra
230 [27] test whether the factor structure of the disgust response in humans reflects the main
231 transmission routes of infection: direct interpersonal contact; interpersonal contact through
232 aerosolized droplets; interpersonal sexual contact; contact with a secondary host or vector;
233 ingestion of contaminated food or water; and contact with a fomite. To do this, they
234 generated a set of stimuli based on cues derived from the epidemiology of disease
235 transmission. Using a factorial analysis approach, they identified patterns of co-variation
236 across these descriptions of infection threats presented to a large sample of people. Six
237 domains emerged from this factorial analysis: atypical appearance, lesions, sex, poor
238 hygiene, off foods and animals. These factors did not exactly mirror the transmission routes
239 of infection but, instead, reflected different kinds of behavioural tasks involved in

240 parasite/pathogen avoidance. These six strategies for parasite avoidance may be universal,
241 and examples in many other species can be found throughout this special edition, for
242 example, fish avoid conspecifics of atypical appearance or with lesions [22], nematodes and
243 primates avoid contaminated foods [18,20], mice avoid sex with infected conspecifics [19],
244 bees are hygienic [21] and birds and ruminants avoid unhygienic environments [17,23].
245 Heterospecific avoidance behaviour has been rarely reported in the animal literature but
246 could be expected to occur when other species serve as vectors or intermediate hosts of
247 specific parasites.

248

249 **(c) Consequences of parasite infection and parasite avoidance**

250

251 When animals fail to behave in ways that minimize their disease risk, because avoidance is
252 too difficult or too costly, then they must bear the consequences in terms of morbidity and
253 mortality. Due to the impact that parasites can have on livestock production, research on
254 faecal-oral parasite avoidance has been focused on domestic ruminants. Much less is
255 known about the dynamics of parasite avoidance in the wild. In their paper, Coulson et al
256 [23] review trade-offs between parasitism and foraging in mammalian herbivores.
257 Mammalian herbivores are infected by parasites such as gastro-intestinal bacteria and
258 nematodes which are acquired via faecal-oral transmission from conspecific or
259 heterospecific faeces during feeding. Studies assessing the fitness costs of such parasites
260 have been difficult to carry out in the wild, however experimental studies manipulating host's
261 parasite load with anthelmintic treatments have been possible in multiple species, with
262 equivocal effects on host foraging behaviour. Coulson et al [23] discuss the limited evidence
263 that exists for herbivores to prioritize faecal avoidance over forage intake in mammalian
264 herbivores, citing for example that eastern grey kangaroos' (*Macropus giganteus*) foraging
265 preference for tall grass is not maintained if patches are faecally-contaminated [53]. The
266 authors suggest the use of new technology including motion sensitive camera traps at
267 latrines and animal-borne video cameras to further investigate the parasite avoidance
268 behaviour of wild herbivores.

269

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

276

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

283

284 **(d) Variation in avoidance responses**

285

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

293

294 **3. New avenues of exploration: Towards consilience**

295

296 Parasite avoidance is a task that has to be accomplished by all living things. Hence
297 inevitably there will be commonalities in the mechanisms, strategies and consequences of
298 parasite avoidance behaviour across Animalia. In our Royal Society meeting on disease
299 avoidance behaviour it was striking how much students of different host-parasite systems
300 had in common, and it was exciting to see specialists in areas as diverse as parasitology
301 and psychology, molecular biology, immunology and behavioural ecology, cognitive ecology
302 and public health, and terrestrial and marine disease ecology share insights and begin to
303 form new collaborations. One product of the meeting is this special edition where we have
304 compiled research, reflections and reviews from scientists working in invertebrates,
305 vertebrates, and humans investigating pathogen and parasite avoidance behaviours from
306 strategic, mechanistic and consequential perspectives. We hope that this theme issue will
307 provide a starting point for establishing a pathogen/parasite avoidance network, and that it
308 will inspire much further investigation.

309

310 Areas for future investigation are multiple. Whilst this edition covers a huge array of
311 strategies employed by hosts to avoid becoming prey to pathogens, there is still no

312 overarching theory or common consensus as to what the basic strategies are. Above, we
313 have suggested that behavioural strategies must include avoiding parasites themselves and
314 cues to their presence in conspecifics, heterospecifics, foods and habitat. Further, parasite
315 avoidance behaviour can also be directed at constructing parasite-retardant niches – which
316 include the skin and the nest.

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

325

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

333

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

344

345 Other major gaps that remain to be addressed include the parasite avoidance behaviour of
346 unicellular organisms and reptiles, the importance of parasite-driven selection in the

347 evolution of sex and sociality, and the many other trade-offs in fitness investment and
348 reproductive opportunity that animals have to make to avoid paying the cost of not avoiding
349 parasites.

350

351 In the longer term, understanding the working of the disgust system across species offers
352 an excellent model for investigating the strategies, mechanisms and consequences of
353 behaviour and could provide a vital contribution towards the understanding and
354 conservation of the ecosystems of our planet.

355

356

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360 many of the papers, and all who participated in the Royal Society meeting from which this special issue emerges. We
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362

363 **Authors' Contributions**

364 C.S., V.C. and R.M. contributed equally.

365

366 **Competing Interests**

367 We have no competing interests.

368

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371

372 **Footnote**

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

378

379 **AUTHOR PROFILES**

380



381 **Cecile Sarabian** is a PhD student in Behavioural Ecology at the
382 Primate Research Institute of Kyoto University. She received a Master's degree in Eco-
383 physiology and Ethology from the University of Strasbourg, France. Her work investigates
384 primate behaviour and parasite infection, with emphasis on parasite/pathogen avoidance
385 strategies in *Papionini* and *Hominini* and the evolutionary origins of hygiene and disgust.
386 She has conducted research on food-processing and faeces avoidance behaviours in
387 relation to parasite infection in Japanese macaques of Koshima island, Japan; sensory cues

388 eliciting revulsion and parasite infection-risk avoidance in long-tailed macaques, mandrills
389 and chimpanzees at the 'Centre International de Recherches Médicales de Franceville',
390 Gabon; and contamination-sensitivity in bonobos at Lola ya Bonobo sanctuary in the
391 Democratic Republic of the Congo. Her work integrates field-experiments, behavioural
392 observations, parasite identification and quantification, and lots of replica faeces.
393

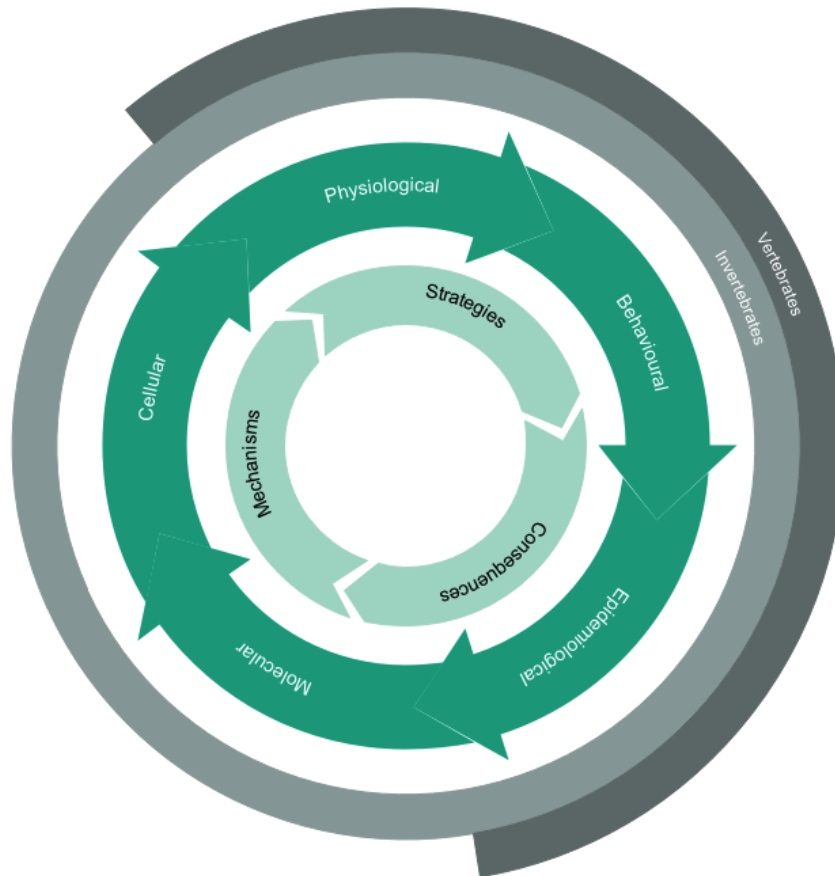


394 **Val Curtis** is Professor of Hygiene at the London School of Hygiene
395 and Tropical Medicine. Trained in engineering, epidemiology and anthropology, she leads
396 the multi-disciplinary Environmental Health Group at LSHTM. Her researches into human
397 hygiene-related behaviour led her to propose the Parasite Avoidance Theory of disgust in
398 2001. Her current work involves applying evolutionary theory to the problem of behaviour
399 change; researching and advising governments, international agencies and industry on
400 improving sanitation, water, hygiene and nutrition-related behaviour. She is author of 'Don't
401 Look, Don't Touch! The Science behind Revulsion' (OUP 2014) and is co-author of 'Gaining
402 control: how human behaviour evolved' (OUP 2015)
403



404 **Rachel McMullan** is a lecturer in the School of Life, Health and
405 Chemical Sciences at The Open University. Following a postdoc at the MRC Laboratory for
406 Molecular Cellular Biology, University College London during which Rachel studied the
407 function of small GTPases in *Caenorhabditis elegans* in neurotransmission Rachel received
408 a Wellcome Trust Research Career Development Fellowship to study behavioural and
409 cellular responses to pathogen infection in *C. elegans*. In 2015 Rachel moved to her current
410 post where she continues to use *C. elegans* as a model to understand the evolution of
411 pathogen avoidance behaviours and their role in protecting hosts.
412

413
414 **Figures**
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Figure 1 Towards a complete understanding of pathogen/parasite avoidance behaviour. As illustrated by the papers in this special issue the evolution of pathogen/parasite avoidance behaviours provides an opportunity to take an interdisciplinary approach in order to fully understand the strategies, mechanisms and consequences of pathogen/parasite avoidance behaviour.

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