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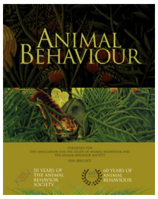

Faecal avoidance and selective foraging: do wild mice have the luxury to avoid faeces?☆

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Host–parasite interactions are a key determinant of the population dynamics of wild animals, and behaviours that reduce parasite transmission and infection may be important for improving host fitness. While antiparasite behaviours have been demonstrated in laboratory animals and domesticated ungulates, whether these behaviours operate in the wild is poorly understood. Therefore, examining antiparasite behaviours in natural populations is crucial for understanding their ecological significance. In this study, we examined whether two wild rodents (white-footed mice, *Peromyscus leucopus*, and deer mice, *Peromyscus maniculatus*), selectively foraged away from conspecific faeces or avoided faeces altogether, and whether faecal gastrointestinal parasite status affected their behaviour. We also tested whether wild mice, when nesting, avoided using material that had previously been used by healthy or parasite-infected conspecifics. Our results, in contrast to laboratory mouse studies, suggest that wild mice do not demonstrate faecal avoidance, selective foraging or selective use of nesting material; they preferred being near faeces and did not differentiate between faeces from parasitized and uninfected conspecifics. Behavioural avoidance to reduce parasite infection may still represent an important strategy; however, mice in our study population appeared to favour the opportunity to feed and nest over the risks of coming into contact with faecal-transmitted parasites. Furthermore, the presence of conspecific faeces may actually provide a positive cue of a good foraging or nesting location. Ultimately, balancing the trade-off of performing antiparasite behaviours to reduce infection with missing an important feeding or nesting opportunity may be very different for animals in the wild facing complex and stochastic environments.

Parasites play a major role in regulating the dynamics of wild animal populations (Anderson & May 1979). Hosts are known to employ a variety of methods, both physiological and behavioural, to avoid or eliminate parasites (Hart 1990, 1992; Loehle 1995). Immune and other physiological responses to parasites, defined here as both macroparasites (helminths, fungi, ectoparasites) and microparasites (viruses, bacteria, protozoans), are relatively well understood, but comparatively fewer studies have focused on specific antiparasite behaviours that can protect the host from infection and the possible fitness consequences of parasitism (Ezenwa 2004; Daly & Johnson 2011; de Roode & Lefèvre 2012). For a particular behaviour to be considered as reducing parasite contact or the likelihood of infection, two criteria must be met: (1) the parasite should have a negative effect on the host's fitness; and (2) the behaviour in question should be shown to be effective in helping an animal to avoid, remove or mitigate parasite infection (Hart 1990).

Animals can exhibit behaviours that may reduce the spread of pathogens to themselves and fellow group members (Moore 2002). Some of these behaviours are employed after parasites are already present. Grooming, for example, serves to remove or reduce ectoparasites and has been documented extensively across mammals (Hart 1990; Cotgreave & Clayton 1994). Similarly, self-medication, in which a species selectively feeds on resources that have medicinal qualities to eliminate or reduce parasite infection levels, has been documented in primates, including ingesting compounds that may be useful against helminths (e.g. Wrangham & Nishida 1983), and recently demonstrated in the ovipositing choices of infected

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monarch butterflies, *Danaus plexippus* (Lefèvre et al. 2012). However, gastrointestinal parasites, commonly spread through faecal–oral transmission, may require that different behaviours be employed to reduce parasite contact and the probability of infection in the first place. It appears that animals that use behavioural strategies to avoid parasite transmission are probably responding to cues from the infected individuals, rather than the direct presence of transmissible parasite stages (Cooper et al. 2000; Kavaliers et al. 2005). One behaviour that may reduce exposure to faecal–orally transmitted parasites is selective foraging, or preferentially foraging away from faeces (Hart 1990).

Selective foraging has been demonstrated to reduce parasite loads in animals (Michel 1955), but behavioural observations are largely limited to domesticated livestock and wild ungulates (e.g. cattle, *Bos taurus*: Michel 1955; domestic sheep, *Ovis aries*: Crofton 1958; Hutchings et al. 1999, 2000, 2002; Cooper et al. 2000; horses, *Equus caballus*: Odberg & Francis-Smith 1976, 1977; reindeer, *Rangifer tarandus*: Moe et al. 1999; van der Wal et al. 2000; wild antelopes: Ezenwa 2004; chamois, *Rupicapra rupicapra*: Fankhauser et al. 2008; exceptions: primates: Freeland 1980; macropodids: Garnick et al. 2010). Therefore, it is unclear how widely this behavioural adaptation occurs in other animals.

Equally, communal or sequential nest use, roosting sites and burrows potentially provide another significant risk for infection by faecal–orally transmitted parasites. Therefore, the detection and avoidance of previously used or faecal-contaminated nest or sleeping sites and materials may minimize parasite transmission and has been extensively studied in bird nesting behaviour (see Mazgajski 2007). However, while some bird species do avoid used or infected nests (e.g. Brown & Brown 1986; Merilä & Allander 1995), others show no avoidance (e.g. Johnson 1996; Blem et al. 1999) or even a preference for previously used nests (e.g. Jackson & Tate 1974; Davis et al. 1994). Wild rodents also use nests communally and sequentially (Wolff & Hurlbutt 1982; Frank & Layne 1992) and have been found to remove old materials from their nests, in subsequent uses, as a method of removing ectoparasites (e.g. house mice, *Mus musculus*: Schmid-Holmes et al. 2001; Brants' whistling rats, *Parotomys brantsii*: Roper et al. 2002). The diversity of behavioural responses to minimize the potential for parasite contact and infection suggests that antiparasite behaviours may represent a cost to the host, and that the benefit of avoiding parasites must outweigh the cost of not performing the behaviour, consequently exposing the host to potential infection (Hart 1990).

Rodents communicate primarily through olfaction, and may use olfactory cues to detect parasitized individuals. In studies of laboratory mice, females consistently spend more time near the urine of healthy males and preferentially mate with healthy individuals over individuals infected with gastrointestinal parasites (Penn & Potts 1998; e.g. *Heligmosomoides polygyrus*: Ehman & Scott 2001; *Eimeria vermiformis*: Kavaliers & Colwell 1995; Kavaliers et al. 1997). Yet, although laboratory mice have been shown to be able to detect parasitized individuals (Kavaliers et al. 2005), it has not been demonstrated whether this occurs in wild individuals or extends to selective foraging or selectivity in nesting sites or burrows.

Wild populations of white-footed mice, *Peromyscus leucopus*, and deer mice, *Peromyscus maniculatus*, are ideal for studying faecal avoidance and selective feeding. First, they live in high-density communities and have a high prevalence of intestinal parasites (Pedersen 2005; Clotfelter et al. 2007). Over 10 species of faecal–orally transmitted gastrointestinal parasites have been found to infect both species of *Peromyscus* at our study site, including helminths and protozoans (Pedersen & Greives 2008). Second, the burrows of these mice contain significant amounts of both faeces and stored food and are used by several individuals over short periods of time (Wolff & Hurlbutt 1982; Wolff 1985a, b; Wolff & Durr 1986), making nest sites likely locations for parasite transmission. Finally, there is evidence that the gastrointestinal parasites that infect *Peromyscus* can have negative fitness consequences. For example, *Eimeria* spp. infection has been associated with lower mass and overwintering survival (Fuller & Blaustein 1996) and, in this study population, antihelminthic treatment can, in part, limit seasonal population crashes (Pedersen & Greives 2008). Thus, mice may benefit from faecal avoidance or selective feeding or nesting to avoid contact and infection with these parasites.

In this study we investigated whether wild *Peromyscus* demonstrate faecal avoidance or differentiate between gastrointestinal parasite-infected or uninfected faeces when feeding or in nesting situations. Understanding behavioural adaptations to parasites in wild animals will provide insights into host–parasite dynamics and parasite-driven regulation of animal behaviours and population dynamics.

METHODS

Study Site

These experiments were conducted at the Mountain Lake Biological Station (MLBS) in Giles County, Virginia, U.S.A. (3722′21′N, 8031′20′W, elevation: 1160 m above sea level). The site consists of oak–maple forest that supports large, coexisting populations of *P. leucopus* and *P. maniculatus* (Wolff 1996; Clotfelter et al. 2007; Pedersen & Greives 2008).

Trapping Methods

Six 0.5 ha grids were trapped for 3 consecutive days every 2 weeks during the summer of 2002. Each grid had 64 Sherman live folding traps (5 × 2 cm and 16.5 cm high, H.B. Sherman; Tallahassee, FL, U.S.A.), spaced 10 m apart. In addition, mice were trapped on a separate 2.25 ha grid, in a similar habitat, once a month. Traps were set at dusk with crimped oats, and checked the following morning. All captured individuals were permanently ear tagged (National Band & Tag, U.S.A.), and species and sex were recorded. All individuals included in experimental trials were adult mice.

Faecal Analysis

For all faecal samples used in the faecal avoidance, selective foraging and nesting material use experiments, a subsample was used to determine infection status. Faecal samples were obtained from individuals, and faecal float analysis (saturated sodium chloride) was used to identify gastrointestinal parasite infection (Pritchard & Kruse 1982). Eggs from each sample, concentrated on a cover slip, were identified to parasite species by scanning five transects under a microscope (100× magnification, Pedersen 2005). Samples without gastrointestinal parasites were identified as 'healthy' and samples that contained one or more of the following gastrointestinal parasites were considered 'parasitized': nematodes including *Aspiculuris americana*, *Capillaria americana* and *Syphacia peromysci*, and two unidentified morphospecies; protozoans including *Eimeria delicata* and *Eimeria arizonensis*; and cestodes including *Hymenolepis diminuta* and *Hymenolepis citelli* (Pedersen 2005; Pedersen & Antonovics 2013). The life cycles of this group of gastrointestinal parasites varies significantly, from the pinworms (*A. americana* and *S. peromysci*), which can be directly infectious after defecation, to the coccidial protozoans (*Eimeria* spp.), which require 10–14 days of development in the soil. The cestodes (e.g. *Hymenolepis* spp.) even require an intermediary arthropod host before they are infectious to the next mouse. We used 1–3-day old faeces, which will not contain infectious stages of many of the