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Selective Defecation and Selective Foraging: Antiparasite Behavior in Wild Ungulates?

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Abstract

Selective defecation and selective foraging are two potential antiparasite behaviors used by grazing ungulates to reduce infection by fecal–oral transmitted parasites. While there is some evidence that domestic species use these strategies, less is known about the occurrence and efficacy of these behaviors in wild ungulates. In this study, I examined whether wild antelope use selective defecation and selective foraging strategies to reduce exposure to gastrointestinal nematode parasites. By quantifying parasite levels in the environment in relation to the defecation patterns of three species, dik-dik (*Madoqua kirkii*), Grant's gazelle (*Gazella granti*), and impala (*Aepyceros melampus*), I found that nematode larval concentrations in pasture were higher in the vicinity of clusters of feces (dung middens) compared to single fecal pellet groups or dung-free areas. In addition, experimental feeding trials in free-ranging dik-dik showed that individuals selectively avoided feeding near concentrations of feces. Given that increased parasite contamination was found in the immediate vicinity of fecal clusters, fecal avoidance could help reduce host consumption of parasites and may therefore be an effective antiparasite behavior for certain species. On the other hand, while the concentration of parasite larvae in the vicinity of middens coupled with host avoidance of these areas during grazing could reduce host contact with parasites, results showing a positive correlation between the number of middens in a habitat and larval abundance at control sites suggest that dung middens might increase and not decrease overall host exposure to parasites. If this is the case, dung midden formation may not be a viable antiparasite strategy.

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Introduction

Parasites can exact extensive costs on their hosts including reductions in growth and fecundity and even death. In response, hosts have developed many

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sophisticated methods of combating parasitic invasion. While immunological defenses are the most commonly cited parasite defense strategies, behavioral defenses against parasites also occur widely and may in fact be the first line of defense for many hosts (Hart 1990, 1994; Moore 2002). Antiparasite behaviors can range from commonplace behaviors that remove or repel parasites such as grooming, fly-repelling and comfort movements (see Hart 1994 and Moore 2002 for review) to fairly complex behaviors that alleviate or prevent infection such as leaf swallowing in chimpanzees (Huffman et al. 1996) and cannibalism avoidance in larval salamanders (Pfennig et al. 1998).

Hart (1992) outlined two criteria that must be met for a behavior to be considered a viable antiparasite strategy. First, the parasite involved must have negative fitness effects on the host, and second, the relevant behavior must effectively reduce or eliminate the parasite. Selective defecation and selective foraging are two behaviors that have been discussed as potential defense strategies used by grazing ungulates to reduce infestation by fecal–oral transmitted parasites (Hart 1990, 1992). While both behaviors are known to occur in domestic animals, evidence that they actually reduce levels of parasitism is scant. For example, domestic horses create permanent defecation sites and it has been suggested that this selective clustering of fecal eliminations in space serves to sequester parasites allowing subsequent avoidance during foraging (Taylor 1954; Ödberg & Francis-Smith 1976). Similar observations have also been made in wild primates (Gilbert 1997), but direct links between selective defecation and reduced parasitism are lacking in both groups. Selective foraging in the form of fecal avoidance has been documented in cattle (Taylor 1954), sheep (Crofton 1957; Cooper et al. 1977, 2000; Hutchings et al. 1998), horses (Ödberg & Francis-Smith 1977), and captive reindeer (Moe et al. 1999). By selectively avoiding grazing near feces, animals are thought to reduce consumption of parasites, thereby lowering their infection rates. Unlike selective defecation, selective foraging has been associated with reduced parasite intake (Michel 1955; Cooper et al. 2000), which suggests that this behavior may serve as an effective antiparasite strategy for grazing ungulates.

Despite the many examples of selective foraging and defecation in domestic animals, there is almost no information about the extent to which these behaviors may be used by wild ungulates as antiparasite strategies. The general assumption seems to be that wild ungulates use similar behaviors to control parasitic infections (e.g. Hart 1990; Møller et al. 1993). The fact that many wild ungulates deposit feces in heavily used dung middens, for example, indicates that selective defecation does occur. However, because middens often serve an important scent-marking role for many species (Leuthold 1977; Estes 1991), an antiparasite function of this behavior cannot be presupposed. Furthermore, since there has been no clear demonstration of fecal avoidance in a wild ungulate, it remains unknown whether this form of selective foraging, which is relatively widespread among domestic species, even occurs in the wild.

To understand more about antiparasite behavior in wild ungulates, I studied selective foraging and defection behaviors in African antelope in relation to gastrointestinal nematode parasitism. Gastrointestinal nematodes are common fecal–oral transmitted parasites of ruminants, and in this study I focused on the 'strongyle' nematodes (Order: Strongylida; Superfamily: Trichostrongyloidea), a group which includes highly pathogenic genera such as *Haemonchus*, *Ostertagia*, *Oesophagostomum*, *Trichostrongylus*, and *Cooperia*. In the typical life cycle of these parasites, eggs are shed in the feces and hatch within 1–2 days as larvae. First and second stage larvae feed on microorganisms in the feces and within days to weeks infective third stage larvae migrate out of the fecal mass onto surrounding vegetation to await ingestion by a susceptible host (Bowman 1999). Strongyle nematodes cause significant morbidity and mortality among domestic livestock worldwide, and the negative effects of these parasites on production in domestic systems are well-documented (Sykes 1994; Urquhart et al. 1996). Increasing evidence also suggests that these parasites negatively impact the condition, fecundity, and survival of wild ungulates (Gulland 1992; Stein et al. 2002).

Given the potential fitness costs of strongyle nematode parasitism and the possible benefits a host could gain from reducing exposure to these parasites, I examined whether selective defecation and foraging serve as important defense strategies in three antelope species: dik-dik (*Madoqua kirkii*), Grant's gazelle (*Gazella granti*), and impala (*Aepyceros melampus*). Since all three species are territorial and use fecal scent-marking to varying degrees to demarcate territory ownership (Estes 1991), I investigated whether this form of selective defecation reduces host exposure to strongyle nematodes by concentrating infective larvae around dung middens and facilitating parasite avoidance during foraging. In addition, since it is unknown whether free-ranging antelope engage in selective foraging (fecal avoidance), I also tested whether individuals selectively avoid foraging near large concentrations of feces in order to reduce parasite intake rates.

Methods

Study Location and Species

This study was conducted at the Mpala Research Center, Kenya (00°17′N, 36°53′E). The Center is located in the semi-arid region of central Kenya in the Laikipia district. Annual rainfall at Mpala ranges from 400 to 500 mm, and the vegetation is dominated by *Acacia* bushland/grassland. Approximately 20 large herbivore species occur at Mpala, 15 of which are bovids. The three study species, dik-dik, Grant's gazelle and impala, are among the most numerous bovid species at the study site. Dik-dik live as monogamous pairs. Both males and females are territorial and both sexes deposit feces in dung middens (Estes 1991). Grant's gazelle and impala are polygynous and individuals can be divided into three distinct classes: territorial males, non-territorial or bachelor males, and females and juveniles. Only territorial males actively defend territories and they create and maintain dung middens within their territory boundaries (Estes 1991). In all three species, territoriality and midden use occur year round at the study site (Ezenwa, pers. obs.).

All three study species have been found to be infected with strongyle parasites at the study site. Adult worms collected and identified from study animals included the genera *Agriostomum*, *Cooperia*, *Cooperioides*, *Gazellostrongylus*, *Haemonchus*, *Oesophagostomum*, *Ostertagia*, and *Longistrongylus* (Ezenwa 2003). Mean strongyle fecal egg counts measured over an 18-month period ranged from 843 ± 90 eggs/g feces (EPG) in dik-dik to 963 ± 39 EPG in impala and 2560 ± 97 EPG in Grant's gazelle (Ezenwa 2003). For comparison, egg counts between 600 and 2000 EPG are considered to be indicative of moderate (4000–10 000) worm burdens in domestic sheep, and counts over 2000 EPG are considered indicative of high ($>10\,000$) worm burdens (McKenna 1987). A sheep with a burden of 5000 *Haemonchus contortus* worms can lose up to 250 ml of blood per day resulting in anemia, weight loss, and weakness (Urquhart et al. 1996). If these parasites have similar effects on wild antelope, then the parasite loads observed for the study species could have important fitness consequences.

Defecation Patterns and Parasite Abundance

To determine the relationship between dung midden use and strongyle abundance in the external environment, I performed strongyle larval counts on pasture vegetation surrounding different dung formations. Counts were done on vegetation surrounding three different feces formations: dung middens (defined as fecal clusters with four or more individual fecal pellet groups deposited on top of or adjacent to each other), single fecal pellet groups, and control areas (areas at least 1.0 m away from any dung pellets). One midden/single/control set of larval counts was done in each of three distinct territories for Grant's gazelle and impala, and in each of four territories for dik-dik. For Grant's gazelle and impala, locations of territories were determined by the presence and behavior of territorial males. Sampling locations within territories were selected by locating active dung middens in areas heavily used by territory occupants (Ezenwa, pers. obs.). These middens were selected as the midden sites, and then appropriate single and control sites were selected in the same vicinity. For dik-dik, the locations of territories were determined by mapping the locations of dik-dik pairs along a road in a densely occupied habitat (Ezenwa, unpubl. data). Clusters of sightings were considered to be likely territories and these areas were searched for dung middens. The distribution of middens was then used to define probable territories. Midden sites used for sampling were selected based on the frequency with which they contained fresh feces. Because dik-dik rarely produce single-pellet groups (Ezenwa, pers. obs.), larval counts were done exclusively on middens and controls for this species. Control sites were selected as described above. For all species, sampling locations (midden, single, or control) within each territory were no more than 20 m apart to control for differences in vegetation structure that might affect larval dispersal. All larval counts were completed between May and August 2001.

To sample nematode larvae on vegetation, grass clippings were taken from a half-meter circle around each sampling point (midden, single-pellet group or control area) until a sandwich-sized (16.51 cm × 8.25 cm) Ziploc® bag was filled. All grass clippings were collected between 09:00 and 11:00 h, soaked in 1.0 l of water with detergent (Tween 80) for 24 h and then nematode larvae were extracted following Lancaster (1970). Lugol's iodine was added to the larval suspension after extraction and all third stage infective (L_3) strongyle nematode larvae were counted using a binocular microscope at 40× magnification. After the extractions, all grass clippings were air-dried and weighed to calculate L_3/kg dry weight herbage for each sampling location.

Midden Use Frequencies

At each Grant's gazelle and impala territory where nematode larvae counts were performed, I also estimated the proportion of fecal pellet groups deposited in middens in that territory. Based on behavioral observations of territory inhabitants, I determined the areas of each territory which were most heavily used and then surveyed fecal pellet groups on the ground in these areas. Surveys began in the center of the heavily used sites and extended outward until at least 10 distinct fecal pellet formations were located. I classified all fecal pellet formations encountered during each survey as being either a midden ($\geq$ 4 pellet groups) or non-midden (1–3 pellet groups), and then used these counts to calculate a midden use frequency for each territory: frequency = number of middens encountered/ total number of fecal pellet formations encountered. Between 10 and 25 fecal pellet formations were used to calculate midden use frequencies for each territory. Midden use was not estimated for dik-dik because the overwhelming majority of fecal pellet groups for this species occur in middens.

Fecal Avoidance Experiments

To investigate the occurrence of fecal avoidance behavior in wild ungulates, I performed feeding trials on free-ranging dik-dik. Trials consisted of placing two piles with three cups each of calf feed (composition: lucerne, bran, low-grade maize, wheat) 1.0 m apart near heavily used dik-dik walkways. One pile of feed was designated as a 'no dung' treatment and the other as a 'dung' treatment. The 'dung' treatment had two cups of completely dried dik-dik fecal pellets placed at three points adjacent to, but not mixed in with the feed, while nothing was done to the 'no dung' treatment. The experimental site was then watched for up to 10 continuous hours to monitor all visits by dik-dik. The duration of all feeding bouts (designated as total time spent by an individual near the experiment site after at least one bite had been taken, but before moving off) and the number of bites taken from either treatment during a feeding bout were recorded, as were the age, sex, and identity of the feeder when possible. For each trial, after the first 50 bites were taken from either treatment, the 'dung' and 'no dung' sides were reversed to control for possible side bias, and observations continued until at least

50 more bites were recorded in the new configuration. All feeding trials were conducted between 7 February and 4 May 2000. The feeding behaviors of at least seven individually distinguishable dik-dik were recorded during the trials, but the actual number of distinct individuals involved is unknown because many were not individually identifiable.

Statistical Analysis

I used STATVIEW 5 for Windows (SAS Institute, Cary, NC, USA) for all statistical comparisons, and significance was accepted at $p \leq 0.05$ for all tests. To compare nematode larval counts around different feces types, I used an analysis of variance (ANOVA) corrected for multiple comparisons using the Fisher's Protected Least Significant Difference (PLSD) test. Counts were log transformed for the analysis. To test for associations between midden use frequencies and larval abundance at control sites, I calculated a standardized larval abundance for all Grant's gazelle and impala territories [e.g. Grant's gazelle, site 1 = (L_3/g dry weight)/(Max L_3/g dry weight) × 100] and compared this to midden use frequency using a Spearman's rank correlation test. Lastly, I used a paired t-test to test for fecal avoidance in dik-dik.

Results

Dung Formation and Larval Abundance

Estimates of infective larvae abundance on vegetation surrounding dung middens, single-pellet groups, and control areas indicate that larval abundance varied with dung formation. For Grant's gazelle feces there was significant variation in abundance of infective larvae across dung types (ANOVA: $F_{2,6} = 6.1$, $p = 0.04$; Fig. 1). Middens produced significantly more larvae than did single-pellet groups (Fisher's PLSD: $p = 0.02$) or control areas ($p = 0.03$), but there was no difference in larval abundance around single-pellet groups and control areas ($p = 0.87$). For impala, differences across all dung types were only marginally significant (ANOVA: $F_{2,6} = 3.6$, $p = 0.09$), however middens did produce significantly more larvae than did controls (Fisher's PLSD: $p = 0.04$). There was no difference between middens and singles ($p = 0.13$), or singles and controls ($p = 0.40$; Fig. 1). Dik-dik dung middens also produced significantly more larvae than did control areas (ANOVA: $F_{1,6} = 11.1$, $p = 0.02$; Fig. 1).

Midden Use and Larval Abundance

When midden use frequencies within Grant's gazelle and impala territories were compared against larval abundances at control sites, standardized larval abundance was positively correlated with midden frequency (Spearman rank: $r_s = 0.93$, $p = 0.04$; Fig. 2).

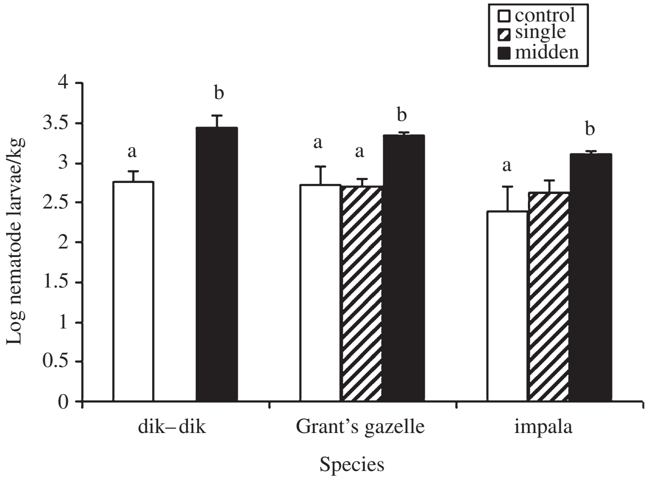

Fig. 1: Infective nematode larvae ± SE on vegetation surrounding control, midden, and single-fecal pellet group sites for dik-dik, Grant's gazelle and impala fecal pellets. Letters (a vs. b) indicate significant differences among treatments within a species

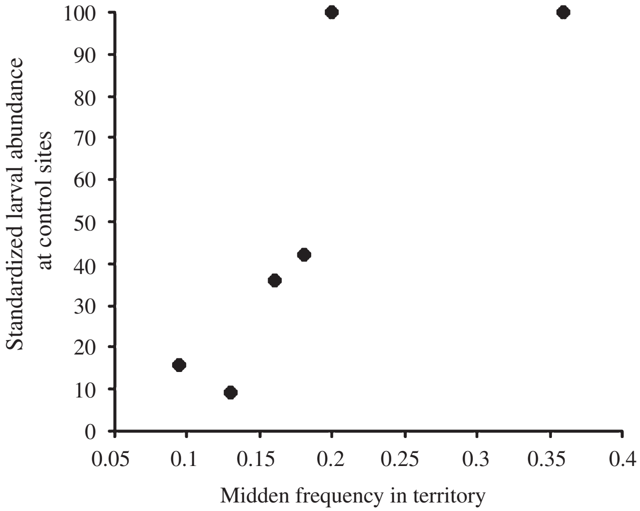

Fig. 2: Relationship between the proportion of middens encountered in Grant's gazelle and impala territories and standardized larval abundance measured at control sites (Spearman's rank correlation: $r_s = 0.93$, $p = 0.04$)

Fecal Avoidance Experiments

Dik-dik feeding trials showed that individuals preferentially avoided feces when feeding. Individuals presented with a choice of calf feed in the vicinity of either ‘dung’ or ‘no dung’ took significantly more bites from the ‘no dung’ treatment (Paired t-test: $t = -3.57$, $df = 30$, $p = 0.001$; Fig. 3).

Discussion

For African antelope, midden formation is thought to serve an important scent marking function (Leuthold 1977). Dung middens have also been hypothesized as having an antiparasite function (see Hart 1990 for review) because they potentially help sequester parasite infective stages to limited areas of pasture reducing host exposure to parasites. In the current study, larval abundance counts around different feces formations showed that dung middens do have higher infective larvae concentrations in their immediate vicinity when compared to single fecal pellet groups and control areas. However, it is unclear whether these high concentrations of larvae actually remain confined to midden sites. The observed positive correlation between the proportion of dung middens in a host territory and larval abundance at control sites suggests that middens may somehow contribute to larval contamination in surrounding areas of pasture. Although this result is correlational and other unexplored factors may influence the observed relationship, the idea that dung middens could increase pasture larval concentrations on a broader scale is feasible under certain conditions.

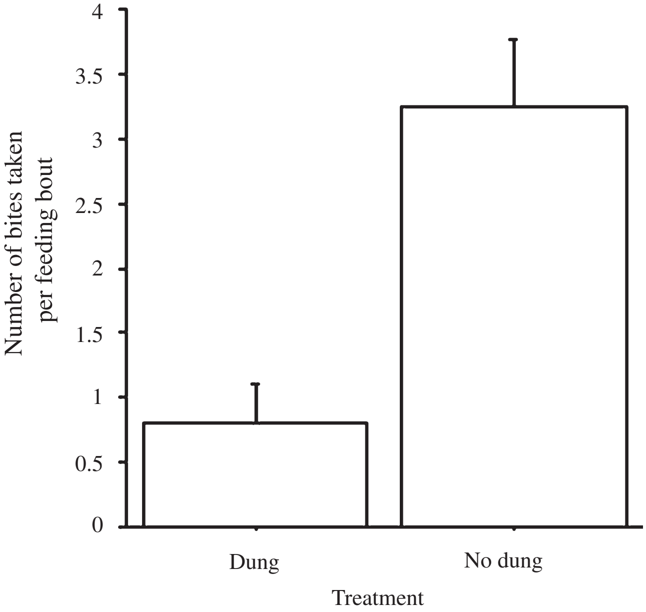

Fig. 3: Number of bites ± SE taken by dik-dik given a choice between ‘dung’ and ‘no dung’ food sources. Significantly more bites were taken from ‘no dung’ treatments ($p = 0.001$)

Because high concentrations of feces and moist conditions inside middens might foster the production of large numbers of infective larvae, dung middens could act as important source populations of infective larvae. While under most conditions larvae actively disperse only a maximum distance of about 1 m (Durie 1961), during wet periods, rain can facilitate the passive dispersal of larvae on a much wider scale. In tropical climates, pasture larvae levels have been shown to be highest during the rainy season when larval dispersal from fecal pats is aided by rain (e.g. Waruiru et al. 1998, 2001). Similarly, rain could be an important mechanism moving large numbers of larvae from midden hotspots to surrounding areas of a host territory. The period during which the larval counts were performed in this study (May–August 2001) was fairly wet at the study site (see Ezenwa 2004a), thus it is possible that rain dispersal could account for the increased larval abundance at control sites in those territories that had more middens. The fact that any larvae were detected at control sites, which were all at least 1 m away from any visible fecal pellets, suggests that active dispersal alone cannot account for the observed dispersion of infective larvae at the study locations. However, since the current study did not include a spatial analysis of dung middens in relation to larval abundance at the controls, additional work is needed to determine if, and to what extent, dung middens affect pasture larval counts on a broad scale.

If dung middens do contribute to larval contamination of non-midden areas as preliminary results suggest, then midden formation is unlikely to be an effective antiparasite strategy. In fact, increased parasitism may be a cost of midden use, and as such, midden-making species might suffer from higher infection rates than species that do not create middens. Results of an associated study comparing strongyle nematode infection rates in territorial and non-territorial bovids support this hypothesis. The study showed that territorial species, a majority of which form dung middens, had significantly higher strongyle infection rates than non-territorial species that do not create middens (Ezenwa 2004b). Furthermore, territorial male Grant's gazelles were found to have significantly higher strongyle egg counts than did either non-territorial males or females, possibly because these males spend more time on territories and in closer proximity to dung middens (Ezenwa 2004b). Both of these findings support the idea that midden-making and increased exposure to dung middens may be associated with higher infection rates. If this is the case, then parasitism could be a major factor limiting the use of dung middens in territorial antelope. This could explain why, in species like dik-dik where both males and females defecate almost exclusively in middens, dung middens are generally placed only on the periphery of territories whereas glandular secretions are used for scent-marking in more central locations (see Hendrichs 1975) despite the fact that these secretions are potentially more costly to produce. To gain a better understanding of the potential costs of midden formation, future studies will explore whether there is in fact a causal relationship between midden use frequency within a territory, overall larval abundance in the environment, and host infection rates. An examination of the relative costs and benefits of midden use will also shed light on the functions of this behavior.

Selective foraging is a second potential antiparasite strategy used by grazing ungulates to reduce parasitism. Several studies show that domestic sheep use fecal avoidance as a cue for parasite avoidance (Hutchings et al. 1998; Cooper et al. 2000), which suggests that selective foraging in relation to dung serves a distinct antiparasite function in these animals. In this study, free-ranging dik-dik exhibited fecal avoidance when given a choice between food placed near clusters of dung and dung-free food. Because gastrointestinal parasites can have extensive negative effects on their hosts (e.g. Gulland 1992; Urquhart et al. 1996; Stein et al. 2002) and these negative effects increase with increasing parasite loads, any reduction in the number of parasites ingested probably directly influences host fitness. Since nematode larval counts surrounding dik-dik dung middens were significantly higher than larval counts in control areas, the avoidance of clusters of dung by individuals in this species could serve to significantly reduce consumption of infective parasite stages. Selective foraging behavior has been shown to reduce parasite intake rates in both domestic sheep (Cooper et al. 2000) and cattle (Michel 1955), thus it is possible that similar behavior in dik-dik also reduces parasite intake rates.

Even if fecal avoidance is an effective antiparasite strategy used by some wild ungulates, there are significant costs associated with this behavior that could lead to individual- and species-level variation in responses to feces. Because selective foraging may, under certain conditions, reduce host nutrient intake rates or increase total foraging time necessary to fulfill nutritional requirements, the costs of avoidance counterbalanced by the benefits in terms of parasite reduction can result in foraging trade-offs between nutrient intake and parasite avoidance (Hutchings et al. 1999, 2000, 2001a, 2001b). Since adequate host nutrition is critical to parasite resistance and resilience (Van Houtert & Sykes 1996), and because parasites themselves disrupt host metabolism and digestive efficiency (Coop & Kyriazakis 2001), an animal's physiological state, including current nutritional status, existing parasite load and immune function are all important determinants of foraging selectivity (Hutchings et al. 1998, 1999, 2000, 2001a, 2001b). Studies on domestic sheep, for example, show that parasitized sheep are more selective than non-parasitized sheep; highly food motivated sheep are less selective than unmotivated sheep; and immune sheep are less selective than non-immune sheep (Hutchings et al. 1998, 1999, 2000, 2001a, 2001b). For wild ungulates, the opportunity costs of selective foraging can be very high, especially when resources are limited or predators are abundant. As a consequence, differences in immune function, nutritional status and parasitism, as well as a variety of ecological factors will contribute to variation in the expression of fecal avoidance behavior.

Differences in species' defecation behaviors will also influence fecal avoidance behavior since defecation patterns directly affect the distribution of parasites in the environment. Species that form dung middens may be more likely to engage in fecal avoidance behaviors if they run a higher risk of infection. Also, if rainfall does play an important role in dispersing larvae away from dung middens, then selective foraging behavior may vary with season and may also occur on a larger scale than was examined in the current study. Future work will investigate the existence of fecal avoidance behavior in a wider range of species, examine host foraging behavior in relation to feces and larval distributions at both fine (patch-level) and coarse (territory-level) scales, and explore relationships between selective foraging behavior and host infection rates. This will help improve our understanding of the behavioral mechanisms wild animals use to combat parasitism.

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