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Smelling fit: scent marking exposes parasitic infection status in the banded mongoose

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Abstract

Preference for uninfected mates is presumed beneficial as it minimizes one's risk of contracting an infection and infecting one's offspring. In avian systems, visual ornaments are often used to indicate parasite burdens and facilitate mate choice. However, in mammals, olfactory cues have been proposed to act as a mechanism allowing potential mates to be discriminated by infection status. The effect of infection upon mammalian mate choice is mainly studied in captive rodents where experimental trials support preference for the odors of uninfected mates and some data suggest scent marking is reduced in individuals with high infection burdens. Nevertheless, whether such effects occur in nonmodel and wild systems remains poorly understood. Here, we investigate the interplay between parasite load (estimated using fecal egg counts) and scent marking behavior in a wild population of banded mongooses *Mungos mungo*. Focusing on a costly protozoan parasite of the genus *Isospora* and the nematode worm *Toxocara*, we first show that banded mongooses that engage in frequent, intensive scent marking have lower *Isospora* loads, suggesting marking behavior may be an indicator trait regarding infection status. We then use odor presentations to demonstrate that banded mongooses mark less in response to odors of opposite sexed individuals with high *Isospora* and *Toxocara* loads. As both of these parasites are known to have detrimental effects upon the health of preweaned young in other species, they would appear key targets to avoid during mate choice. Results provide support for scent as an important ornament and mechanism for advertising parasitic infection within wild mammals.

Key words: Isospora, olfaction, parasite, scent, scent preferences, Toxocara.

One of the major costs of social behavior is the risk of pathogenic infections, including those caused by parasites (Loehle 1995; Altizer et al. 2003). As such, a variety of behavioral mechanisms have evolved to minimize parasite exposure and to avoid infection (Kavaliers et al. 2005b), and hence parasites are now considered to play major roles in social organization including breeding dynamics. Here parasitic infection can have an important influence on sexual selection as infectious pathogens have the potential to affect not only host growth, survival, and health (Coltman et al. 1999), but also behavior (Poulin 1994; Poulin 1995; Klein 2003). This may in turn affect a hosts' ability to locate, attract, and/or copulate with potential mates. Therefore, mechanisms to detect and avoid highly parasitized mates are assumed advantageous across species.

In avian systems, there is a wealth of research into the ability of bright and conspicuous plumage to advertise health and fitness (Hamilton and Zuk 1982; Petrie 1994; Hale et al. 2009), although

the evidence for this hypothesis is mixed (Hamilton and Poulin 1997). Female choice based upon such traits selects for healthier mates including those of low parasite burden (Loehle 1997; Roulin et al. 2001; Buchholz 2004; Moreno-Rueda and Hoi 2011). This may benefit females not only directly by reducing their likelihood of contracting costly parasitic infections (Loehle 1997), but also indirectly by providing offspring with genes for parasite resistance if this trait is heritable (Hamilton and Zuk 1982; Moller 1990). There is also evidence that males prefer visually ornamented females, such as in the barn owl *Tyto alba*, where spotty plumage indicates lower parasite loads (Roulin et al. 2001).

Mammals tend not to possess such elaborate visual ornaments, although there are exceptions such as secondary sexual coloration of primates which are believed to function in mate choice (Waitt et al. 2003). However, when tested in mandrills *Mandrillus sphinx*, neither facial coloration nor rump swellings appeared related to parasite load despite being sexually selected traits (Setchell et al. 2006, 2009, 2011). Nevertheless, mate choice based directly upon infection status does still occur. Laboratory and captive rodents are consistently observed to avoid mating with individuals infected with parasitic nematodes, viruses, and other microorganisms (Penn and Potts 1998b; Zala et al. 2004; Kavaliers et al. 2005a). In rodents, olfactory signals appear to allow mate discrimination on the basis of infection (Penn and Potts 1998 a, 1998b; Gosling and Roberts 2001; Arakawa et al. 2011). This is unsurprising considering the predominant role of odor signals within mammalian communication (Kavaliers et al. 2005b; Wyatt 2014). In one example Zala et al. (2004) showed that male wild-derived (but captive) mice infected with *Salmonella enterica* bacteria have reduced marking rates and their scent appears less attractive to females. This suggests that scent marking behavior may act as an indicator of infection whilst the scent itself also encodes infection status.

Unfortunately, caveats of previous research include an almost exclusive focus on laboratory or captive rodents with little taxonomic diversity or consideration of wild systems. Odor presentations also tend to be choice-tests in experimental arenas that may not accurately reflect scent marking behavior as it would occur in the wild (Hurst et al. 1994) which makes it difficult to extrapolate findings to natural situations. Additionally, some frequently cited examples of parasitic avoidance focus on bacteria (Zala et al. 2004, 2015) or viruses (Penn and Potts 1998a). Although these organisms have important health implications and may also constitute parasites in the broad sense, the mechanisms by which they influence scent composition and marking behavior will likely differ from gastrointestinal parasites (Kavaliers et al. 2005a, 2005b). This is an important discrimination to make because wild mammals, particularly carnivores, are often heavily infected by gastrointestinal parasites (Pedersen et al. 2007) suggesting these pathogens could have considerable impacts upon social and sexual behavior including mate choice (Poulin 1994).

We aim to overcome these limitations by investigating whether scent communication can encode parasitic information in the banded mongoose. This cooperative breeder provides a novel opportunity for such research as the wild focal population can be sampled for gastrointestinal parasites (via fecal sampling) and is habituated to human presence allowing targeted odor presentations to be conducted without disturbing natural behavior. Despite both sexes exhibiting mate choice (Nichols et al. 2010; Cant et al. 2013), banded mongooses are sexually monomorphic, lack visual ornaments, and thus appear limited in terms of visual cues advertising quality. However, both sexes do participate in extensive olfactory marking (Jordan 2009; Jordan et al. 2010) providing a potential mechanism through which parasitic infection status may be encoded. Scent marking events, such as latrines, are common occurrences (Müller and Manser 2007; Jordan 2009) and previous research suggests scent is likely utilized for within-group communication (Jordan et al. 2010), particularly intrasexual competition (Müller and Manser 2007, 2008; Jordan et al. 2011a). However, it is currently not known whether odor cues also contain fitness-related information such as parasitic infection status, which could assist in mate choice.

To address whether scent marking behavior is influenced by parasitic infection in the banded mongoose, we first investigated whether fecal egg counts of 2 common parasites (*Isospora* and *Toxocara*) correlated with scent marking behavior during natural marking bouts. We then investigated whether the parasites may be detected via scent by presenting individuals with odors from differentially parasitized opposite sex group members. We predicted that: 1) if parasite load impacts marking behavior, then more heavily infected individuals should engage in fewer social marking bouts and deposit fewer scent marks; and (2) if parasite burdens are detectable via scent, behavioral aversions should occur in response to the odors of highly parasitized individuals.

Materials and Methods

Field site and study species

The banded mongoose is a small (<2 kg) diurnal carnivore, common throughout sub-Saharan Africa, which lives in large mixed-sex groups of 5–40 individuals, mean 29 (Cant et al. 2013). Groups contain a 'core' of ~1–5 dominant breeders of each sex, which reproduce regularly (up to 4 times per year), but younger subordinates breed alongside dominants when environmental conditions are good (Nichols et al. 2012). Within social groups, reproduction is synchronized; females come into estrous within a week of each other and give birth together, on the same night in more than 60% of breeding attempts (Hodge et al. 2009) . The resulting litters are raised communally by the group, with both breeders and non breeders contributing to pup care (Cant et al. 2013). During estrus, dominant males attempt to mate-guard females, following them closely and chasing off rivals. However, females are able to refuse unwanted matings and also to evade their mate-guard and mate with other males (Cant 2000). For further details of banded mongoose reproduction, behavior and demography, see Cant et al. (2013).

In banded mongooses, scent is primarily used for within-group communication, rather than for territory defense (Jordan et al. 2010). Previous studies, focused on over-marking behavior, found that scents are sexually dimorphic (Jordan et al. 2011a). Both male and female adults are more likely to over mark the scents of same-sex individuals, suggesting that over marking may be involved in intrasexual competition (Jordan et al. 2011a). Supporting this idea, Jordan et al. (2011b) found that males that over marked more had greater mating success.

The current study used a wild but habituated banded mongoose population in Queen Elizabeth National Park, Uganda (0°12′S; 27°54′E). This population has been monitored continuously since 1995 under licenses from the Ugandan Wildlife Authority, Ugandan National Council for Science and Technology. All experimental procedures have been approved by the University of Exeter's Ethical Review Committee. Full details of the population, habitat, and climate are described elsewhere (Cant 2000). All mongooses are habituated to close (<5 m) human observation and identified by unique shaves in their fur (for full details see Cant 2000). Shaves are

maintained during routine trapping events where individuals are caught by trained field staff in baited Tomahawk traps and anaesthetized with isoflurane (Jordan et al. 2010). No fatalities or health concerns have arisen from trapping procedures across the long-term study's duration. Every effort is made to minimize stress during the trapping process, but it is likely that capture raises stress levels. Due to this, no observations or scent presentations were made on a group within 24 h of the capture of any group members. Pups are first trapped at around 4 weeks of age and, under anesthetic, are given a unique identifier (a passive integrated transponder (PIT) tag or, pre 2001, a tattoo) and are sexed by examination of the genital region (Gilchrist 2008; Jordan et al. 2010). Groups are visited by trained observers approximately every 2 days meaning accurate ages, group compositions, and life history information is available.

Parasite analysis

Fecal samples for parasite analysis were obtained between May and August 2014. Samples were collected directly after deposition by scooping the feces up in a clean plastic bag. The sample was then homogenized and half returned to the field to avoid disturbing natural scent marking. The remaining half was transferred into a 50 mL falcon tube containing approximately 20 mL of 5% formalin and stored at room temperature. Fecal samples were analyzed by a modified MacMaster technique (Dunn and Keymer 1986; Coles et al. 1992; Cringoli et al. 2004) which involves several wash stages and a final suspension within 15 mL of saturated saline. A 0.3 mL aliquot of the resulting solution was transferred to a McMaster slide. Eggs per gram (EPG) of feces were calculated as $(15/0.3)Y/X$, where Y represents the sum of all ova counted across the 2 chambers of the Macmaster slide and X represents the total weight of fecal matter from which the ova were obtained (Dunn and Keymer 1986). Ova were identified using the veterinary parasitology literature (Frenkel and Smith 2003; Adl et al. 2005; Bowman 2014; Leclaire and Faulkner 2014).

Faecal egg count is a commonly used method to assess parasite loads in the wild, yet the method has well-known limitations. For example, fecal egg counts often face criticism as a measure of parasite load due to high variability within individuals sampled (Villanua et al. 2006; Gasso et al. 2015). Egg shedding loads can vary with the life stage of the parasite, coinfection, environmental conditions, and the physiological condition of the host (Dorchies et al. 1997; Villanua et al. 2006; Jolles et al. 2008; Raharivololona and Ganzhorn 2010). This may be a particular issue for nematode worms, as the counts in feces reflect not only the number of mature worms, but also their fecundity and patterns of shedding ova. Furthermore, ova can migrate and mature in other tissues besides the intestine, which may further decouple ova counts from worm/larvae numbers (Urquhart et al. 1996). However, assessing the variation in egg counts provide a method to compare the relative parasite loads in a system where true parasite burdens are impossible to assess (Gillespie 2006); it would not have been feasible for us to sacrifice individuals to gain comprehensive adult parasite counts from the gastrointestinal tract. Furthermore, for the purpose of this study, fecal egg count is a direct indication on the parasite ova shedding pattern of a particular individual. It, therefore, indicates the infectiousness of the individual in question; the more eggs in feces, the more contagious that individual is. The number of eggs in feces is therefore very relevant, at least in terms of direct avoidance of infection, even if less so in terms of sexual advertising of an individual's capability to resist or fight off infection.

We took several measures to maximize the usefulness of our fecal egg counts. First, we used average ova counts which are likely to minimize the effect of within-individual fluctuations in egg counts owing to parasite fecundity and provide a comparable estimate of parasite load across individuals for this short-term period. Second, as exact exposure levels may vary between social groups due to variation in territories and proximity to humans and other animals, we controlled for group identity in all analyses. Finally, for the duration of the study (May to August 2014) climate remained consistently warm and dry with negligible rainfall, and all groups patrolled consistent territories. Thus, the effect of weather fluctuations, abnormal foraging patterns, territory shifts, or other known stressors on average fecal egg counts is also expected to be minimal. Nevertheless, we emphasize the correlative nature of our results and that we cannot dismiss the possibility that exposure levels may also differ between individuals within social groups.

In this study, we focused on 2 pathogens that are both common in banded mongoose fecal samples and also have demonstrated negative effects in other species 1) a coccidian of the genus *Isospora*, and 2) a *Toxocara* nematode species. *Isospora* were present in 100% and *Toxocara* in 61% of samples collected during this study period. *Isospora* are spore-forming protozoans of the subclass Coccidia. In other species, their resulting infection (coccidiosis) damages the cells lining the gut wall, leading to diarrhea and dehydration (Urquhart et al. 1996) which may consequently compromise reproductive success (Hill et al. 2005; Hakkarainen et al. 2007), body condition (Hill et al. 2005), and survival (Alzaga et al. 2007). *Toxocara* are nematode worms which reside in the host's small intestine where they may cause anemia and malnutrition, and in many host mammals *Toxocara* ova can migrate to other tissues including the lungs, liver, and uterus (Urquhart et al. 1996). The latter is particularly problematic for breeding females as ova are able to infect developing fetuses, causing chronic and often fatal infections after birth (Lee et al. 2010). Indeed, the most severe effects of both parasites are felt by pre-weaned young (Eustis and Nelson 1981; Urquhart et al. 1996; Lindsay et al. 1997; Kirkpatrick 1998; Mateo 2003; Mundt et al. 2006; Bowman 2014). Therefore, *Isospora* and *Toxocara* would appear key parasites to avoid during mate choice in terms of safeguarding reproductive success and offspring fitness.

Is natural scent marking behavior correlated with parasite burdens in the banded mongoose?

Behavioral data collection. To investigate whether scent marking behavior reflects parasitic infection, we observed social marking events within 2 geographically separated social groups (known as 1B and 1H). Marking bouts were filmed on a handheld camera (Panasonic 5 Access Hybrid O.I.S, Full HD) for the first 2 h of foraging (as the group left the den) during 2 separate mornings per-week between 28 May and 31 July 2014. From these films, three key measures of marking behavior were recorded: 1) the frequency of marking bouts where a mongoose was present at the marking site but did not deposit a scent mark (termed "present but inactive"); 2) the frequency of marking bouts where a mongoose was present and actively sniffing or deposited at least one scent mark but fewer than 5 scent marks (termed "active"); and 3) the frequency of marking bouts where an individual deposited 5 or more scent marks (termed "intense marking"). The upper quartile of marks deposited in the same bout is 5 marks. A scent mark was defined as any behavior that appeared capable of depositing an olfactory cue. Such behaviors included chin or anal-rubbing, defecating, urinating, chewing, scratching, and licking but not sniffing. Parasites are known to have

variable effects upon host behavior (Poulin 1994), and thus the 2 former parameters (presence and activity at marking bouts) were included to evaluate whether parasitic infection influences general behavioral patterns such as presence at social marking bouts. We focused on intense marking behavior, as previous studies of other mammals including primates and prosimians (Irwin et al. 2004; Droscher and Kappeler 2014), mustelids (Clapperton 1989; Begg et al. 2003), and ungulates (Gosling 1987; Brashares and Arcese 1999) find that social marking events appear to be attended by group members indiscriminately of age, sex, or dominance factors, and that individual differences generally appear when considering the frequency and intensity of marking behaviors (Rich and Hurst 1998; Brashares and Arcese 1999; Rich and Hurst 1999; Begg et al. 2003). Preliminary observations in the banded mongoose found that the vast majority of group members attended and partook in marking events. Intensive scent marking (>5 marks per bout), however, displayed much greater individual variability. Although 47% of banded mongooses deposited >5 scent marks per bout on more than 2 occasions, only 31% did so on more than 4 occasions, and only 22% on more than 6 occasions. Thus, intensive scent marking appears restricted to a subset of the population, and therefore may incur metabolic or opportunity costs.

Female banded mongooses become sexually mature around 7–8 months, first giving birth as early as 9 months old. Males have poor reproductive success until around 2 years of age due to competitive exclusion by older individuals (Nichols et al. 2010), however young males do show interest in estrous females (Cant 2000). We, therefore, excluded individuals less than 6 months from the analyses as they are unlikely to be using scent to assess potential mates. The final dataset comprised 20 individuals aged >6 months from each social group (40 individuals in total), which were observed more than a total of 102 marking events (61 in group 1B, 41 in group 1H).

Parasite data collection. To accompany behavioral data, weekly fecal parasite samples for each of the 40 individuals were collected during the study period (May to July 2014). These samples were used to calculate the mean EPG count of *Isospora* oocytes and *Toxocara* ova for each individual within the 2 focal groups. Note that parasite loads were unknown at the time of film scoring, so all marking data were collected blind to the infection status of individuals.

Statistical analysis. To test the effect of mean parasite load upon scent marking behavior, models were constructed in R (version 3.0.2). In total, 3 models were constructed per parasite, with the response variables as the frequency of marking bouts where an individual was either 1) present but inactive, 2) active, or 3) intensely marking. Parasite load, rank, sex, and group were fitted as explanatory terms and all second-order interactions were included in initial models. Banded mongooses appear to have an age-based dominance hierarchy, with the oldest group members of each sex generally being dominant over younger individuals (Cant et al. 2013). Rank was, therefore, included as a proxy measure for dominance. The oldest member of each sex within each group was assigned the rank of 1, the next oldest 2 and so on. Models were fitted in full and were then simplified using the step-wise method of sequentially removing each nonsignificant term ($P > 0.05$). To model *Isospora* load, General Linear Models (LMs) were constructed using the package lme4 (Bates et al. 2008). Models were fitted with a maximum likelihood convergence criteria and Gaussian error distribution. The *Toxocara* data did not conform to normal distributions and thus was multiplied by 1,000 and analyzed by a model fit by penalized quasi-likelihood (glmPQL) with a negative binomial error distribution, built within the MASS package (Venables and Ripley 2002).

Can parasitic infection be detected via odor cue?

Odor collection. During the course of our study, anal-gland secretions (AGS) were the most commonly deposited odor cues, suggesting they are a good candidate to encode important information regarding behavioral decision-making. Furthermore, previous studies (Jordan et al. 2010, 2011a, 2011b) have found AGS to encode information such as sex and individual identity. AGS were collected between 29 May and 31 July 2014 during routine trapping events, following the methods of Jordan et al. (2010). Briefly, individuals were anaesthetized and the anal region was cleaned with cotton wool. A glass vial was placed over each of the 2 gland openings in turn and the gland was gently squeezed to express ~150 μL of liquid. Secretions were collected in 2 mL snap-cap glass vials that were cleaned by soaking for several hours in methanol, air-drying then soaking in detergent and warm water (1:1,000 dilution), rinsing and allowing to air dry again. Secretions were vortexed to mix, labeled, and transferred to liquid nitrogen for storage. To avoid contamination, sterile nitrile gloves were worn and changed between individual banded mongooses. The examiner's fingers never came into contact with the secretion nor the top of the glass vials. We cannot exclude the possibility that anesthetization impacted on the composition of the AGS, but as all samples were collected in the same way, the effect if there is any, should be the same in all individuals, and therefore is not expected to influence or bias results.

Odor presentations. Between 1 June and 2 August 2014, 84 odor presentations were conducted in the field to test whether banded mongooses respond differently to the scent of opposite sex group members based upon *Isospora* or *Toxocara* infection. Presentations were conducted within 2 well-habituated study groups (1B and 1H) and to maintain relevance to mate choice, individuals were always presented with AGS from the social group to which they belong. AGS samples were transferred to a thermos flask of ice on the morning of the presentation. Samples were fully defrosted directly before presentations, spread upon a clean ceramic tile using an autoclaved cotton swab, and presented directly to the recipient individual. Presentations were conducted when the recipient was at least 1 m away from other conspecifics and was actively foraging. No odors were presented during resting periods, aggression, social bonding, or interactions between groups. After a predator alarm or social marking event involving the recipient, or over half the group, observers waited at least 20 min to ensure presentations were not influenced by these events. If an intergroup interaction occurred, all presentations were abandoned for at least 24 h, or longer if the animals were still showing unusual behavior such as increased vigilance behavior, failure to forage, or increased scent marking.

Responses to the presentations were filmed using a handheld camera (Panasonic 5 Access Hybrid O.I.S, Full HD) and scored after the field session. To address whether olfactory cues may encode information pertaining to parasite infection, 3 measures of response to odor presentations were considered. "Duration" represented the time before mongooses returned to normal behavior (ceased vigilance, left 1 m radius around presentation, and returned to foraging or group activity). "Contact" referred to the duration a mongoose remained within 30 cm of the tile on which the odor was presented. Finally, "Vicinity Marking" referred to the number of scent marks

recipients deposited around the odor (within 30 cm of the tile), but not directly on top. Marking response was categorized this way as previous research suggests that when odors are used for mate choice and self-advertisement, scent marks are placed adjacent to, rather than directly over the original marks (Wolff et al. 2002). This is believed to maximize the identities of both scent markers, whereas direct over marking can obliterate the original scent and is thus generally considered to function in competition (Rich and Hurst 1999; Wolff et al. 2002). Indeed, previous work on banded mongooses suggests that over marks are used for intersexual competition, hence may not be important for mate advertisement (Jordan et al. 2010, 2011a). In addition, Jordan et al. (2011a) investigated responses to 2 banded mongoose scents on the same site and found that the sex of the top or most recent scent was more important than that of the bottom or original scent in determining over marking response, indicating that over marks do to some extent mask the scents below.

Parasite data collection. For each odor donor, fecal samples (3–6 per individual) were collected per individual within a 7-day-window either side of AGS odor sample collection. This allowed the calculation of mean EPG *Isospora* and *Toxocara* loads for each odor donor. As fecal ova counts are often variable within individuals (Gasso et al. 2015), this was considered the most robust method for generating comparable *Isospora* counts. Measures of odor donor parasite load were assessed upon return from the field and thus were unknown during fieldwork and odor presentations, which removed the risk of observer and expectation biases. All fecal samples were collected in the mornings, reducing the impact of circadian rhythm on oocyte shedding, hence increasing the comparability of our samples between individuals (Martinaud et al. 2009).

Statistical analysis. Due to the distribution of average *Isospora* and *Toxocara* load, their effects upon marking behavior were analyzed within models fit by glmPQL with a binomial error distribution built in the MASS package of R version 3.0.2 (Venables and Ripley 2002). The 3 response terms were the duration of the response (duration), the duration a mongoose remained within 30 cm of the odor (contact), and the number of scent marks recipients deposited around the odor (vicinity marking). In separate models, the EPG load of each parasite was multiplied by 1,000 (to create full, positive integer values) and fitted as an explanatory variable alongside the sex, age, and rank of odor donors as parasite loads may vary with such life history parameters. The identity and group of the odor donor was included as a random factor as certain animals yielded larger AGS samples that could be split and used in multiple presentations. Specifics of the recipient did not require inclusion as all were sexually mature adults of opposite sex and familiar to their odor donors. Initial models included all second-order interactions, however, nonsignificant terms were removed using the backward step-wise method of model simplification.

Results

Is natural scent marking behavior correlated with parasite burdens in the banded mongoose?

Group marking events occurred on average every 17 min in the first 2 h of foraging. In 49% of these bouts, every group member over 6 months of age was present at the marking site and was either sniffing or actively scent marking.

Whilst we did not find a significant relationship between *Isospora* load and presence or activity within marking bouts, *Isospora* load did impact intensive marking behavior (>5 marks per bout) in interactions with both sex (LM: $t = 2.462$, $P = 0.019$, Table 1, Figure 1) and social group (LM: $t = 4.203$, $P = 0.0002$, Table 1, Figure 1). In support of our predictions, the frequency of intense marking was significantly higher in individuals of lower *Isospora* load, with the exception of female individuals within 1 of the 2 social groups (group 1H), among which no individual attended intensive marking bouts more than 3 times (Figure 2). The interactions of *Isospora* load with both sex and group identity seem, therefore, likely to reflect properties of the dataset and "missing" datapoints owing to the lowered marking activity of females in this group.

Individuals with higher *Toxocara* ova burdens were significantly more likely to be present but inactive at marking bouts (LM: $t = 2.942$, $P = 0.003$) compared with individuals with lower levels of infection. Although a nonsignificant trend suggests highly infected individuals are less active in marking bouts (LM: $t = -1.879$, $P = 0.06$), there was no significant difference in marking activity or intense marking relating to *Toxocara* burdens. In models for both *Isospora* and *Toxocara*, female banded mongooses were present but inactive in significantly more bouts than males, whilst males were more likely to be scent marking and intensively marking than females (Table 1). Note that there was no correlation between *Toxocara* and *Isospora* loads (LM: $t = 0.124$, $P = 0.902$).

Can parasitic infection be detected via odor cue?

Scent marking behavior in response to opposite sex odor presentations was correlated significantly with the parasite burdens of odor donors (Table 2). In initial models, the *Isospora* load and age of the odor donor interacted to significantly predict marking response (GLMM: effect size $= 1.889 \times 10^{-9}$, SE $= 9.269 \times 10^{-10}$, $t = 2.038$, $P = 0.042$). Here, vicinity marking declined as the odor donor's infection status increased, however the effect was skewed by 1 older odor donor with a very high *Isospora* burden. When this outlier was removed, the interaction dropped out, however results still maintain a significant negative correlation between *Isospora* load and marking behavior (GLMM: $t = -1.990$, $P = 0.047$, Table 2, Figure 2). In fact, the scent of all individuals with high *Isospora* loads (>250 EPG) received fewer than 10 scent marks. This supports our predictions that recipients should show less interest in the odors of heavily parasitized conspecifics.

The sex and *Toxocara* load of odor donors also interacted to influence marking behavior (GLMM: $t = 2.190$, $P = 0.029$, Table 2, Figure 3). Fewer vicinity marks were deposited over male odors (by females) as their *Toxocara* load increased but this trend was not apparent when considering female odors.

Female odors provoked lower contact durations in both datasets and less scent marking than male odors within in the *Isospora* dataset (Table 2). The odors of top ranking donors received significantly more marks than those of lower ranked individuals in both datasets, and individuals who were relatively young for their rank also received more marks (Table 2). Finally, no factors included in the models had significant effects upon the duration before returning to normal foraging behavior.

Discussion

Results suggest that in the banded mongoose, natural scent marking behaviors are influenced by parasite burden, with highly infected individuals being less likely to mark intensively. This supports our first

Table 1. The relationship between *Isospora* and *Toxocara* burdens and marking behavior at social marking bouts

Model testing	Fixed effect	Effect size	Estimate (SD)	*t* value	*P* value
Frequency of bouts present but inactive	Intercept	2.727	0.481		
	Sex (female)	**2.323**	**0.697**	**3.335**	**0.002**
	Social group (1H)			−1.179	0.246
	Rank			0.307	0.761
	Isospora load			−0.616	0.542
	Intercept	0.944	0.131		
	***Toxocara* load**	**5.30×10^{-6}**	**1.80×10^{-6}**	**2.942**	**0.003**
	Sex (female)	**0.502**	**0.174**	**2.895**	**0.003**
	Social group (1H)			−0.859	0.390
	Rank			0.307	0.759
Frequency of bouts active	Intercept	21.359	1.514		
	Sex (female)	**−5.464**	**1.779**	**−3.072**	**0.004**
	Social group (1H)	**−7.172**	**1.779**	**−4.033**	**2.0×10^{-4}**
	Rank			−1.514	0.140
	Isospora load			−0.361	0.720
	Intercept	3.080	0.099		
	Sex (female)	**−0.361**	**0.124**	**−2.912**	**0.004**
	Social group (1H)	**−0.473**	**0.123**	**−3.850**	**1.0×10^{-4}**
	Rank			0.924	0.356
	Toxocara load			−1.879	0.060
Frequency of bouts intensively marking(5+ marks deposited)	Intercept	7.194	0.553		
	Rank			−1.125	0.269
	***Isospora* load**	**−0.042**	**0.008**	**−5.145**	
	Sex (female)	**−3.042**	**0.717**	**−4.245**	
	Social group (1H)	**−3.980**	**0.694**	**−5.733**	
	***Isospora* load: Sex**	**0.024**	**0.010**	**2.462**	**0.019**
	***Isospora* load: Social group**	**0.038**	**0.009**	**4.203**	**2.0×10^{-4}**
	Intercept	1.727	0.145		
	Sex (female)	**−0.827**	**0.222**	**−3.721**	**2.0×10^{-4}**
	Social group (1H)	**−0.824**	**0.215**	**−3.833**	**1.27×10^{-4}**
	Rank			0.290	0.772
	Toxocara load			−1.042	0.298

The sample size was 40 individuals more than 6 months of age, living in 2 social groups. A total of 102 marking bouts were observed. Full models considered the relationship between marking behaviors and EPG parasite load, sex, group, and all second-order interaction between fixed effects. Bold text denotes terms remaining significant within the minimal model. The table details the intercept of the minimal model and the *P* values upon which fixed effects were removed during the backward step-wise process of model simplification. Effect sizes are not reported when there is no significant effect of the variable, as the variable is not included in our final models.

prediction that scent marking behavior may encode information regarding donor infection status. Furthermore, our scent presentation experiments found that behavioral aversions in the form of reduced vicinity marks occurred in response to the odors of highly parasitized individuals, supporting our second prediction that odor may communicate parasite infection status. Our study provides novel evidence of odor-based parasite discrimination in a wild, nonmodel species.

Banded mongooses that frequently deposited more than 5 scent marks per bout (intensive scent marking) showed significantly lower *Isospora* loads than conspecifics that marked less. This suggests that scent marking may be considered as an indicator trait signaling lower *Isospora* burdens. Olfactory advertisement of quality may function in a similar way to elaborate plumage which often signals parasite resistance in birds (Petrie 1994; Hale et al. 2009). For example, in house sparrows, females preferentially mate with males who have larger wing bars. Such males also have larger uropygial glands which are involved in resistance against chewing lice, a common parasite of this species (Moreno-Rueda and Hoi 2011). Thus, choice based on an attractive advert allows females to select better quality mates. Indeed, male banded mongooses who mark most frequently also secure more mating opportunities (Jordan 2009, 2011a). Our results enrich this finding as intense scent marking appears to act as an indicator trait for reduced *Isospora* infection, thus providing a trait by which scent marking can inform mate choice.

An exception to this trend were females from group 1H, which showed no decrease in intensive marking activity, stressing the importance of controlling for social and life history factors when considering behavioral reactions to odor presentations. However, the lack of correlation in this group seems to reflect differences in behavior and parasite load, rather than a different effect: these individuals show overall lower frequencies of intensive marking behavior and low *Isospora* loads (very few individuals had more than 500 EPG; see Figure 2) .Overall, based on our results intensive scent marking, therefore, appears limited to banded mongooses of low *Isospora* load. This suggests scent marking may be used to signal low parasitic infection status to potential mates.

Individuals with higher *Toxocara* burdens were present but not marking in significantly more bouts than individuals of lower infection levels and activity at marking bouts declined (nonsignificantly) with increasing *Toxocara* infection. However, in contrast to *Isospora* results, there was no correlation between *Toxocara* load and intense marking. It may be that *Toxocara* has fewer immediate effects upon host behavior, indeed *Toxocara* ova can lie dormant

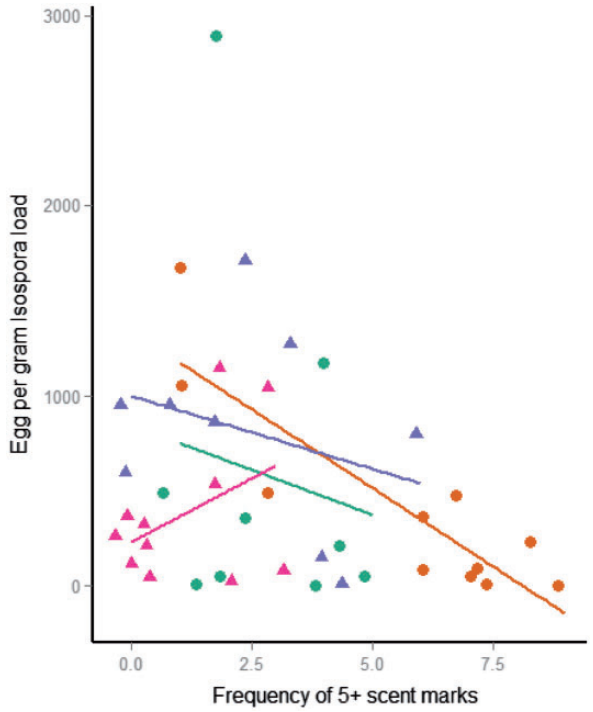

Figure 1. The relationship between *Isospora* load and intensive marking behavior. Points show raw data (circles = male, triangles = female). Lines (green for social group 1B females, orange 1B males, purple for 1H females and pink for 1H males) were calculated by linear regression of *Isospora* load upon the frequency of depositing >5 marks per bout. Results were based upon 102 observations of group marking events within 2 social groups containing 40 individual banded mongooses aged >6 months. In general, individuals with lower *Isospora* loads engaged in intense marking (>5 marks per bout) significantly more frequently than individuals of higher *Isospora* load. The exception to this is females within group 1H (purple line, triangular points).

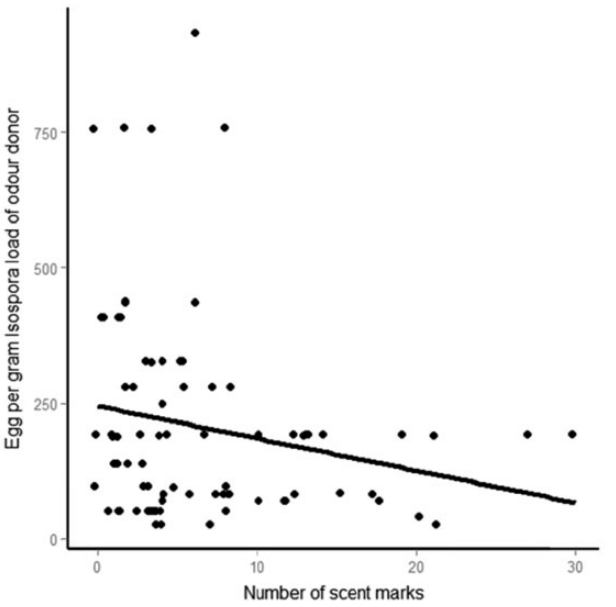

Figure 2. The relationship between *Isospora* load and marking behavior to presented odors. Recipients deposited fewer marks toward opposite sex odors as the *Isospora* load of the odor donor increased. Points show average EPG *Isospora* counts for each odor donor, and lines were fit by linear regression of EPG load against scent marking.

in bodily tissues for several years before causing notable health concerns (Urquhart et al. 1996). Therefore, the impact on the host, and possibly effects on odor cues, may vary with the stage of infection. Furthermore, tolerance to these parasites may also differ.

Differences in the possible impacts of *Isospora* and *Toxocara* may also occur due to the differing reliability of ova counts to reflect actual parasite burdens. In protozoan, single-cell parasites including *Isospora*, oocysts shed in feces directly represent the number of sexually reproducing parasites, whereas the ova of nematode worms may be shed at differing intensities dependent of the life stage and fecundity of the parasite as well as condition of the host (Villanua et al. 2006; Gasso et al. 2015; Rafalinirina et al. 2015). *Toxocara* ova can also migrate and mature in other tissues besides the intestine which temporarily decouples ova counts from worm/larvae numbers (Urquhart et al. 1996) meaning ova counts may not be as reliable an indicator of parasitic infection as *Isospora* oocytes. A more controversial explanation would be to suggest that *Toxocara* parasites are able to manipulate host behavior for their own benefits (Poulin 1994). Indeed, attending social events such as marking bouts should increase parasite transmission due to contact with multiple individuals. However, under this assumption one would also expect *Toxocara* burdens to be higher in active and intensive scent markers, which is not the case.

In support of our second prediction, odor presentation results suggest that banded mongooses are able to discriminate infection status via scent. Recipients significantly reduced vicinity marking around odors of increasing parasite burdens when considering both *Toxocara* and *Isospora* infections. This is an exciting result as, to the best of our knowledge, it provides the first evidence that a wild, nonmodel mammal can discriminate odors on the basis of infection. However, note that, due to being carried on a wild population, our results are correlative so cannot conclusively demonstrate cause and effect. Future work would benefit from using antiparasitics to experimentally manipulating parasite levels in this species, and hence reveal any causal link.

As vicinity marks are often used in mate choice and self-advertisement (Wolff et al. 2002), reduced vicinity marking behavior toward highly parasitized opposite sex odors suggests that parasites may play a part in mate choice in the banded mongoose. Avoiding highly parasitized mates should provide direct fitness benefits to both sexes as it is likely to minimize the risk of contracting an infection through close contact. Additional fitness benefits to avoiding heavily parasitized mates may arise if susceptibility to parasite infection is heritable. In several species including feral Soay sheep *Ovis aries* (Smith et al. 1999), barn swallows *Hirundo rustica* (Moller 1990), and kittiwakes *Rissa tridactyla* (Boulinier et al. 1997) significant heritable variation for parasitic resistance has been shown. Although we do not currently have the data to test this possibility in the banded mongoose, future studies considering the heritability of endoparasitic resistance in this species will allow more detailed investigations into the benefits of choosing less infected mates.

For *Isospora*, reduced marking toward the odours of highly parasitized individuals was evident across the dataset. However, when considering *Toxocara* infection, male odors received significantly fewer vicinity marks as their infection status increased, yet male reactions to female odors did not change with female infection status. The responsiveness of females but not males to infection status could occur due to the potential costs of females becoming infected with

Table 2. The relationship between odor donor *Isospora* and *Toxocara* burdens and recipient responses to presented odors

Model testing	Fixed effects	Effect size	Standard error	*Z* value	*P* value
Duration before return to normal behavior	Intercept (*Isospora* model)	3.478	0.962		
	Donor sex (Female)	0.282	0.258	1.092	0.275
	Donor *Isospora* count			0.418	0.676
	Donor rank			−0.315	0.753
	Donor age (in days)			−0.704	0.481
	Intercept (*Toxocara* model)	3.870	0.878		
	Donor sex (female)	0.261	0.250	1.041	0.298
	Donor *Toxocara* count			−0.357	0.721
	Donor rank			−1.319	0.187
	Donor age (in days)			−0.863	0.388
Duration of contact	Intercept (*Isospora* model)	3.149	1.133		
	Donor sex (female)	**−0.632**	**0.301**	**−2.100**	**0.036**
	Donor age (in days)			−0.959	0.338
	Donor *Isospora* count			1.300	0.194
	Donor rank			0.482	0.630
	Intercept (*Toxocara* model)	2.828	0.338		
	Donor sex (Female)	**−0.503**	**0.243**	**−2.070**	**0.039**
	Donor age (in days)			−1.582	0.114
	Donor *Toxocara* count			−0.467	0.641
	Donor rank			−0.841	0.401
Vicinity marking	Intercept (*Isospora* model)	5.411	1.052		
	Donor *Isospora* count	-1.057×10^{-5}	5.311×10^{-6}	**−1.990**	**0.047**
	Donor sex (female)	**−0.676**	**0.283**	**−2.394**	**0.017**
	Donor age (in days)	-8.716×10^{-4}	3.326×10^{-4}	**−2.620**	**0.009**
	Donor rank	**−0.534**	**0.145**	**−3.675**	2.00×10^{-4}
	Intercept (*Toxocara* model)	7.071	0.990		
	Donor sex (female)	−0.583	0.337	−1.730	
	Donor *Toxocara* count	-1.460×10^{-5}	5.726×10^{-6}	**−2.550**	
	Donor age (in days)	-1.318×10^{-3}	2.794×10^{-4}	**−4.718**	2.39×10^{-6}
	Donor rank	**−0.821**	**0.148**	**−5.552**	2.83×10^{-8}
	***Toxocara* count*Donor sex**	-5.706×10^{-5}	2.605×10^{-5}	**−2.190**	**0.029**

The output of GLMMs testing the relationship between the response of opposite sexed conspecifics to presented odors and parasite burden, odor sex, age, and age rank. *Toxocara* results were based upon 85 odor presentations to familiar opposite sex conspecifics. The *Isospora* dataset included 81 presentations as 1 odor donor, used in 4 presentations, was excluded from the analysis on the basis of his extremely high *Isospora* burden. All second-order interactions were included in original models but if nonsignificant, they were removed during the backward simplification process. Nonsignificant fixed effects are presented alongside the *P* values upon which they were removed from the models. All intercepts refer to minimal models. Effect sizes are not reported when there is no significant effect of the variable, as the variable is not included in our final models.

Toxocara. Several species of *Toxocara* can lie dormant in uterine tissue and infect offspring during gestation (Urquhart et al. 1996), causing chronic and often fatal infections after birth (Lee et al. 2010). Females may, therefore, benefit from avoiding highly infected males as mates. Alternatively, these sex differences could be due to differences in the variation in parasite burden between the sexes, which may also reflect the differential costs of infection depending on sex. *Toxocara* burdens show greater variability within male donors suggesting female aversion toward higher infection burdens could be a biologically relevant response to avoid highly parasitized males. However, there was less variation in female *Toxocara* counts so it is possible that discrimination of female odors on the basis of parasite load may not be behaviorally possible or necessary. In most research investigating the ability of scent cues to encode infections, the animals have been experimentally infected (Kavaliers et al. 2003, 2005a, 2014; Roberts et al. 2014; Zala et al. 2015). This allows greater variation between infected and uninfected individuals meaning any parasite-mediated aversion to their scent cues should be more obvious. However, experimental manipulations of parasite load, for example through experimentally infecting individuals, may result in levels of infection not found in the wild, and so may not be biologically relevant.

While banded mongooses appear to respond to differences in parasite infection level based on odor, the mechanism by which they may do this is not currently clear. In birds, several coccidian parasites are recognized to reduce plasma protein levels and significantly decrease internal pH (Chapman 2014). Protein and pH differences are likely to alter the chemical profile of odors (Drea et al. 2013) providing a way for individuals to discriminate between the infection status of donors. It is, therefore, possible that banded mongooses are using similar cues to detect the parasite burden of odor donors directly. Alternatively, as parasite burden affects intensive marking behavior (at least for *Isospora*), it is possible that banded mongooses gain information about the parasite load of their group mates from their marking behavior and respond accordingly when presented with their scents. Indeed, previous studies (Jordan et al. 2011a, 2011b, 2011c) found that banded mongoose scents are individually identifiable through chemical analysis and also by banded mongoose group members, providing a means to recognize group mates from scents deposited during marking bouts. Furthermore, males who intensely scent marked had greater mating success (Jordan et al. 2011b), suggesting that banded mongooses may adjust their mating behavior in accordance with scent encounter rate. Future studies involving both the chemical analysis of scents and of

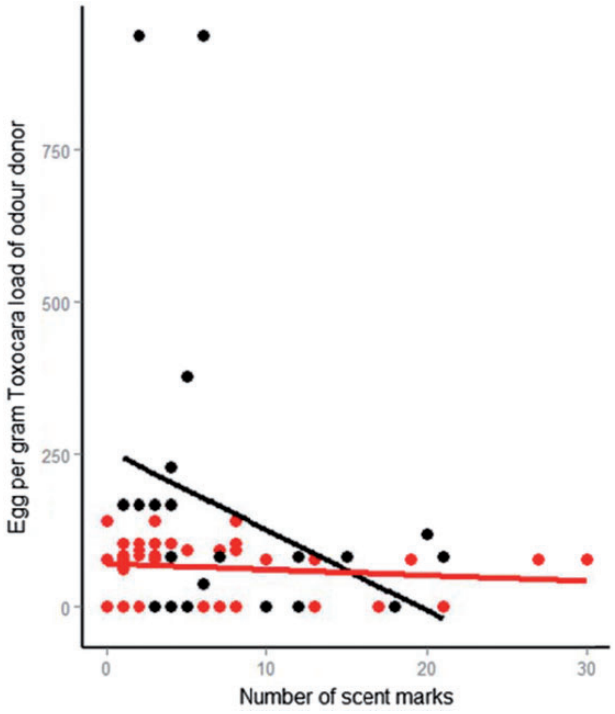

Figure 3. The relationship between odor donor sex, *Toxocara* load and reactions to opposite sex presented scents. Recipients deposited more marks toward male odors as their *Toxocara* load decreased (black points). This trend was not as strong when considering female odors (red points). Points represent average EPG *Toxocara* counts for each odor donor, lines fit by linear regression of egg load against scent marking.

presentations of scents of differentially parasitized unfamiliar individuals will allow us to determine whether parasite load could be identified chemically or via previous association in the banded mongoose.

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Author contributions

J.M. designed the study, collected scent and parasite data, analyzed the data and wrote the first draft of the manuscript; M.A.C. supervised field data collection; E.I.K.V. supervised parasite data collection, identification. and analysis; H.J.N. supervised the study, provided assistance with statistical analysis, and helped draft the manuscript. All authors commented on the manuscript.

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