Gastrointestinal parasites in relation to host traits and group factors in wild meerkats *Suricata suricatta*

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SUMMARY

Meerkats are one of the most endearing of South African's wildlife celebrities and one of the most highly studied social mammals. However, although parasites are widely recognized as important regulatory factors in animal population, basic knowledge on meerkats' parasites is lacking. Here 100 fresh fecal samples of wild meerkats were examined for the presence of endoparasitic infection. Endoparasitic taxa identified by the presence of eggs or oocysts included *Toxocara suricattae*, *Oxynema suricattae*, *Pseudandrya suricattae*, *Cystoisospora* sp. and *Eimeria* sp. Non-specific diagnoses were made for parasites in the Order Strongylida, Order Spirurida and coccidian based on the morphology and size of the eggs and oocysts. The prevalence of infection with *T. suricattae* and the strongylate species increased with age, while prevalence of coccidia and intensity of infection by the strongylate species increased with decreasing group size, suggesting that stress associated with living in smaller group may increase susceptibility to parasitism. Moreover, parasite communities were more similar between individuals from the same group than between individuals from different groups, suggesting an important role of the environment in parasite infestation. We did not detect any differences between males and females. This study represents the first detailed report of gastrointestinal parasites in wild meerkats, and is a key starting point for future studies on the effect of endoparasite load in the life history of this species.

Key words: Endoparasites, meerkats, group size, toxocara, strongylate.

INTRODUCTION

Infection by endoparasitic organisms is an important component in the dynamics of wild animal populations. Effects on vital demographic parameters such as decreased survival and fecundity have been described (Anderson and May, 1978; Hudson *et al*. 1992*a*; Stirnadel and Ebert, 1997; Krams *et al*. 2013). In numerous free-ranging wildlife species, the distribution of intestinal parasitic infection is affected by extrinsic or intrinsic factors such as environmental conditions, population density and host age, sex or condition (Setchell *et al*. 2007; Thurber *et al*. 2011; Oates *et al*. 2012). For instance, individuals may be more parasitized when living in larger home ranges because they encounter more parasite-dense areas (Nunn and Dokey, 2006), or during years of low food availability because of nutritional stress (Thurber *et al*. 2011).

Meerkats, *Suricata suricatta*, are one of the most endearing of South Africa's wildlife celebrities and one of the most highly studied social mammals. Although parasites may be important regulatory factors in their life history, basic knowledge on their fauna is limited to taxonomic descriptions of individual parasite species, and host-parasite checklists (Warren, 1970; Lynch, 1980; El-Gayar *et al*. 2008). To the best of our knowledge, systematic study of the parasites infecting meerkats at the population level has not been undertaken. Likewise, a photographic atlas illustrating the diagnostic stages of endoparasitic species infecting meerkats has never been published. Here we describe and illustrate the distribution of endoparastic infections in a wild population of meerkats based on the detection of eggs and oocysts found in freshly collected feces and an investigation of the host traits affecting individual infection risk. We test whether age and sex of the host, and size of the host group are associated with parasite prevalence. In addition, as meerkats live in territorial groups (van Staaden, 1994; Doolan and Macdonald, 1997), we expect individuals from the same group to host more similar parasite assemblage than individuals from different groups.

MATERIALS AND METHODS

Study site

This study was conducted on a wild population of meerkats at the Kalahari Meerkat Project in the

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Table 1. Number of samples, percentages of individuals sampled within the group, and number of females and males sampled within the group, for each studied group

	Period 1			Period 2		
Group identity	Number of samples	% of individuals sampled within the group	female #; male #	Number of samples	% of individuals sampled within the group	female #; male #
A	3	12%	1; 2	7	30%	4; 3
B	5	31%	3; 2	7	49%	3; 4
C	7	40%	2; 5	0		
D	9	28%	5; 4	3	10%	2; 1
E	7	24%	5; 2	9	34%	6; 3
F	1	7%	1; 0	0		
G	2	10%	0; 2	2	12%	1; 1
H	6	32%	5; 1	3	39%	2; 1
I	3	10%	1; 2	5	20%	1; 4
J	11	42%	7 : 4	5	19%	3 : 2
K	0			4	22%	2; 2
L	1	4%	0; 1	0		

Kuruman River Reserve (26°58′S, 21°49′E), on ranchland in the South African Kalahari desert. Data were collected in March–April 2011 (period 1) and November 2011 (period 2). Most individuals were habituated to observation from <2 m.

Sample collection

Fecal samples (mean ± SE weight: 3·62 ± 0·20 g) were collected immediately after defecation and stored at ambient temperature in plastic tubes filled with 15 mL 10% buffered neutral formalin. We collected 100 fecal samples (54 samples in period 1 and 46 samples in period 2) from a total of 12 groups (Table 1). Ten individuals (3 males and 7 females from 5 groups) were sampled during period 1 and resampled during period 2, while the remaining individuals were sampled only once. We sampled 54 females aged between 39 days and 7·3 years (mean ± SE: 1.7 ± 0·3 years), and 46 males aged between 41 days and 6·2 years (mean ± SE: 1·3 ± 0·2 years). At the time of our study, dominant individuals were older than all other individuals (>4·5 years *vs* <3·5 years), except for two dominant females aged 2·4 years and 3·1 years, one of which having just acquired dominancy. Age was therefore highly confounded with social status and we decided to consider only the age factor. Age and sex of sampled meerkats were equally distributed among periods ($t_{98} = -0{\cdot}40$, $P = 0{\cdot}69$ and $\chi^2 = 0{\cdot}01$, $P = 0{\cdot}94$).

Fecal sample analyses

Fecal samples were processed for microscopic analysis using the centrifugal sucrose flotation method as described by Zajac and Conboy (2012). Wet mount preparations were microscopically examined at ×200,

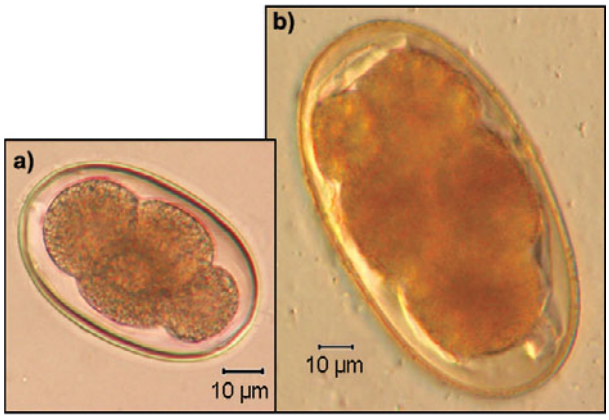

Fig. 1. Pictures of two strongyle-like eggs; (a) the small type and (b) the large type.

followed by ×400 for confirmation of parasite identification. Endoparasitic species were identified to taxonomic order, family and genus based on their diagnostic morphology and measurements made with a calibrated ocular micrometer. When possible, species level identifications were accomplished using published host-parasite checklists (Round, 1968; Lynch, 1980). The distribution of parasitic infections in the host was analysed based on prevalence and taxa richness of the infracommunity (Bush *et al*. 1997). Variance in prevalence of the strongylate species was very low and parasite intensity for infection with the Strongylate species was therefore estimated, albeit imprecisely, by semi-quantification based on the following predefined subjective scores: 1 (very few eggs), 2 (a few eggs), 3 (moderate abundance of eggs), 4 (many eggs) and 5 (an extremely high amount of eggs). The scale of intensity gave an idea of the presence of the taxon in the fecal sample, but may not be directly related to the number of individuals in the host animal (the intensity of infection;

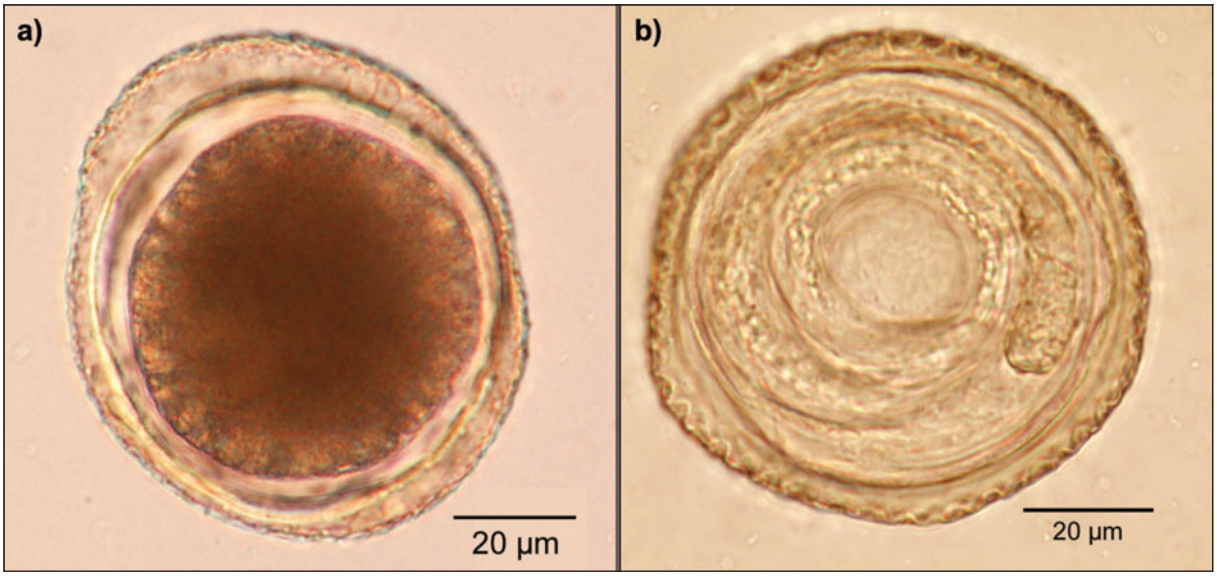

Fig. 2. *Toxocara suricattae* (a) with a zygote and (b) with a larva.

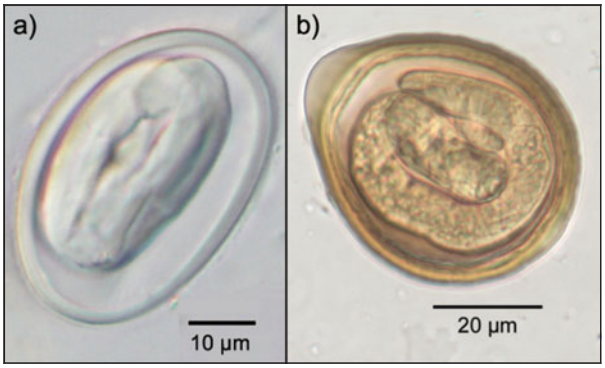

Fig. 3. Spirurida eggs: (a) the small ovoid transparent type and (b) the gnathostoma-like type. Note the characteristic thick shell and larvae within.

Gillespie, 2006). Scoring was done blind to meerkat identity.

Statistical analyses

Taxa richness and strongyle infection intensity were analysed using a linear mixed model (LMM), while the prevalence of each taxon was analysed using generalized linear mixed models (GLMM) with binomial error (i.e. 0 when no egg of the taxon was found and 1 when at least one egg of the taxon was found in the host). Sex, age, group size (measured as the mean number of individuals in the group over the 3 months before sampling), period (period 1 or period 2), time of sampling (morning or afternoon) and the interaction between sex and age were included as fixed effects, and group identity was included as a random factor. We did not include meerkat identity as a random factor as 90% of meerkats were sampled only once. All these analyses were conducted within SAS version 9.1. We used

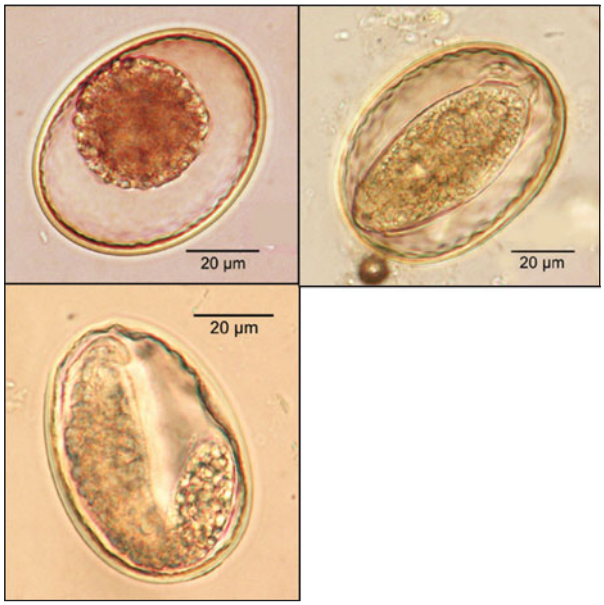

Fig. 4. *Oxynema suricattae*.

2-tailed type-3 tests for fixed effects, and the Satterthwaite correction for the calculation of fixed effects degrees of freedom (Littell *et al*. 2006).

To determine if individuals from the same group hosted more similar parasite assemblage than individuals from different groups, we used permutation *t*-tests. For each host individual, parasite assemblage was described as a vector based on presence/absence of each parasite taxon, and the Jaccard distance was used to describe dissimilarity in parasite assemblage between each dyad of meerkats. We used permutation *t*-test with 5000 permutations to compare within-group distances to between-group distances. Permutation *t*-test and measures of the Jaccard distances were performed with the R statistical software (R Development Core Team, 2008).

Fig. 5. *Pseudandrya suricattae*.

All analyses were conducted with a significance level set to $\alpha = 0{\cdot}05$. Values are expressed as mean ± S.E. throughout.

RESULTS

Description of endoparasite diagnostic stages

Strongylate eggs (Nematoda, Strongylida). These eggs exhibit morphology characteristic of species in the Order Strongylida. They are ovoid with a thin translucent shell and contain a morula. At least two types of Strongylate eggs were observed, those measuring 66 µm × 42 µm, and others measuring 123 µm × 71 µm (Fig. 1). The smaller eggs were frequently observed (i.e. in 88% of samples) and may be ascribed to the parasite species *Arthrocephalus gambiensis* (Ortlepp, 1925) described from a Gambian mongoose. Eggs of the family Ancylostomidae are comparable in size, and have been reported variously from related genera in the African Feliformia (Round, 1968). The larger eggs are characteristic of parasite species in the families Strongyloidea and Trichostrongyloidea and were occasionally embryonated. As they were observed in 4 female meerkats only, they were excluded from the statistical analyses.

Toxocara suricattae (Ortlepp, 1940) (Warren, 1970) (Nematoda, Ascaridida). These eggs exhibit morphology typical of the genus with a pitted subspherical thick shell. The eggs are round-shaped and contain a very dark one-celled zygote or occasionally a larva (egg size: 80 µm × 71 µm; Fig. 2a and b).

Spirurid eggs (Nematoda, Spirurida). Two types of eggs were observed. Small (45 µm × 30 µm), ovoid, thick-shelled, transparent eggs containing a larva (Fig. 3a) are morphologically consistent with *Vigisospirura whitei* listed by Lynch (1980), and have been previously attributed to meerkats (Round, 1968). Larger (58 µm × 44 µm), brown, thick-shelled eggs with a distinct polar plug containing a larva were classified as Gnathostoma-like eggs (Fig. 3b). These large eggs were only observed in a single individual. Eggs of similar morphology have not been previously described from host genera in the family Herpestidae.

Oxynema suricattae (Monnig, 1931) (Inglis, 1955) (Nematoda, Oxyurida). The most common pinworm egg found in meerkats is characterized by an oblong egg (egg size: 74 µm × 55 µm) containing a distinctive embryo with a small protuberance on the distal end. The shell is thick and may be associated with fecally derived detritus on its surface. Occasionally, the eggs contain a one-celled zygote or a larva, instead of the embryo (Fig. 4).

Pseudandrya suricattae (Ortlepp, 1938) (Baer, 1959) (Cestoda, Hymenolepididae). These eggs exhibit morphology typical of the Hymenolepididae. They are round-shaped with a transparent membrane enclosing a hooked oncosphere (egg size: 49 µm × 39 µm; Fig. 5).

Coccidia. Several types of coccidia were found (Fig. 6). The most common is an isosporid coccidia (oocyst size: 29 µm × 25 µm; Fig. 6a and b), which seems to be morphologically similar to the coccidia *Cystoisospora timoni* described in recently imported and long-resident zoo-housed meerkats (El-Gayar *et al*. 2008). Round and ovoid shapes of the *Cystoisospora* sp. oocyst were observed. Round coccidia (size: 34 µm × 30 µm; Fig. 6c) with 6–9 sporocysts were found in 5 samples from 3 groups. Large oblong brown coccidia (size: 47 µm × 34 µm; Fig. 6d) with a thick shell and a fuzzy surface were found in 6 samples from 4 different groups. Sporulated eimeriid coccidia were found in one sample (size: 33 µm × 18 µm; Fig. 6e).

Relation with host traits and group factors

Evidence of parasitic infection was found in all individuals, except in the youngest pup. Taxa richness per individual ranged from 0 to 6 parasite taxa per sample with a mean of 3·13 ± 0·13 per individual and increased with age ($F_{1,91\cdot2} = 10{\cdot}68$, $P = 0{\cdot}0015$; Fig. 7). Taxa richness was higher in November than in March/April (3·49 ± 0·19 taxa *vs* 2·84 ± 0·16 taxa; $F_{1,96\cdot9} = 8{\cdot}75$, $P = 0{\cdot}0039$). Taxa richness did not vary with sex of the host, group size or time of sampling.

Similarly, strongyle fecal egg counts increased with meerkats' age ($F_{1,94\cdot6} = 13{\cdot}08$, $P = 0{\cdot}0005$; Table 2). Strongyle-like eggs were absent in the feces of pups less than 2 month old ($n = 5$) and infection prevalence was 50% in pups aged between 2 and 4 months

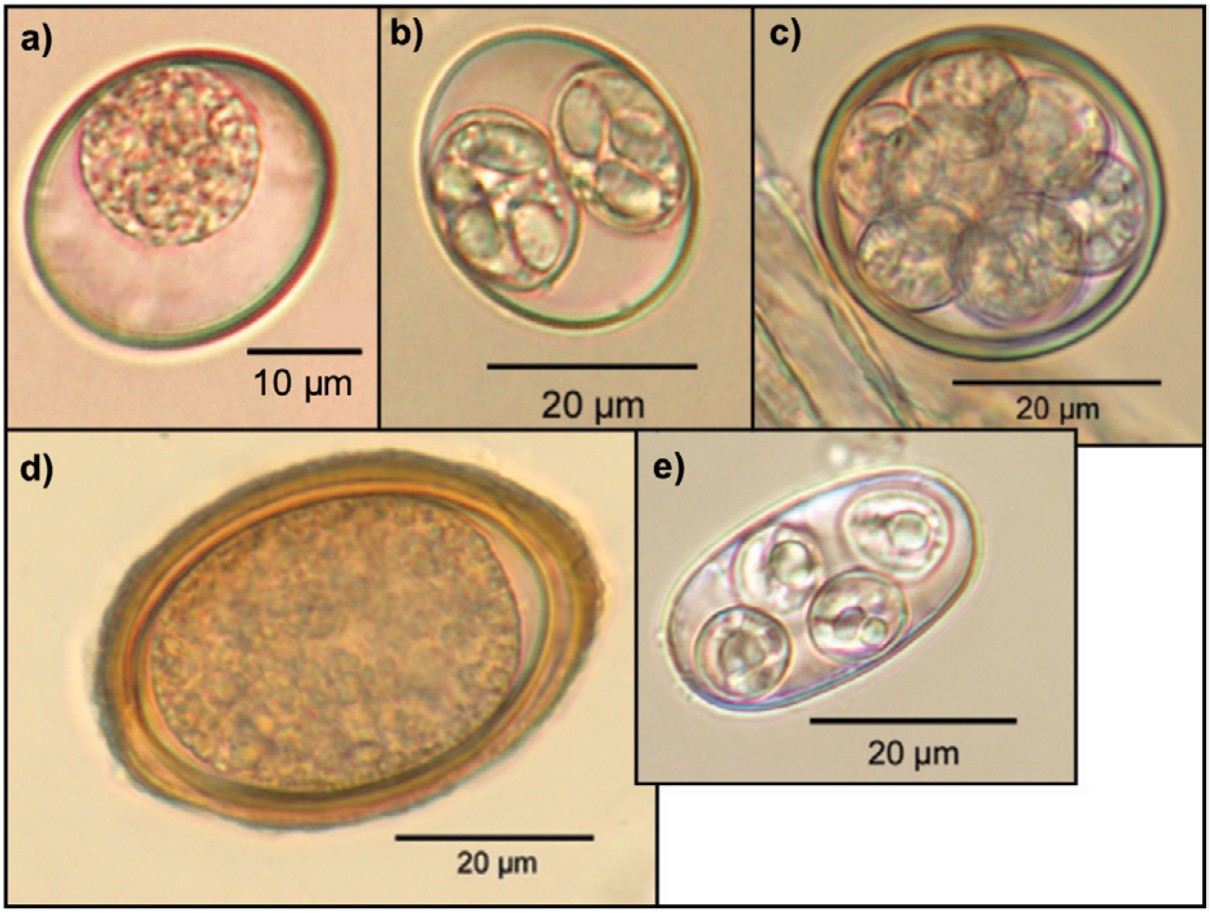

Fig. 6. Coccidia oocysts: *Cystoisospora* species (a, b), coccidia oocyst with multiple sporocysts (c), large brown coccidia (d), and *Eimeria* oocyst (e).

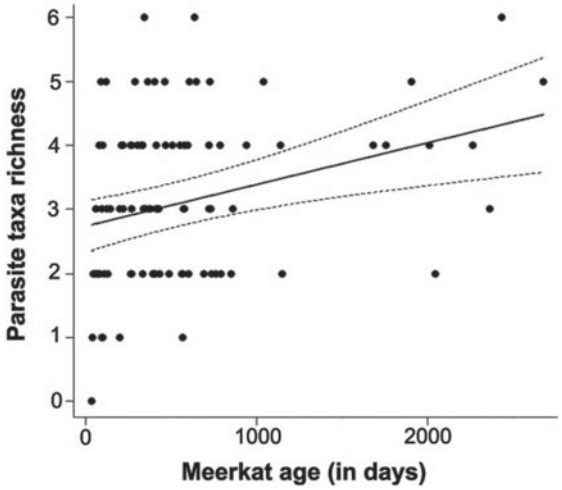

Fig. 7. Parasite taxa richness according to meerkat age. Lines show GLMM prediction and 95% confidence bands.

($n = 16$) and was 100% in all individuals of other age groups. The occurrence of *Toxocara* eggs in the feces of infected hosts increased with meerkats' age ($F_{1,98} = 8{\cdot}92$, $P = 0{\cdot}0036$; Table 2). *Toxocara* eggs were absent in the feces of individuals less than 80 days old.

Prevalence of tapeworm infection in the host population was seasonally distributed ($F_{1,98} = 6{\cdot}97$, $P = 0{\cdot}0096$). Fecal samples collected in November were 3·5 times more likely to be positive for infection than samples collected in March–April (prevalence in November: 38 ± 7% *vs* prevalence in March–April: 11 ± 4%). Strongyle fecal egg counts were higher when samples were collected in the morning than in the afternoon (2·42 ± 0·17 eggs *vs* 1·96 ± 0·18 eggs; $F_{1,91{\cdot}6} = 5{\cdot}59$, $P = 0{\cdot}02$). None of the parasite prevalences were associated with the sex of the host.

Strongyle fecal egg counts and occurrence of coccida oocysts decreased with group size ($F_{1,10{\cdot}5} = 6{\cdot}00$, $P = 0{\cdot}033$; Fig. 8a and $F_{1,11{\cdot}7} = 6{\cdot}18$, $P = 0{\cdot}029$; Fig. 8b). Meerkats from the same group hosted more similar parasite assemblage than meerkats from different groups (permutation *t*-test: $t_{505,4346} = -4{\cdot}02$, $P < 0{\cdot}0001$, Fig. 9).

DISCUSSION

The prevalence of endoparasitic infection in this population of wild meerkats was high. All meerkats except one were parasitized. Such prevalence is fairly typical of wild mammals (e.g. Müller-Graf, 1995;

Table 2. Per cent prevalence of parasite taxa identified by eggs or oocysts detected by examination of fecal samples from pups, juvenile, adult subordinates and adult dominants. Although age was analysed as a continuous variable, it is displayed here as a discrete variable for illustrative purposes. 95% confidence limits were calculated using bespoke software (courtesy of Professor J.M. Behnke and Dr F.S. Gilbert, University of Nottingham) based on the tables of Rohlf and Sokal (1995)

Parasite taxon	Pup (< 3 months) ($n = 13$)	Juvenile (3–12 months) ($n = 33$)	Adult subordinate ($n = 43$)	Adult dominant ($n = 11$)
Toxocara suricattae	8% ($CL_{95} = 0$–34)	36% ($CL_{95} = 24$–51)	40% ($CL_{95} = 24$–56)	73% ($CL_{95} = 41$–92)
Oxynema suricattae	62% ($CL_{95} = 34$–83)	45% ($CL_{95} = 32$–60)	47% ($CL_{95} = 31$–64)	64% ($CL_{95} = 33$–87)
Pseudandrya suricattae	0% ($CL_{95} = 0$–23)	39% ($CL_{95} = 26$–54)	19% ($CL_{95} = 9$–35)	18% ($CL_{95} = 3$–50)
Strongylate nematode	38% ($CL_{95} = 17$–66)	85% ($CL_{95} = 71$–93)	100% ($CL_{95} = 90$–100)	100% ($CL_{95} = 74$–100)
Spirurida nematode	23% ($CL_{95} = 7$–52)	21% ($CL_{95} = 11$–36)	28% ($CL_{95} = 15$–45)	55% ($CL_{95} = 27$–80)
Coccidia oocysts	69% ($CL_{95} = 41$–89)	73% ($CL_{95} = 58$–84)	70% ($CL_{95} = 53$–83)	73% ($CL_{95} = 41$–92)

Behnke *et al*. 1999; Lilly *et al*. 2002). This meerkat population is overall healthy and stable (Bateman *et al*. 2013), with no clinical symptoms related to the degree of parasite infection (personal observations). However, in many species, subclinical parasitism is common and associated with impaired nutrition, inadequate feeding behaviour, restricted travel due to energy deficits or inability to compete for resources and escape predation (Parkins and Holmes, 1989; Hudson *et al*. 1992*b*; Alzaga *et al*. 2008). Detailed studies are therefore needed to properly evaluate the impact of parasitism on meerkat behaviour and fitness.

We found that prevalence of infection with coccidia and fecal egg counts for strongyle-type nematode parasites were negatively correlated with group size. This finding is in contrast with other studies showing that, in several species, including rhesus monkeys *Macaca mulatta*, bank swallows *Riparia riparia* and several African bovids with closed-group structures, parasite intensity or prevalence increases with group size (Hoogland and Sherman, 1976; Phillippi and Clarke, 1992; Ezenwa, 2004; see review in Côté and Poulin, 1995, and Patterson and Ruckstuhl, 2013). In large groups, transmission of directly and indirectly transmitted parasites is expected to be higher than in small groups, as host proximity and the number and duration of conspecifics contacts usually increase (Alexander, 1974; Patterson and Ruckstuhl, 2013). On the other hand, smaller groups may be at a disadvantage in resource competition, with restricted foraging opportunities, poor quality forage, reduced ability to defend resource-rich loci, and vulnerability to predation (Foster and Treherne, 1981; Krause and Ruxton, 2002). In cooperative species, *per capita* energy expenditures associated with caring and provisioning for pups may be greater in smaller groups (Clutton-Brock *et al*. 1998). Accordingly, in meerkats, adult mortality is higher in small groups than in large groups, and smaller groups are more at risk of group extinction, especially during years of low food availability (Clutton-Brock *et al*. 1999). It is therefore reasonable to interpret factors associated with small group size as stressors that may exacerbate meerkat susceptibility to parasitism.

The occurrence of infection with *Toxocara suricattae* and Strongylate nematode parasites increased with age. The pattern of infection with *T. suricattae* stands in marked contrast to the life cycle biology documented for *Toxocara canis*, and *Toxocara cati* where susceptible hosts are infected prenatally by the transplacental route or by the lactogenic route as neonates (Soulsby, 1982). In this study, the age of the youngest meerkat infected with *T. suricattae* was 83 days old. Although one cannot exclude that the prepatent period of *T. suricattae* is longer than the one of *T. canis* and *T. cati* (i.e. 30–35 days and 56 days respectively; Dryden, 1996), the pattern found in

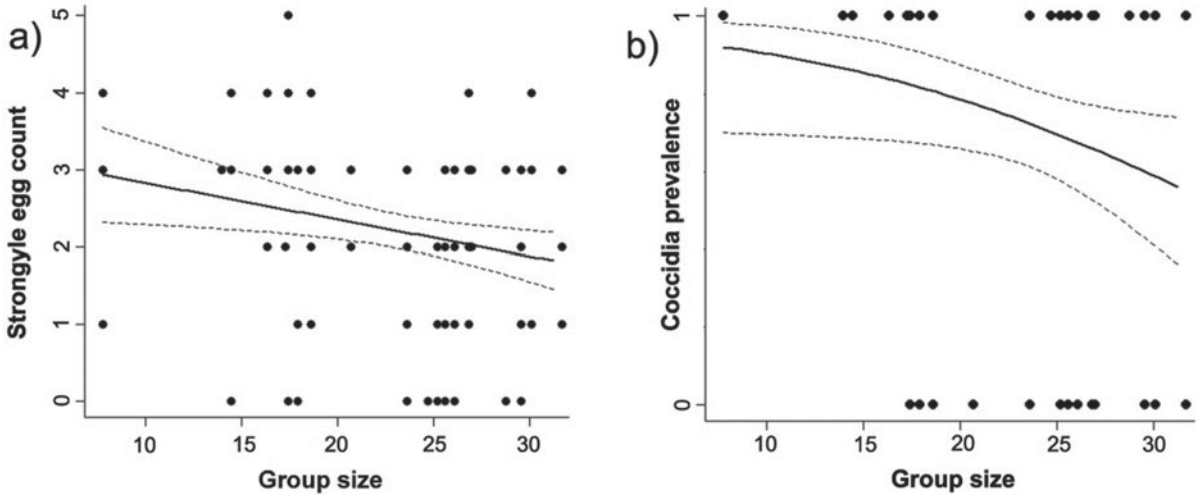

Fig. 8. Strongyle egg count (a) and coccidia prevalence (b) according to group size. When the three outliers (group size of group H period 2 = 7·8 individuals) are removed, the correlation remains significant for strongyle egg count ($F_{1,9\cdot2} = 6\cdot75$, $P = 0\cdot029$), while it tends to be significant for coccidia prevalence ($F_{1,10\cdot5} = 4\cdot53$, $P = 0\cdot058$). Lines show GLMM prediction and 95% confidence bands.

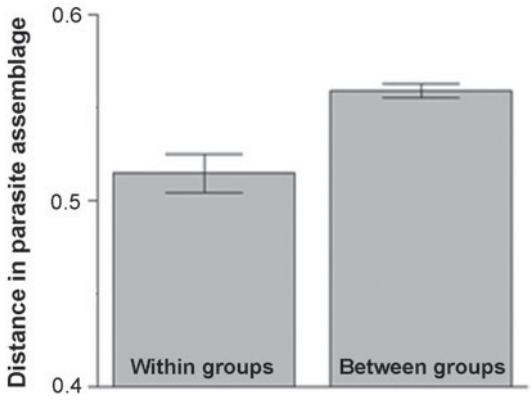

Fig. 9. Mean Jaccard distance (± S.E.) in parasite assemblage in dyads of meerkats from the same group (i.e. within groups) and dyads of meerkats from different groups (i.e. between groups).

meerkats may indicate that vertical transmission of infective parasites does not occur in this host species. Meerkat pups are likely infected by direct ingestion of the embryonated eggs that are picked up on their fur when they begin using communal latrines from their third month of life (van Staaden, 1994).

The increase of strongyle egg counts with age in meerkats is in accord with other studies. In African elephants *Loxodonta africana* and plain zebra *Equus quagga*, strongyle egg count is lower in younger family group members than in older animals (Thurber *et al*. 2011; Fugazzola and Stancampiano, 2012). The pattern of infection observed in this study suggests chronic exposure, and accumulation of infective parasite stages over time. The development of acquired immunity by the host facilitated by chronic exposure to the parasites may further mitigate the intensity of parasite burdens in adult hosts and susceptibility to adverse health effects (Hudson and Dobson, 1997).

The tapeworm, *Pseudandrya suricattae*, was the only parasite with a seasonal distribution. Fecal samples collected in November were 3·5 times more likely to be positive for tapeworm eggs than samples collected in March/April. Infection with this parasite is the direct result of consumption of Coleoptera that serve as obligate intermediate hosts for the parasite. In a study of meerkat dietary preferences, Coleoptera accounted for 58% of the invertebrates identified in stomach contents and were the predominant food item consumed during the winter months (May–July) (van Staaden, 1994). The presence of tapeworms in the November-collected samples may be a residual effect of the winter diet. It is not surprising that seasonality was not observed with the other parasitic species identified. Each of the nematode parasite species, with the exception of the Spirurida, have direct life cycle biology and infections are characteristically associated with the ingestion or skin penetration of infective eggs or larvae from fecally contaminated loci. The Spirurida, however, have an indirect life cycle biology and utilize a variety of insects, including Coleoptera, as obligate intermediate hosts. The lack of seasonality observed with this species may be a reflection of the long prepatent period of spirurids (Quentin, 1969; Sen and Anantaraman, 1971) and its persistence within the host (Soulsby, 1982).

Although sex differences in parasitism are commonly observed (Zuk and McKean, 1996; Turner *et al*. 2012), we did not detect any differences between male and female meerkats. A lack of sex differences has also been observed in several species, such as Kafue lechwes *Kobus leche kafuensis* (Munyeme *et al*. 2010), New Zealand sea lions *Phocartos hookeri*

(Castinel *et al*. 2007) or cats and dogs (Visco *et al*. 1978; Becker *et al*. 2012). Sex differences are usually attributed to ecological, morphological or physiological differences between males and females. For instance, larger home range, larger size or high testosterone levels have often been considered as factors causing higher parasite load in males. Meerkats are however sexually monomorphic (van Staaden, 1994; Clutton-Brock *et al*. 2002) and, although only males frequently prospect outside the territory (Doolan and Macdonald, 1996; Young *et al*. 2007), subordinate females are often evicted from the group, when like males, they may experience nearby territories (Clutton-Brock *et al*. 2008).

Meerkats living in the same group host more similar parasite assemblage than meerkats living in different groups. As a territorial species, meerkats from the same group share the same environment and diet and are thus exposed to similar parasites. In addition, our study population lives on different ranchlands, which differ in the livestock they host. Some groups of meerkats are thus mainly in contact with goats, gemsbok *Oryx gazella* or eland *Taurotragus oryx* while others are mainly in contact with cattle or ostrich *Struthio camelus*. Land use by livestock may affect environmental conditions and hence parasite assemblage development in meerkats.

In conclusion, our study is the first detailed report on gastrointestinal parasites in meerkats and identifies several potential factors affecting parasite infection. It is a key starting point for future studies on the effect of endoparasite load in the life history of this species. Necropsy and molecular genetic analyses would however be needed to further identify each parasite species.

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