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Host social behavior and parasitic infection: a multifactorial approach

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I examined associations between several components of host social organization, including group size and gregariousness, group stability, territoriality and social class, and gastrointestinal parasite load in African bovids. At an intraspecific level, group size was positively correlated with parasite prevalence, but only when the parasite was relatively host specific and only among host species living in stable groups. Social class was also an important predictor of infection rates. Among gazelles, territorial males had higher parasite intensities than did either bachelor males or females and juveniles, suggesting that highly territorial individuals may be either more exposed or more susceptible to parasites. Associations among territoriality, grouping, and parasitism were also found across taxa. Territorial host genera were more likely to be infected with strongyle nematodes than were nonterritorial hosts, and gregarious hosts were more infected than were solitary hosts. Analyses also revealed that gregariousness and territoriality had an interactive effect on individual parasite richness, whereby hosts with both traits harbored significantly more parasite groups than did hosts with only one or neither trait. Overall, study results indicate that multiple features of host social behavior influence infection risk and suggest that synergism between traits also has important effects on host parasite load. *Key words:* Bovidae, group size, group living, parasite prevalence, parasite richness, strongyle nematodes, territoriality. *[Behav Ecol 15:446–454 (2004)]*

Host behavior plays an important role in mediating exposure to parasites (Alexander, 1974; Hart, 1990; Moore, 2002). In particular, host social behavior is recognized as having significant effects on the transmission of contagious or contact-transmitted parasites (Freeland, 1976; Loehle, 1995; Møller et al., 1993). For instance, because grouping promotes contact between susceptible and infected individuals, increasing host group size is correlated with both increased prevalence (percentage of hosts that are infected) and intensity (number of parasites in each infected host) of contagious parasites across a wide range of taxa (Coté and Poulin, 1995). In a few cases, grouping behavior has also been correlated with increased parasite richness (the number of parasite species in a host population) (Freeland, 1979; Ranta, 1992), further highlighting the capacity for social behavior to modify infection risk.

Grouping behavior in itself is only one feature of host social behavior. Many other components of sociality also have the potential to affect parasitism levels, especially those behaviors that directly foster contact between susceptible hosts and parasites, yet there is very little empirical evidence of relationships between infection rates and social factors other than grouping behaviors. Past studies examining the links between sociality and parasite load have generally focused on group living and/or group size (Brown and Brown, 1986; Brown et al., 2001; Hoogland, 1979; Hoogland and Sherman, 1976; Møller, 1987; Moore et al., 1988; Rubenstein and Hohmann, 1989), and thus, the role other components of host social behavior play in the dynamics of infection remains relatively obscure. In the present study, I undertake a more comprehensive analysis of the relationship between social organization and parasitism by using the behavioral flexibility present across African Bovidae to test the effects of multiple components of host social structure on parasite infection rates.

Social organization in African bovids is determined by two major behaviors, grouping and territoriality. Grouping behavior influences the degree to which individuals associate with one another, and territorial behavior affects the spatial distribution of individuals within a population. Both behaviors influence rates of contact between individuals, potentially affecting parasite transmission. All bovids can be classified as either gregarious (G) or solitary (S), and either territorial (T) or nonterritorial (NT), and when these traits are combined, most species fall into one of four distinct groups: (1) solitary/territorial, (2) solitary/nonterritorial, (3) gregarious/territorial, or (4) gregarious/nonterritorial (Estes, 1974). Among gregarious species there is significant within and between species variation in group size and levels of group stability (Jarman, 1974; Leuthold, 1977), and this variation could translate to differences in parasite transmission at both levels. Within gregarious/territorial species, individuals can be subdivided into three distinct social classes: territorial males (T), bachelor males (B), and nursery herd members (N) (Estes, 1974). These classes denote age, sex, and behavior, but also reflect intraspecific gradations in territoriality. Territorial males defend patches of habitat against other males, whereas nursery herds composed of females and juveniles wander through these territories at will, associating with defending males when they are within his territory (Estes, 1974; Jarman, 1974). Bachelor males include young males as well as adult males without territories who wander throughout the territorial mosaic, often on the fringes of defended territories (Estes, 1974; Jarman, 1974). These differences in behavior between social classes may lead to potentially interesting intraspecific differences in infection risk.

Taking advantage of the behavioral variation described above, I examined the relationships between the following behavioral traits and infection rates with fecally-dispersed, gastrointestinal parasites both within and across bovid species.

(1) Group size (intra-specific comparison): Because of the increased contact between hosts in larger groups, group size should be positively correlated with parasite prevalence, intensity, and possibly richness. The strength of any such relationships, however, may be

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affected by other host traits such as group stability (e.g., group size is more likely to influence infection rates in hosts that live in closed groups in which there is relatively little mixing between groups compared with species in which intergroup mixing is more frequent), as well as certain parasite traits such as host specificity (e.g., levels of infection by host-specific parasites are more likely to vary with host group size than are infections by multispecies [generalist] parasites).

(2) Social class (intraspecific comparison): Confinement in space resulting from the territorial behavior of certain males may increase their exposure to parasitic contaminants, thereby increasing parasite prevalence and intensity in this group. In some instances, the increased isolation effected by territoriality may limit exposure to novel parasites, reducing host parasite richness (Freeland, 1976), but this effect is unlikely in this case because territorial males continually associate with females (nursery herd members) and are therefore also exposed to any novel parasites females contract outside of the territory. Thus, no effect of social class on parasite richness is expected.

(3) Gregariousness (interspecific comparison): Because levels of aggregation, and therefore parasite transmission opportunities, are higher among gregarious species, these species should have higher parasite prevalence, and possibly richness, than do solitary species.

(4) Territoriality (interspecific comparison): Confinement in space should increase parasite prevalence in territorial relative to nonterritorial species owing to increased levels of contamination experienced by territory dwellers. However, isolation effects may lead to a reduction in parasite richness in territorial species.

(5) Gregariousness + territoriality (interspecific comparison): Because both behaviors potentially increase parasite prevalence independently, species with both traits may have higher infection rates than do species with only one trait or neither of the traits.

METHODS

Study population and sampling

This study was conducted at the Mpala Research Center, Kenya (00°17′ N, 36°53′ E). The Center is located in the semiarid region of central Kenya and is home to more than 20 large mammal species. The basic ecology of the study site is described in Ezenwa (2003b). The African Bovidae is composed of 11 tribes (Estes, 1991), seven of which are represented in this study. Eleven species were studied, including representatives from all four social types: solitary/territorial—dik-dik (*Madoqua kirkii*), klipspringer (*Oreotragus oreotragus*), steinbuck (*Raphicerus campestris*); solitary/nonterritorial—bushbuck (*Tragelaphus scriptus*); gregarious/territorial—Grant's gazelle (*Gazella granti*), Thomson's gazelle (*Gazella thomsoni*), waterbuck (*Kobus defassa*), impala (*Aepyceros melampus*), hartebeest (*Alcelaphus buselaphus*); and gregarious/nonterritorial—buffalo (*Syncerus caffer*), eland (*Taurotragus oryx*).

Fecal sampling was used to assess gastrointestinal parasite infection rates for all 11 species. Samples were collected monthly from August 1999–July 2000 and March–August 2001. During monthly sampling periods, host groups were located by driving a continuous road transect, beginning each morning at 0600 h and ending at approximately 1100 h. Groups were defined as close associations of conspecifics having a high degree of coordination in activity over an extended period of time. Agonistic interactions between males and reproductive interactions between males and females were also used to define group membership in certain instances. When a group was located, group size and composition were recorded, and the group was observed until defecations occurred. For each defecation, the age, sex, and social class of the defecating individual were recorded along with the position of the fecal sample when possible. This process continued until a sufficient number of defecations were observed and sample collection could commence. In some cases it was not possible to record individual defecator information, and instead after the study group vacated an area, the area was searched for fresh fecal samples. In these instances, only fecal pellet groups judged to be from the particular species under observation were collected, and only pellet groups at least 6 inches or more apart were considered to be independent samples. The maximum number of samples collected during this type of sampling never exceeded the number of individuals in the group so as to reduce the probability of any single individual being sampled more than once. To ensure adequate sampling of host groups, whenever possible I collected at least 20 fecal samples from groups that exceeded 20 individuals and at least 10 samples from groups of less than 20 individuals, based on results of sampling studies of domestic ungulates that suggest that between 10 and 20 fecal samples provide a reliable assessment of herd infection rates (Brunsdon, 1970; Cabaret et al., 1986; Chartier, 1991; Gasbarre et al., 1996). For solitary cryptic species such as the dik-dik and klipspringer, I collected individual fecal samples from dung-middens in known territories along the sampling transects. Over the course of the study, a total of 1987 fecal samples were collected with 8–692 samples collected per species.

Parasitological analysis

To quantify parasite output in host feces, I used a modification of the McMaster fecal egg counting technique with saturated sodium chloride as the flotation solution (Ezenwa, 2003b; MAFF, 1980). Parasites could not be identified to the species level with this method, but eight distinct parasite groups were distinguishable, including three nematode genera (*Capillaria* spp., *Strongyloides* spp., and *Trichuris* spp.), two cestode genera (*Moniezia* spp. and *Thysaniezia* spp.), lungworms (Nematoda: Protostrongylidae), strongyles (Nematoda: Strongylida), and coccidia (Apicomplexa: Eimeriidae). Trematodes were not detected with the methodology used. The cestodes and lungworms require intermediate hosts for transmission, but all other parasites are transmitted directly from host to host and are therefore likely to be influenced by host social behavior. Strongyles and coccidia were the most frequently observed parasites, and both of these groups were comprised of numerous species. Based on adult worms recovered from necropsies of 17 dead animals representing seven of the 11 study species, at least nine different genera and 14 different species were involved in the strongyle infections. The recovered strongyle genera included the following: *Agriostomum, Cooperia, Cooperioides, Gazellostrongylus, Haemonchus, Impalaia, Longistrongylus, Oesophagostomum,* and *Ostertagia* (Ezenwa, 2003b). Between one and seven different strongyle species were recovered per host species, and approximately 54% of these strongyles infected more than one host species, suggesting that these parasites are relative generalists within the host group (Ezenwa, 2003b). Very little information exists on the species diversity of coccidia in wild African bovids; however, studies in related taxa such as cattle, sheep, and goats suggest that coccidia as a group are relatively more host specific than are the strongyles (Bowman, 1999; Levine and Ivens, 1986). Evidence from other groups such as rodents also indicate that even within distinct subfamilies and tribes, coccidia can be

Table 1
Parasitological variables for 11 bovid species

Host	Total samples collected	N (subsamples)	Strongyle prevalence (%)	Coccidia prevalence (%)	Mean individual richness	Total richness
Buffalo	60	15	86.7	13.3	1.1	4
Bushbuck	13	13	61.5	38.5	1	2
Dik-dik	231	15	73.3	6.7	0.87	3
Eland	149	15	86.7	6.7	0.93	2
Grant's gazelle	382	15	100	20	1.4	3
Thomson's gazelle	39	15	100	20	1.4	4
Gazelles (average)	—	—	100	20	1.4	3.5
Hartebeest	222	15	86.7	53.3	1.7	3
Impala	692	15	93.3	26.7	1.5	4
Klipspringer	14	14	85.7	7.1	0.93	2
Steinbuck	8	8	87.5	12.5	1	1
Waterbuck	177	15	93.3	66.7	1.5	2

All variables were calculated by using 15 (except in cases where $n < 15$) subsamples randomly selected from the total number of samples collected per species; values for Grant's and Thomson's gazelle were averaged because genus was used as the level of phylogenetic independence.

highly genus-specific compared with many helminths (Decker et al., 2001; Hnida and Duszynski, 1999; Wilber et al., 1998).

Prevalence and intensity analyses included only strongyle and coccidian parasites. Mean strongyle eggs (epg) and coccidian oocysts (opg) per gram feces were used as indicators of the numbers of these parasites in infected hosts (parasite intensity). Although the exact relationship between fecal egg counts and the number of adult parasites is unclear, egg counts can provide a valuable noninvasive means of assessing relative infection rates across groups of hosts (Bryan and Kerr, 1989; McKenna, 1981). However, because a variety of factors influence the number of eggs emitted in feces, including host resistance, fecal output rate, and differential parasite fecundity, analyses of epg and opg counts were restricted to the intraspecific comparisons in this study. Prevalence of strongyle and coccidia infections among hosts was calculated as the percentage of fecal samples infected with each parasite type out of the total number of samples examined. For parasite richness determinations, the presence of all eight recorded parasite types, including both directly and indirectly transmitted groups, was used to calculate two measures of parasite richness: the total number of parasite types per host species (total richness) and the number of parasite types per individual within a species (individual richness). In all cases, each fecal sample was treated as independent for calculation of parasitological variables for each host species or group within a host species.

Statistical analysis

Group size analyses were performed by using samples collected from six gregarious species over the entire study period (sample size range = 39–692). Each individual fecal sample was assigned a group size score based on the size of the host group from which the sample was collected. I then tested relationships between group size and strongyle/coccidia intensity, prevalence, and individual richness by using linear regression tests. Because each hypothesis (e.g., group size versus strongyle intensity) was tested independently on each host species, I used the sequential Bonferroni method to adjust significance levels in order to minimize the probability of committing type I errors (Rice, 1989). The resulting α-levels for evaluating the lowest to highest p values for each set of tests were: $p < .0083$, .01, .0125, .017, .025, and .05. For the above analyses, I calculated all dependent variables (parasitological variables) for each group size category within a species by taking the average over all individuals (samples) within the category. Strongyle and coccidia prevalences were normalized by using arcsine transformations and egg and oocyst counts were $\log_{10}(x + 1)$ transformed. I also tested associations between the probability of obtaining a significant group size versus parasite prevalence result and species group structure type using chi-square tests. Host species were classified as being either open-group or closed-group species based on descriptions of social structure presented in Estes (1991).

I performed all social class analyses using data from the two gazelle species (Grant's gazelle and Thomson's gazelle). Chi-square tests were used to test the relationship between social class and parasite prevalence. ANOVAs adjusted for multiple pairwise comparisons with the Student-Neumann-Keuls (SNK) test were used to test the relationship between social class and parasite intensity and individual richness.

Interspecific comparisons included all 11 host species. For these analyses, strongyle prevalence, coccidia prevalence, total richness, and individual richness were calculated for each species by using 15 samples selected randomly from the total number of samples collected per species (range = 8 to 692) (Table 1). For those species for which fewer than 15 samples were collected over the course of the study, all available samples were included. This random subsampling procedure was used to control for variations in sample size across species because measures of parasite prevalence and richness can be influenced by sampling intensity (Gregory and Blackburn, 1991; Gregory et al., 1996). I tested relationships between gregariousness and territoriality and strongyle prevalence, coccidia prevalence, total parasite richness, and mean individual richness by using two-way ANOVA tests. For these tests, coccidia prevalence was arcsine transformed, and significance was accepted at $p < .05$.

Although cross-species comparative analyses generally benefit from some type of phylogenetic correction, in the present study the standard independent contrasts method for correcting for phylogenetic effects (Felsenstein, 1985) could not be used because it resulted in too few degrees of freedom for successful analysis. Therefore, in place of standard methods, I used simple correlational analyses to assess the dependence of species parasitological variables on degrees of relatedness between species before performing any cross-species comparisons. To do this, divergence times between all possible pairs of species were calculated from a consensus tree of the African

Table 2

Mean and range of group sizes in six bovid species used for group size analyses

Species	Mean ± SE	Range
Buffalo	11.4 ± 2.7	1–30
Eland	17.3 ± 4.6	1–50
Grant’s gazelle	13.1 ± 1.5	1–26
Hartebeest	7.0 ± 1.1	1–13
Impala	23.1 ± 3.1	1–60
Thomson’s gazelle	4.6 ± 1.0	1–8

Bovidae (Brashares et al., 2000) and compared with species’ differences in parasitological variables by using Spearman rank correlation tests. Also, for cross-species comparisons, I used genus as the level of independence for all tests in order to limit any potential type I errors. Consequently, scores for Grant’s gazelle (*G. granti*) and Thomson’s gazelle (*G. thomsoni*) were averaged and used as a single sample for comparative analyses (Table 1).

RESULTS

Intraspecific comparisons

Group size and infection rates

Mean group size per host species ranged from four to 23, and there was considerable within-species variation in the size of groups (Table 2). Group size was not correlated with strongyle prevalence, strongyle intensity [log (epg + 1)], coccidia intensity [log (opg + 1)], or individual richness in any host species (Table 3). In contrast, coccidia prevalence increased significantly with group size in buffalo and hartebeest, but not in any other species (Table 3 and Figure 1). When I examined whether the probability of finding a correlation between group size and coccidia prevalence was associated with species group structure (closed versus open groups), I found that significant positive correlations between coccidia prevalence and group size were more common in species classified as closed-group species ($\chi^2 = 6.0$, df = 1, $p = .01$) (Table 4).

Social class and infection rates

All of the Thomson’s gazelles sampled in this study were infected with strongyle nematodes, so there was no variation in strongyle prevalence with social class in this species. Likewise, social class had no effect on strongyle prevalence in Grant’s gazelle ($\chi^2 = 0.73$, df = 2, $p = .7$). Coccidia prevalence also did not differ with social class in either species (Grant’s gazelle: $\chi^2 = 1.46$, df = 2, $p = .48$; Thomson’s gazelles: $\chi^2 = 0.97$, df = 2, $p = .62$). However, because juvenile Grant’s gazelles tend to be infected with coccidia more often than are adults (Ezenwa, 2002), I repeated the Grant’s gazelle analysis with only adults but still found no social class effect (Grant’s gazelle adults: $\chi^2 = 2.49$, df = 2, $p = .29$).

ANOVA tests showed no correlation between social class and individual parasite richness in either gazelle species (Grant’s gazelle: $F = 0.30$, df = 2,197, $p = .74$; Thomson’s gazelle: $F = 1.24$, df = 2,32, $p = .30$). However, there was a significant effect of social class on strongyle intensity in Grant’s gazelle (ANOVA: $F = 3.49$, df = 2,196, $p = .03$) (Figure 2A). Territorial males had significantly higher strongyle loads than did both nursery herd members and bachelor males (SNK: T > N, B), but nursery herd members and bachelor males did not differ in egg loads (SNK: N = B). Although there was no corresponding effect in Thomson’s gazelle ($F = 1.3$, df = 2,32, $p = .29$) (Figure 2A), territorial males did have higher mean egg counts than did other classes (mean ± SE: T = 3.31 ± 0.25; B = 3.13 ± 0.24; N = 3.03 ± 0.45). Coccidia intensity, on the other hand, was significantly influenced by social class in Thomson’s gazelle ($F = 9.24$, df = 2,5, $p = .02$) (Figure 2B). Territorial males had significantly higher oocyst counts than did nursery herd members and bachelors (SNK: T > N, B), but there was no difference between bachelors and nursery herd members (SNK: N = B). This effect was not apparent in Grant’s gazelles ($F = 0.18$, df = 2,42, $p = .84$) (Figure 2B), even after correcting for possible effects of host age ($F = 1.22$, df = 2, 33, $p = .31$).

Interspecific comparisons

Phylogenetic analyses

Analyses to explore the relationship between parasitological scores and host phylogenetic relatedness showed that phylogeny had no effect on the variables used in the present study. If parasitological variables were correlated with phylogenetic relatedness, hosts that diverged more recently from each other should share more parasites (negative slope); however, divergence time between all possible host pairs was not correlated with the number of parasite taxa groups shared between host species (Spearman rank correlation: $r_s = .18$, $n = 55$, $p = .18$). Furthermore, if there were phylogenetic effects, more recently diverged pairs should have smaller differences in parasite richness and prevalence (positive slope). However, more closely related species were no more likely to have similar mean individual richness ($r_s = -.03$, $n = 55$, $p = .83$), strongyle prevalence ($r_s = .15$, $n = 55$, $p = .26$), or coccidia prevalence ($r_s = .13$, $n = 55$, $p = .35$) than were more widely divergent species.

Gregariousness, territoriality, and infection rates

Strongyle nematode infections were more prevalent among gregarious hosts compared with solitary hosts (ANOVA: $F = 18.3$, df = 1,6, $p = .005$) (Figure 3) and among territorial hosts compared with nonterritorial hosts ($F = 10.3$, df = 1,6, $p = .02$)

Table 3

Regression results for host group size vs. parasitological variables for six gregarious bovid species

	Strongyle prevalence				Strongyle intensity				Coccidia prevalence				Coccidia intensity				Individual richness			
Host species	F	df	r^2	p	F	df	r^2	p	F	df	r^2	p	F	df	r^2	p	F	df	r^2	p
Buffalo	0.19	1,11	.14	.67	0.05	1,10	.005	.83	25	1,11	.71	.0005*	0.38	1,2	.27	.65	3.84	1,11	.28	.09
Eland	0.57	1,11	.05	.47	0.05	1,10	.006	.82	6.42	1,11	.39	.03	3.27	1,5	.45	.14	3.37	1,11	.25	.1
Hartebeest	2.76	1, 2	.2	.12	7.9	1,12	.42	.02	22.6	1,12	.67	.0006*	2.07	1,9	.21	.19	0.11	1,12	.1	.75
Thomson’s gazelle	—	—	—	—	0.21	1,6	.04	.66	3.21	1,6	.39	.13	6.65	1, 5	.63	.06	3.27	1,6	.4	.13
Grant’s gazelle	0.27	1,24	.01	.61	1.67	1,24	.07	.21	0.45	1,24	.02	.51	4.96	1,18	.23	.04	1.75	1,24	.07	.2
Impala	0.31	1,28	.01	.58	0.22	1,28	.008	.64	0.54	1,28	.02	.47	0.84	1,24	.04	.37	0.05	1,28	.002	.83

* $p_1 < .0083$, $p_2 < .01$ (Bonferroni adjusted significance levels).

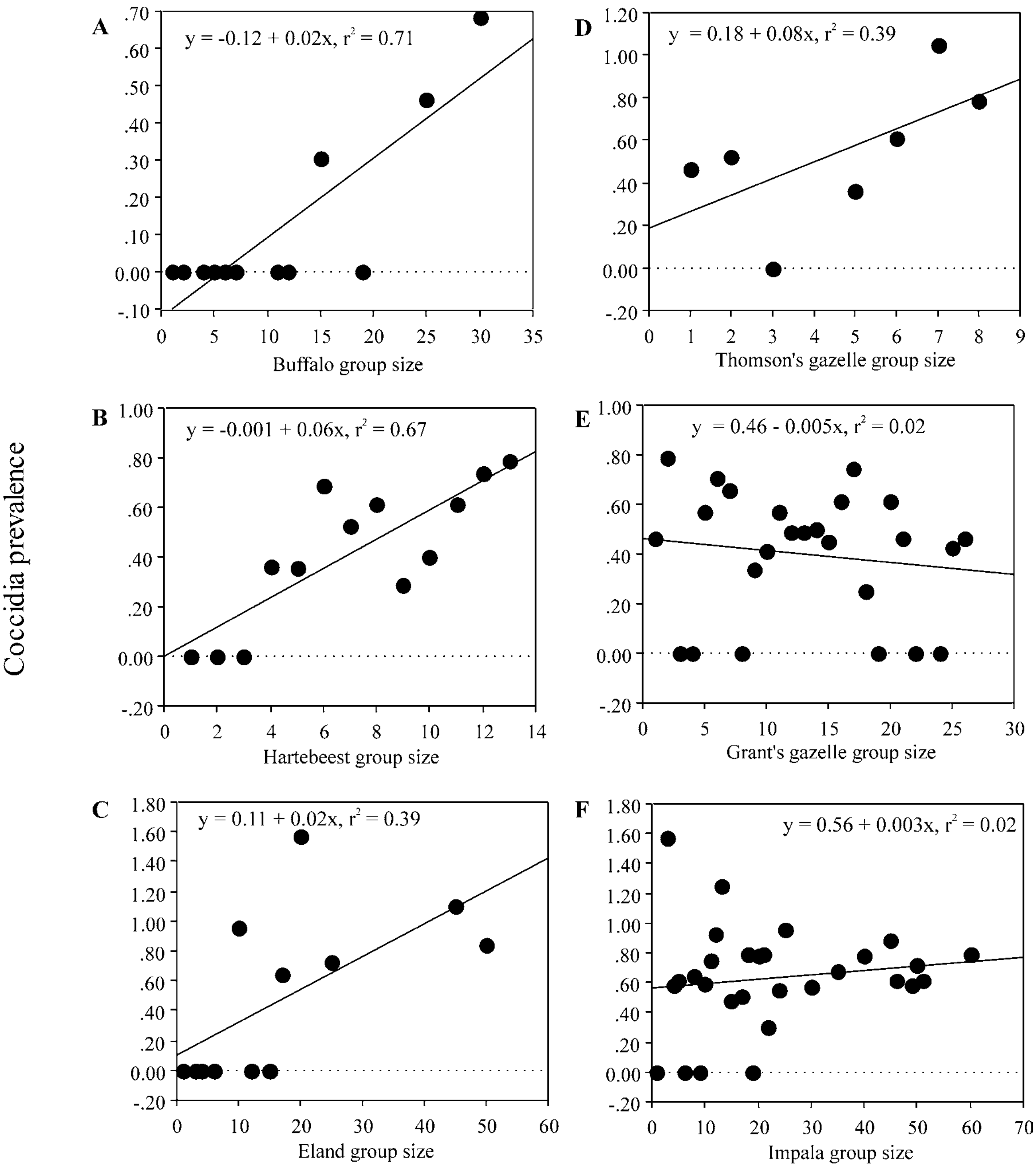

Figure 1

Relationship between host group size and arcsine transformed coccidia prevalence in six gregarious host species: buffalo (A), hartebeest (B), eland (C), Thomson's gazelle (D), Grant's gazelle (E), and impala (F). Group size was significantly correlated with coccidia prevalence in buffalo and hartebeest ($p < .001$).

(Figure 3), but there was no significant interaction between the two traits ($F = 2.73$, df = 1,6, $p = .15$) (Figure 3). Neither trait nor the interaction between traits had any effect on coccida prevalence (G versus S: $F = 0.04$, df = 1,6, $p = .86$; T versus NT: $F = 0.09$, df = 1,6, $p = .77$; interaction: $F = 0.03$, df = 1,6, $p = .87$) or total richness (G versus S: $F = 1.91$, df = 1,6, $p = .22$; T versus NT: $F = 0.13$, df = 1,6, $p = .74$; interaction: $F = 0.03$, df = 1,6, $p = .88$). However, both gregarious hosts ($F = 15.1$, df = 1,6, $p = .008$) (Figure 4) and territorial hosts ($F = 8.04$, df = 1,6, $p = .03$) (Figure 4) had significantly higher mean individual richness than did solitary and nonterritorial hosts, respectively, and this effect was driven by a significant interaction between the two traits ($F = 13.6$, df = 1,6, $p = .01$).

DISCUSSION

Grouping behavior and parasite infection

Grouping behavior and group size have been linked to increases in prevalence of contact-transmitted parasites in a variety of species (Hoogland, 1979; Moore et al., 1988; Phillippi and Clarke, 1992; Poulin, 1991a), and although the same trend holds for bovids in the present study (Table 5), other factors also influence this relationship. Gregarious bovid genera were more likely to be infected with strongyles than were solitary genera, demonstrating that grouping behavior has an important impact on strongyle infection rate in this group. However, neither strongyle prevalence nor intensity

Table 4

Host species group structure type and relationship between group size and coccidia prevalence

Host species	Group structure (open- or closed-group species)	Positive correlation between group size and coccidia prevalence?
Buffalo	Closed	Yes
Eland	Open	No
Hartebeest	Closed	Yes
Thomson's gazelle	Open	No
Grant's gazelle	Open	No
Impala	Open	No

Species are classified as closed (stable) or open (unstable) group based on the degree of exchange between groups.

increased linearly with group size in any species, which might reflect the fact that many strongyle nematodes are generalist parasites that infect multiple host species (Boomker et al., 1986; Ezenwa, 2003b; Zaffaroni et al., 2000). Because strongyle cross-transmission between host species may frequently occur among bovids, contact with heterospecifics also affects rates of exposure to these parasites (Ezenwa, 2003b). As such, differences in contact with heterospecifics could obscure predicted differences in strongyle prevalence across groups. Past studies have shown that associations between group size and infection rates can depend on parasite traits such as transmission mode (e.g., monoxenic versus heteroxenic; Moore et al., 1988) and mobility (e.g., contagious versus mobile; Coté and Poulin, 1995; Rubenstein and Hohmann, 1989), and results documented here suggest that parasite specificity is another trait that influences this relationship.

For coccidia, the more host specific of the two major parasite groups focused on in the present study, prevalence was not associated with gregariousness at the cross-genera level. Because the coccidia observed across hosts probably represent several distinct species, differences in the strategies of parasites infecting different host species such as variations in peak oocyst shedding times (Ezenwa, 2003a) could have influenced the results of interspecific comparisons. Within species, however, coccidia prevalence increased with group size as predicted, but only in a subset of study species. Species with relatively stable, closed-group structures, such as buffalo (Sinclair, 1977) and hartebeest (Dowsett, 1966; Ezenwa VO, personal observation), showed a strong increase in prevalence with group size, whereas in species with very fluid group membership (open-group species), there was no relationship. In open-group species such as impala and Grant's gazelle, in which males frequently enter and leave bachelor herds as they leave nursery groups or obtain territories and nursery groups roam freely throughout male territories breaking up and re-forming often, group membership tends to be dynamic (Jarman and Jarman, 1973; Walther, 1972). As a consequence of this fluidity and the constant exchange between groups, the actual group size being experienced by individuals in these systems is much higher than is reflected by simple static estimates of group size. This may account for why there was no clear relationship observed between prevalence and group size in open-group species. This idea is supported by the fact that associations between coccidia prevalence and group size were significantly more likely to occur in species classified as closed-group species.

The potential for the degree of group stability to affect the group size/parasite load relationship has been discussed previously (Coté and Poulin, 1995), and Freeland (1979) postulated such a mechanism to explain differences in the relationship between protozoan richness and group size in savannah baboons compared with rain forest primates. However, the present study reports the first empirical evidence suggesting that relationships between parasite prevalence and group size do indeed vary depending on host group stability. In addition to group stability, other behavioral traits that increase effective group size, including elements of species mating systems such as sexual promiscuity between members of different groups (Freeland, 1976) and lekking behavior, may also influence observed relationships between parasitism rates and group size.

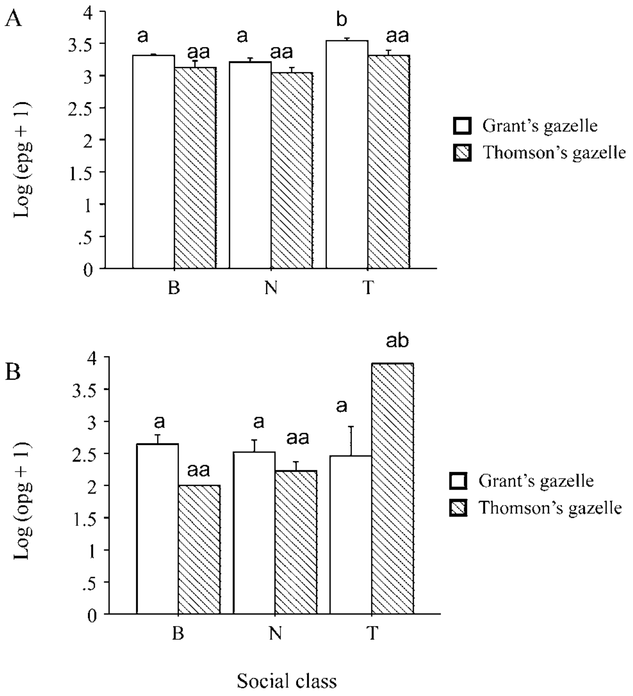

Figure 2
Mean strongyle intensity [log (epg + 1) ± SE] (A) and coccidia intensity [log (epg + 1) ± SE] (B) in Grant's and Thomson's gazelle social classes (T indicates territorial male; B, bachelor male; and N, nursery herd member). Grant's gazelle territorial males (*b*) had significantly higher strongyle egg counts than did both bachelors and nursery members (*a*), and Thomson's gazelle territorial males (*ab*) had significantly higher oocyst counts than did both bachelors and nursery members (*aa*).

Territoriality and parasite infection

Strongyle nematode infections were more prevalent among territorial genera than nonterritorial genera (Table 5), which is most likely a direct result of continuous host exposure to built-up fecal deposits on territories and increased contact between hosts and parasites under these conditions. Past hypotheses suggest that territoriality should decrease contact-transmitted parasite infection rates and may have evolved as a mechanism to avoid infection (Freeland, 1976; Møller et al., 1993). Although territoriality may limit contacts with outsiders, thereby decreasing exposure to novel parasites, study results suggest that exposure to existing parasites, especially ones spread by environmental contamination, might actually increase as a result of territorial behavior. Increased strongyle and coccidia intensities observed in territorial male gazelles compared with bachelor males and nursery herd members support the result of the comparative analysis. Repeated defecation within territories by both males and females leads to the build-up of parasites in these areas, and the fact that territorial male gazelles are by definition more sedentary than

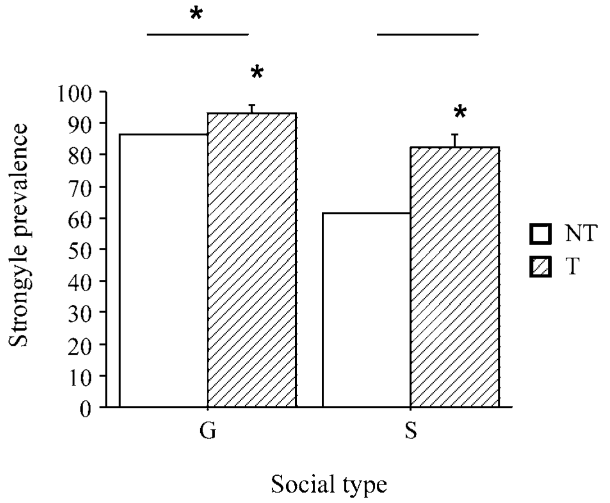

Figure 3
Mean strongyle prevalence (±SE) in bovid genera with differing social behaviors (G indicates gregarious; S, solitary; T, territorial; and NT, nonterritorial). Prevalence was significantly higher in gregarious genera compared with solitary genera and in territorial genera compared with nonterritorial genera ($p < .05$).

are the other social classes (Walther, 1972), and as such are continually re-exposed to the high levels of parasites within territory boundaries, may explain their higher parasite loads. Nursery herd members and bachelor males, on the other hand, are less confined to specified territories and experience a more diversified range of conditions (e.g., heavily trafficked territories and less-used corridors between territories), which may decrease their overall exposure rate relative to that of territorial males.

It is also possible that increased susceptibility to infection could account for the higher parasite load observed in territorial male gazelles. Territorial males, as a consequence of the demands of territory defense, including chasing and fighting other males and the continuous herding of females, may be in much poorer condition than are other individuals, making them more susceptible to infection. In addition, territorial holders may have elevated levels of testosterone and/or cortisol, both of which can have suppressive effects on the immune system (Alexander and Stimson, 1988). Such lowered immunological competence could also influence parasite susceptibility, but at this stage, more work is needed to tease apart the potential interrelationships among host behavior, physiology, and infection rate in this system. Another alternative explanation for the increased parasite load of territorial males could be that territorial males are exposed to more parasites as a consequence of differences in their feeding behavior. Others have suggested that individuals who spend more time feeding ingest more fecal-oral transmitted parasites (Halvorsen, 1986; Hausfater and Watson, 1976), but there was no evidence of differences in feeding behavior between social classes in either Grant's or Thomson's gazelles at the study site (Ezenwa, 2002). Time spent feeding was similar across all social classes in both species, and furthermore, there was no difference in average feeding height between the classes, which could be important if individuals feeding nearer to the ground are more likely to ingest parasites. Therefore, in this case, differences in feeding behavior cannot account for the difference in infection rates observed across social classes.

Both comparative and species-level analyses suggest that there are important links between bovid territorial behavior and gastrointestinal parasitism. Other studies looking at traits related to host mobility such as migration in butterflies (Altizer et al., 2000) have also found that less mobile hosts tend to have higher contagious parasite burdens. Although we often think of large ungulates as being highly mobile, elements of their social structure, such as territoriality, can significantly restrict the mobility of certain individuals and groups, contributing to variations in the risk of infection by parasites that accumulate in the environment. Thus, along with group size and group living, territoriality and social class also seem to be important factors shaping levels of parasite exposure and possibly susceptibility in bovids.

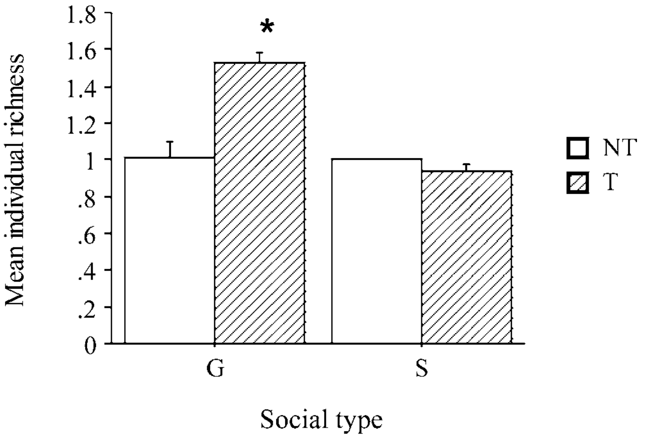

Figure 4
Mean individual parasite richness (±SE) in bovid genera with differing social behaviors (G indicates gregarious; S, solitary; T, territorial; and NT, nonterritorial). Gregarious-territorial genera had significantly higher richness than any other social type ($p = .01$).

Determinants of parasite richness

Unlike parasite prevalence and intensity, there is no consensus as to whether parasite richness is influenced by grouping behaviors. Although there are exceptions, in general, most studies have found no association between grouping behavior and parasite richness across a variety of parasite types (see Gregory et al., 1991; Poulin, 1991b). For the most part, these studies used species-level richness as the lone measure of parasite richness, but Watve and Sukumar (1995), in a study examining correlations between ecological variables and intestinal parasite richness in mammals used several measures of richness (e.g., individual host richness/infracommunity richness; host population-level richness), found that different measures of richness were not necessarily correlated with one another. This suggests that using more than one index of parasite richness might be a useful means of gaining additional information on relationships between host social behavior and parasite colonization rates, so in the present study, two components of gastrointestinal parasite richness were tested—individual-level richness (individual richness) and population-level richness (total richness). Within species, neither group size nor social class was correlated with individual richness; and across species, although neither gregariousness nor territoriality had an effect on total richness, there was a strong interactive effect of both traits on individual richness (Table 5). Gregarious-territorial hosts had significantly higher individual richness levels than did hosts of any other social type. This synergism may arise because gregariousness allows for more novel parasite types to be introduced into groups as new members join, and territoriality, by increasing contact between hosts and parasites, enhances the probability that

Table 5

Summary table of the major study results showing observed associations between behavioral predictor variables and three measures of host parasite load

		Parasite intensity		Parasite prevalence		Parasite richness	
Predictor variable	Level of comparison	Strongyles	Coccidia	Strongyles	Coccidia	Total	Individual
Group size	Intraspecific	NR	NR	NR	+[a]	NR	NR
Social class	Intraspecific	+[b]	+[b]	NR	NR	NR	NR
Gregariousness	Interspecific	—	—	+	NR	NR	NR
Territoriality	Interspecific	—	—	+	NR	NR	NR
Gregariousness + territoriality	Interspecific	—	—	NR	NR	NR	+

NR indicates no relationship; +, significant positive relationship; +[a], correlation observed only in closed-group species; and +[b], territorial males were the social class with higher parasite intensities.

these new parasites actually establish themselves within groups. As a result, gregarious-territorial individuals tend to have more diversified intestinal parasite faunas. This finding indicates that traits affecting both exposure to novel parasites and establishment rates of these parasites within groups are important determinants of individual-level richness. Differences in the results of the two parasite richness analyses also suggest that a distinct set of rules govern species- and population-level richness versus individual-level richness. In past studies, host phylogenetic relationships have been shown to be important determinants of species-level parasite richness across various vertebrate taxa, often confounding apparent ecological patterns (Morand and Poulin, 1998; Poulin, 1995). In the present study, because of the high level of relatedness between host taxa, phylogenetic factors probably played a minor role in richness analyses; nevertheless, results suggest that even in cases in which species-level richness is phylogenetically constrained, individual-level richness could in fact be ecologically determined. Given that the parasite richness scores used in the present study were calculated at a fairly coarse taxonomic level, however, additional work using finer classifications of parasite richness is needed to test the generality of this observation.

Parasitism and the evolution of sociality

Many investigators have suggested that contagious parasites play a role in the evolution of host group size and that increases in this type of parasitism can be costs of sociality (Alexander, 1974; Brown and Brown, 1986; Hoogland, 1979; Hoogland and Sherman, 1976; Møller, 1987; Poulin, 1991a; Rubenstein and Hohmann, 1989; Shields and Crook, 1987). Patterns of coccidia infection across buffalo, eland, and hartebeest groups indicate that there are threshold group sizes below which coccidia are unable to invade groups. Thresholds for buffalo and eland are around a group size of seven, and hartebeest have a threshold of around three (Figure 1). Interestingly, these thresholds are all well below the respective mean group size for each of these species, which suggests that if coccidia are exerting strong downward pressure on bovid group size, the benefits of maintaining group sizes above threshold levels outweigh the costs of coccidian parasitism. Despite this fact, an upper limit on bovid group size may be set, in part, by the negative effects of increasing coccidian parasitism.

To infer evolutionary consequences from relationships between parasitism and sociality, the parasites in question must have demonstrable fitness effects on the host. Strongyle parasitism increased as a function of both gregariousness and territoriality in study species, and these parasites, which included highly pathogenic genera such as *Haemonchus* and *Ostertagia*, have documented negative effects on wild bovids (Gulland, 1992; Stein et al., 2002). Previous work on the bovid populations in this study indicates that strongyle intensities increased in several species when host immunity was weakened due to undernutrition (Ezenwa, 2002). If hosts mount continuous immune responses against these parasites under normal conditions, an increase in strongyle parasitism may well be a definitive cost of both gregariousness and territoriality, and might therefore influence the evolution of both of these traits in bovids.

Patterns that emerge from nonphylogenetically controlled comparative studies sometimes do not hold up once phylogeny is taken into account (Harvey and Pagel, 1991; Nunn and Barton 2001). In this study, interspecific comparisons are made between very closely related species, necessitating careful analysis to ensure independence. Phylogenetic tests show that divergence time between study species was not correlated with any of the measures of parasitism examined, suggesting that observed differences in these traits were shaped primarily by host ecology. Furthermore, exploratory analyses done at the tribe level with reduced statistical power showed very similar results to the genus-level analyses presented here (Ezenwa, 2002). In combination, this is fairly convincing evidence that the patterns observed in this study were not due to the confounding effects of phylogeny. This is the first attempt to examine relationships between social organization and parasitism comparatively in bovids, and when data become available on a wider range of species, standard comparative methods can be used to verify the results detailed here. Nevertheless, this work provides new information on the links between social behavior and parasitic infection in wildlife. In addition to group size and gregariousness, social class and territoriality emerge as equally important determinants of gastrointestinal parasite infection risk (Table 5). Elements of group structure that determine effective group size are shown to affect the degree to which grouping behavior can be used to predict infection rates. And for the first time, it is evident that interactions between behavioral traits affect host parasite load.

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