Habitat overlap and gastrointestinal parasitism in sympatric African bovids

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SUMMARY

Gastrointestinal parasite infections are widespread among wild ungulates. Because many of these parasites infect multiple host species, inter-specific interactions among hosts potentially play an important role in parasite transmission dynamics in ungulate communities. In this study, the effects of inter-specific contact on parasitism rates in 11 sympatric African bovids was examined using habitat overlap among species as a measure of cross-species contact rates. Across individual hosts, strongyle nematode abundance increased with increasing numbers of bovid species occupying a habitat. Furthermore, comparative analyses show a positive association between strongyle prevalence and level of habitat overlap across taxa. These findings suggest that among sympatric bovids, contact between species contributes significantly to the transmission of generalist nematode parasites. For a more host-specific parasite group, coccidia, parasite abundance and individual probability of infection declined in hosts living in bovid rich habitats. This pattern may reflect enhanced inter-specific competition among parasites in these areas. Finally, similar to strongyle abundance, individual parasite richness also increased among hosts occupying habitats with higher numbers of bovid species. No association between habitat overlap and parasite richness was detected at higher taxonomic scales, however, which suggests that contact between host species may not contribute to parasite colonization of new host taxa.

Key words: Bovidae, gastrointestinal parasites, strongyle nematodes, parasite abundance, parasite prevalence, parasite richness.

INTRODUCTION

Parasites and pathogens represent an increasing threat to natural populations (Harvell *et al*. 1999; Daszak, Cunningham & Hyatt, 2000), and recently, attention has been focused on examining methods by which disease threats can be managed in free-ranging wildlife (Woodroffe, 1999; Lafferty & Gerber, 2002). To assess and manage wildlife disease risks effectively, baseline information on patterns of infection in natural populations is critical. To date, many field studies have examined within-population infection patterns by focusing on the effects of factors such as host behaviour (Brown & Brown, 1986; Rubenstein & Hohmann, 1989), demography (Halvorsen, 1986; Hausfater & Watson, 1976), and genetics (Shykoff & Schmid-Hempel, 1991; Müller-Graf, Woolhouse & Packer, 1999) on infection rates. However, far fewer studies (e.g. Dobson, 1995) have looked at the effects of community level interactions on infection rates despite the fact that many parasites infect and are transmitted by multiple host species within the same community. To understand the dynamics of generalist parasite infections, a community level approach is needed because both inter-specific as well as intra-specific processes influence transmission. This is particularly true for parasites that accumulate in the external environment, like many fecal-borne gastrointestinal parasites for which physical contact between hosts is not required for successful transmission and spatial overlap between sympatric hosts is sufficient for cross-species parasite transmission to occur.

Gastrointestinal parasites are among the most widespread parasites of ruminants. In domestic animals these parasites often have detrimental effects on host growth and development, and can increase mortality especially among young animals (Bowman, 1999). Evidence from non-domesticated species suggests that these parasites also play a role in regulating free-ranging ungulate populations (Gulland, 1992), thus understanding the dynamics of parasitic infections in the wild may be critical to understanding host population dynamics. From studies of both domestic and wild ruminants we know that many gastrointestinal parasites infect multiple host species (Sachs & Sachs, 1968; Bindernagel, 1970; Waruiru *et al*. 1995; Zaffaroni *et al*. 2000) and that cross-species parasite transmission can occur between sympatric ungulates (Preston *et al*. 1979). Therefore, in ungulate communities where sympatric hosts share parasites, interactions between host species may influence within-species infection rates. In such cases, host species cannot be studied solely as independent units if accurate predictions of infection risks are to be made.

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This study examines the largely ignored effects of cross-species contact on gastrointestinal parasite transmission in free-ranging African ungulates. The African Bovidae are a highly diverse, yet closely related group of ruminants that share a high degree of ecological overlap as a result of extensive niche partitioning (Gwynne & Bell, 1968; McNaughton & Georgiadis, 1986). This allows multiple species to exploit similar habitats and explains the astonishing bovid diversity apparent on any typical African savanna. African bovids also share many common gastrointestinal parasites (Round, 1968) making them an excellent model system for studying the effects of inter-specific contact on parasite infection risk. In this paper, patterns of gastrointestinal parasitism in 11 sympatric bovid species are reported and community level interactions, measured as habitat overlap among host species, have been tested to see whether they influence parasite infection rates at the individual and species levels. For parasites shared across host species (generalist parasites), it is expected that increasing overlap among species will correlate with increased rates of infection. However, this pattern is unlikely to hold for parasites that are not shared among hosts (specialist parasites). Because of the expected increase in transmission of generalist parasites, increased habitat overlap among species should also be positively correlated with parasite taxa richness.

MATERIALS AND METHODS

The study site

This study was conducted at the Mpala Research Center (00° 17′ N, 36° 53′ E) located in Central Kenya. The Mpala Research Center is contiguous with Mpala Ranch, and both encompass a 22 000 ha area. Annual rainfall at Mpala ranges from 400 mm in the northern half of the ranch to 500 mm in the southern portion, and the vegetation is characteristic of a semi-arid savanna. Mpala ranch is dominated by 2 major soil types red sandy loam soil and black cotton soil formed from volcanic rock. The study was done on the southern half of the ranch where vegetation is mainly composed of *Acacia* bushland/grassland, dominated by *Acacia drepanolobium* in the black cotton areas and *A. mellifera*, *A. etbaica*, *A. brevispica*, *A. nilotica*, *Euclea divinorum* and *Croton dichogamous* in red clay areas. Two major rivers, the Ewaso Nyiro and Ewaso Narok flow through Mpala and the riverine habitats are dominated by *Acacia xanthophloea* stands.

Mpala Ranch is home to a wide variety of mammalian species, 20 of which are large herbivores. Fifteen of these species are bovids including dik-dik (*Madoqua kirkii*), Grant's gazelle (*Gazella granti*), Thomson's gazelle (*Gazella thomsoni*), waterbuck (*Kobus defassa*), impala (*Aepyceros melampus*), buffalo (*Syncerus caffer*), eland (*Taurotragus oryx*), bushbuck (*Tragelaphus scriptus*), hartebeest (*Alcelaphus buselaphus*), klipspringer (*Oreotragus oreotragus*), steinbok (*Raphicerus campestris*), oryx (*Oryx gazella*), mountain reedbuck (*Redunca fulvorufula*), common duiker (*Sylvicapra grimmia*), and greater kudu (*Tragelaphus strepsiceros*). The non-bovid ungulates include Grevy's and Plains zebra (*Equus grevyi* and *E. burchelli*), giraffe (*Giraffa camelopardalis*), warthog (*Phacochoerus africanus*), and elephant (*Loxodonta africana*). In addition to wild herbivores, the ranch also houses domestic stock, of which there are approximately 3000 cattle and 500 sheep, goats, camels, and donkeys. Common carnivores at Mpala include lions (*Panthera leo*), leopards (*Panthera pardus*), spotted hyenas (*Crocuta crocuta*), black-backed jackals (*Canis mesomelas*), and bat-eared foxes (*Otocyon megalotis*).

The study animals

The family Bovidae is made up of the hollow-horned ruminants including all antelopes, sheep, goats, and cattle. The African Bovidae are composed of 11 tribes (Estes, 1991), 7 of which are represented by species in this study including: dik-dik, klipspringer, steinbuck (Neotragini); Grant's gazelle and Thomson's gazelle (Antilopini); waterbuck (Reduncini); hartebeest (Alcephalini); impala (Aepycerotini); bushbuck, eland (Tragelaphini); and buffalo (Bovini). Although each of the study species occupies a slightly different niche in terms of habitat preference and resource use, spatial overlap between species is considerable. The extent of host species overlap was quantified by conducting animal censuses along a series of transects across the study area and recording the location (GPS coordinate) of all species sightings. Transects were censused on 4 consecutive mornings (starting at 06.00 h) and 4 consecutive evenings (starting at 16.00 h) in both April 2001 and May 2001. In addition, *ad libitum* observations were made between April and August 2001. ArcView GIS (3.2) was used to overlay all GPS readings onto a digitized map of Mpala Ranch (Fig. 1). The map was then divided into a system of 1 km^2/grids to represent habitat sectors and the number of species observed per surveyed grid was used as a measure of species habitat overlap for all analyses.

Sample collection

To assess the gastrointestinal parasite burden of live animals, fecal samples were examined for the presence of helminth eggs, larvae and coccidian oocysts. Sampling was carried out by driving a continuous road transect to locate study groups. Animals were usually located either before leaving their sleeping sites, or shortly thereafter and for each herd, the

species and location were recorded and all fresh fecal droppings were collected. Location data were used to assign each fecal sample to the appropriate 1 km^2 habitat grid. For cryptic species, such as dik-dik and klipspringer, dung middens in well-characterized territories along sampling transects were marked and routinely checked for fresh fecal samples. All samples were collected and stored in individually labelled plastic bags. Sampling was conducted every 4 weeks from August 1999 to July 2000, and again from March 2001 to August 2001. The majority of fecal samples (98%) were collected between 06.00 and 11.00 h in order to control for any effects of time of day on egg or oocyst shedding (Ezenwa, 2003). Each species was sampled every month when possible, but not all species could be sampled with the same regularity. Over the course of the entire study 1987 samples were collected.

Parasitological analysis

To quantify fecal parasite output, I used a modification of the McMaster egg counting technique (MAFF, 1980) to determine the number of strongyle eggs (epg) and coccidian oocysyts (opg) excreted per gram of feces for each sample. Non-strongyle eggs and lungworm larvae were also quantified when observed. Three grams (wet weight) of each sample were weighed and placed in a labelled vial. The sample was then homogenized in 42 ml of water, sieved to remove large debris and 15 ml of the strained sample was then centrifuged and the pellet was re-suspended in saturated sodium chloride solution (specific gravity 1·2). After agitation, an aliquot was taken from the centre of the centrifuge tube and pipetted into a single chamber of a McMaster slide, and the tube was then agitated a second time to fill a second chamber. Two chambers were counted for each sample and the counts were averaged to determine e.p.g. and o.p.g. values. For the calculation of all epidemiological variables, each fecal sample was considered to be independent.

In addition to egg counts, several study species found dead were necropsied in order to recover adult helminths. All necropsies were carried out as outlined by Bowman (1999). In brief, the abomasum, small intestine and large intestines were extracted from the cadaver and the contents rinsed out into separate buckets. Water was then added to each bucket and the contents mixed thoroughly. After 5 min the supernatant was poured off and this procedure was repeated 2 more times or until all the large debris was removed. Using a Petri dish and a high-powered light source, the sediment was then systematically searched for worms. Necropsies were performed on the following species with sample sizes in parentheses: impala (5), dik-dik (4), hartebeest (3), buffalo (2), eland (1), Grant's gazelle (1), and klipspringer (1). All recovered worms were preserved in 95% ethanol for storage until identifications could be made.

Terminology and statistical analysis

The epidemiological terms used in this study follow after Margolis *et al.* (1982) with some modification. (1) Abundance: total number of individuals from a particular parasite taxon in a single host individual. In this study parasite abundances were measured using fecal egg/oocyst counts and are reported as eggs/oocysts per gram feces (epg/opg). Mean abundance refers to the total number of individuals of a particular parasite taxon in a sample of hosts divided by the total number of hosts examined. (2) Prevalence: (number of individuals of a particular host species infected with a particular parasite divided by number of hosts examined) $\times 100$. Total prevalence refers to the percentage of individuals infected with at least 1 parasite taxon. (3) Richness: number of parasite taxa present in a host species. Individual richness describes the number of parasite taxa per individual for each host species. Since parasites were not distinguished to species level in this study, parasite taxa richness refers to higher taxonomic levels.

Prevalence was calculated for all parasites, and all parasites found were included in estimates of parasite taxa richness. Only the most prevalent parasite taxa (strongyles and coccidia) were used to calculate parasite abundance. Since macroparasites tend to be aggregated in most host populations (Crofton, 1971; Shaw, Grenfell & Dobson, 1998), the variance-to-mean ratio ($VMR = s^2/\mathrm{m}$) and the parameter of the negative binomial distribution (corrected moment estimate of $k = [m^2 - (s^2/m)]/(s^2 - m)$) were used to evaluate levels of parasite aggregation among host populations (see Gregory & Woolhouse, 1993). Because parasite distributions were aggregated, e.p.g. and o.p.g. counts were $\log_{10}(x+1)$ transformed for statistical analyses.

To determine whether species habitat overlap influences parasite infection rates, all fecal samples were assigned a habitat overlap score (=number of bovid species in habitat) based on the habitat grid in which the sample was collected. The effects of habitat overlap on strongyle abundance, coccidia abundance and individual richness were evaluated using Model I ANOVAs subject to Tukey-Kramer tests for multiple comparisons (Sokal & Rohlf, 1995). The effect of habitat overlap level on the probability of infection with strongyles or coccidia was also tested using logistic regression (Likelihood ratio test). For species level comparisons, mean overlap scores for each host species were calculated by averaging the habitat overlap scores of all individuals within a species and then the association between degree of habitat overlap and strongyle prevalence, coccidian prevalence, and parasite taxa richness across species

Table 1. Helminth parasites recovered from necropsies and the hosts infected

Parasite taxonomic group	Parasite species	Buffalo ($n=2$)	Dik-Dik ($n=4$)	Eland ($n=1$)	Grant's Gazelle ($n=1$)	Hartebeest ($n=3$)	Impala ($n=5$)	Klipspringer ($n=1$)
Strongyle Nematodes	*Agriostomum gorgonis*	X		X			X	
	Cooperia rotundispiculum		X				X	
	Cooperia spp.				X			
	Cooperia verrucosa		X				X	X
	Cooperioides hamiltoni						X	
	Gazellostrongylus lerouxi				X			
	Haemonchus spp. *hybrids*	X				X	X	
	Haemonchus contortus	X	X				X	
	Haemonchus mitchelli					X		
	Haemonchus placei		X					
	Impalaia tuberculata	X				X		
	Longistrongylus curvispiculum		X				X	
	Oesophagostomum columbianum		X					
	Ostertagia spp.	X	X	X				
Other Nematodes	*Protostrongylus africanus*					X		
	Setaria nelsoni	X						
	Skrjabinema spp.		X			X		
	Trichuris spp.		X					
Cestodes	*Stilesia hepatica*						X	
Trematodes	*Cotylophoron macrosphinctris*	X						

was examined. For all analyses, prevalence data were arcsine transformed and parasite richness values were log transformed. Because phylogeny can act as a confounding variable in comparative analyses (Harvey & Pagel, 1991), 2 sets of analyses were performed, phylogenetically controlled comparisons as well as ordinary comparisons using species values. Phylogenetically independent contrasts (Felsenstein, 1985) were calculated with the statistical package CAIC (Purvis & Rambaut, 1995) for use in phylogenetic comparisons. Contrasts were calculated based on a bovid phylogeny obtained from Brashares, Garland & Arcese (2000) and equal branch lengths were assumed to standardize contrasts. All associations between sets of contrasts were tested with regressions forced through the origin (Garland, Harvey & Ives, 1992). Since parasite richness estimates can be influenced by sampling effort (Gregory, Keymer & Harvey, 1991, 1996) multiple regression tests were used in all parasite richness analyses to control for the effects of sample size. Significance was accepted at $P \leqslant 0{\cdot}05$ for all statistical analyses excluding multiple comparison tests.

RESULTS

Parasites found in hosts

Eggs and/or larvae of 8 parasite taxa were detected from fecal analyses. The helminths included 3 nematode genera (*Strongyloides* spp., *Trichuris* spp., and *Capillaria* spp.), 2 cestode genera (tapeworms: *Moniezia* spp., and *Thysaniezia ovilla*), and indistinguishable species of the lungworm family Protostrongylidae, and the nematode order Strongylida referred to collectively as 'strongyles'. Variation in egg characteristics of *Moniezia* spp. and *Trichuris* spp. suggest that several species were responsible for infections both within and across bovid species. The 'strongyles' represent several different genera and species. Except for the Protostrongylids that have intermediate mollusc hosts, the nematodes all have a direct life-cycle and infection occurs through ingestion of either infective larvae or eggs. In the case of *Strongyloides* spp., transmammary infection can also occur or larvae can penetrate the skin of the host. The cestodes have an indirect life-cycle and infection occurs through accidental ingestion of arthropod intermediate hosts. Protozoa from the class Coccidia were also detected in fecal samples. While these parasites were indistinguishable to species level, they most likely were various species from the genus *Eimeria*. The coccidians also have a direct life-cycle, and infection occurs through ingestion of infective oocysts.

Fifteen different helminth genera and 19 species were recovered from necropsies of 7 different bovid species (Table 1). Out of 15 parasites classified to the species level, 6 (40%) infected more than 1 host species, and 3 (20%) infected up to 3 species (Table 1). The most common parasites identified from the study species were strongyle nematodes, and out of 11 strongyles identified to the species level, 6 (54%) infected more than 1 host species

Table 2. Parasite prevalence and richness for 8 parasite taxa in 11 sympatric bovid species

	Buffalo ($n=60$)	Bushbuck ($n=13$)	Dik-Dik ($n=231$)	Eland ($n=149$)	G. gazelle ($n=382$)	Hartebeest ($n=222$)	Impala ($n=692$)	Klipspringer ($n=14$)	Steinbuck ($n=8$)	T. gazelle ($n=39$)	Waterbuck ($n=177$)
Total prevalence	86·7	76·9	86·1	93·9	100	92·3	97·7	85·7	87·5	100	98·9
Strongyles	85	61·5	84·4	88·6	99·7	86·5	96·4	85·7	87·5	100	90·4
Coccidia	11·7	38·5	9·09	21·5	22	26·1	36·1	7·14	12·5	23·1	55·4
Protostrongylidae	1·67	0	0	0	2·62	32	4·91	0	0	2·56	0
Trichuris spp.	0	0	0·43	0·67	7·33	0	0	0	0	7·69	1·13
Strongyloides spp.	0	0	0	0	1·05	0	15·3	0	0	10·3	0
Moniezia spp.	1·67	0	0	4·03	0	0	2·75	0	0	0	0
Capillaria spp.	0	0	0	0	0·52	0	0	0	0	0	0
Thysaniezia ovilla	0	0	0	0	0	0	0·43	0	0	0	0
Parasite richness	4	2	3	4	6	3	6	2	2	5	3
Mean individual richness	1	1	0·94	1·1	1·3	1·4	1·6	0·93	1	1·4	1·5

(Table 1). Between 1 and 9 helminth parasites were identified from each individual host species and hosts shared between 0% and 100% of their parasites with 1 or more other species.

Patterns of infection across host species

Host species were infected with between 2 and 6 different parasite taxa and total prevalence (proportion of individuals infected with at least 1 parasite) rates ranged from 76·9% to 100% across all hosts (Table 2). The most prevalent parasite taxa were strongyles, followed by coccidia. Both of these parasite groups infected all host species, and rates of infection varied from 61·5% to 100% for strongyles and from 11·7% to 55·4% for coccidia (Table 2). Prevalence of the other 6 parasite groups also varied across host species (Table 2).

Strongyle abundance as measured by fecal egg counts was generally high across species. Mean egg counts exceeded 500 e.p.g. in 6 out of the 11 species, and 3 species had egg counts near or above 1000, which would be classified as heavy infections in livestock (Table 3). Coccidia abundance was more variable, and mean oocyst counts ranged from 7 to 7846 (Table 3). Two indices of aggregation indicate that both strongyle and coccidia infections were aggregated across host species. For strongyle egg counts, variance-to-mean ratios (*VMR*) exceeded 50 in all species and the negative binomial parameter (k) <1 in 8 out of 11 species indicating that in each species relatively few individuals were highly infected while most had moderate to low level infections (Table 3). Coccidia distributions were also aggregated; *VMR*s exceeded 100 and $k<1$ in all species (Table 3).

Effects of habitat overlap on infection rates: individual level analyses

Across most of the study area, multiple bovid species were present in the same habitats (Fig. 1A). Bovid species were observed in 44 habitat grids (1 km^2) and the number of species observed per grid (habitat overlap score) ranged from 1 to 7 (mean = 3; Fig. 1B). When all individual fecal samples were assigned an overlap score, habitat overlap was found to have a significant effect on strongyle abundance with abundance increasing with the number of bovid species in the habitat (ANOVA: $F_{6,1978}=8{\cdot}64$, $P<0{\cdot}0001$; Fig. 2A). Individuals in habitats with 7 recorded host species had significantly higher mean strongyle abundance rates than individuals occupying most habitats with fewer species (Tukey-Kramer test: $7>1, 2, 4, 5$; Fig. 2A). Mean strongyle abundance also tended to be significantly lower for individuals in habitats with 1 recorded species (Tukey-Kramer test: $1<3, 7$; Fig. 2A). Habitat overlap also had a significant effect on coccidia abundance, but in this case abundance tended to decrease with the number of species in the habitat ($F_{6,1975}=4{\cdot}12$, $P<0{\cdot}0004$;

Table 3. Mean abundance of strongyles (e.p.g.) and coccidia (o.p.g.) in 11 host species, and 2 indices of parasite aggregation: variance-to-mean ratio (*VMR*) and the negative binomial parameter (*k*)

	e.p.g.			o.p.g.		
	Mean ± S.E.	*VMR*	*k*	Mean ± S.E.	*VMR*	*k*
Buffalo	349 ± 54·0	502	0·68	29·2 ± 18·1	672	0·026
Bushbuck	53·8 ± 15·5	57·7	0·87	7846 ± 7734	99 102	0·002
Dik-Dik	843 ± 90	2223	0·37	316 ± 173	21 955	0·010
Eland	517 ± 43·9	556	0·92	295 ± 117	6930	0·036
Grant's Gazelle	2560 ± 97·2	1411	1·81	293 ± 63·2	5186	0·054
Hartebeest	218 ± 16·2	266	0·82	108 ± 31·1	1978	0·050
Impala	963 ± 38·7	1080	0·89	1159 ± 246	36 075	0·031
Klipspringer	421 ± 131	566	0·67	7·14 ± 7·14	100	$2{\cdot}86 \times 10^{-6}$
Steinbuck	456 ± 162	463	0·86	—	—	—
Thomson's Gazelle	1717 ± 188	807	2·10	254 ± 197	6427	0·011
Waterbuck	522 ± 38·7	508	1·03	1029 ± 286	14 076	0·070

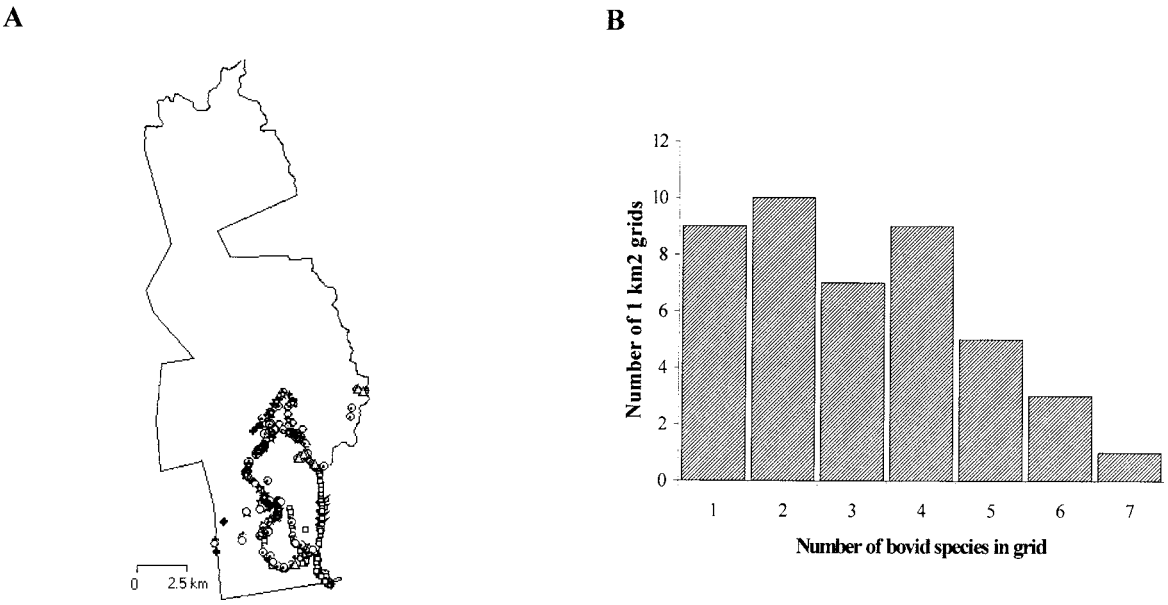

Fig. 1. (A) Map of Mpala Ranch showing GPS locations of 11 bovid species recorded during transect surveys of the study area. Different symbols represent different study species; symbols are highly clustered due to high levels of overlap among species. (B) Histogram showing the number of bovid species recorded per 1 km^2 habitat grid in a total of 44 grids where study species were observed.

Fig. 2B). Although no individuals in habitats with 1 recorded species were infected, individuals in habitats with 2 host species had significantly higher abundance rates than individuals in habitats with more species (Tukey-Kramer test: 2 > 3, 5, 7; Fig. 2B). Analysis of parasite richness across hosts showed that similar to strongyle abundance, habitat overlap also had a significant positive effect on individual parasite taxa richness ($F_{6,1975} = 2{\cdot}41$, $P = 0{\cdot}025$; Fig. 3).

Despite the significant effect of species habitat overlap on strongyle abundance, overlap score was not correlated with the probability of an individual being infected by strongyles (Likelihood ratio test: $\chi^2 = 2{\cdot}25$, D.F. = 1, $P > 0{\cdot}1$). However, the probability of being infected by coccidian parasites declined with the number of bovid species in the habitat ($\chi^2 = 5{\cdot}59$, D.F. = 1, $P = 0{\cdot}018$).

Habitat overlap and parasite prevalence and richness: comparative analyses

Both phylogenetic and non-phylogenetic analyses show that habitat overlap was significantly positively correlated with strongyle prevalence (phylogenetic: $n = 10$ sets of contrasts, $r = 0{\cdot}65$, $P = 0{\cdot}03$, Fig. 4A; non-phylogenetic: $n = 11$ species, $r = 0{\cdot}83$, $P = 0{\cdot}002$), indicating that species with higher levels of contact with heterospecifics are more likely to become infected. On the other hand, there was no correlation between coccidia prevalence and habitat overlap in either phylogenetic ($n = 10$, $r = 0{\cdot}34$, $P = 0{\cdot}30$, Fig. 4B) or non-phylogenetic analyses ($n = 11$, $r = 0{\cdot}3$, $P = 0{\cdot}37$). After controlling for sampling effort, parasite taxa richness was marginally associated (+) with species overlap score in the non-phylogenetic analysis ($n = 11$, standardized regression

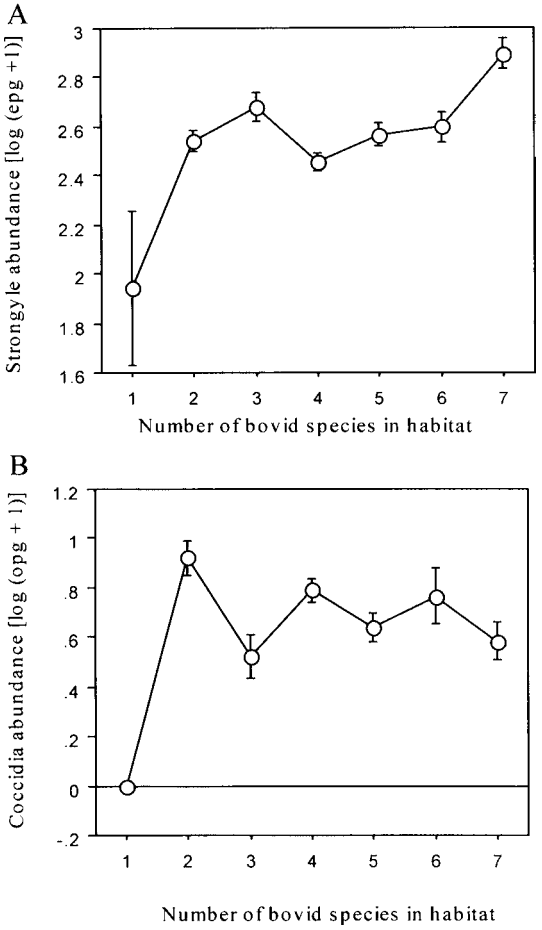

Fig. 2. Comparison of strongyle abundance [log(e.p.g.+1)]±S.E. (A) and coccidian abundance [log(o.p.g.+1)]±S.E. (B) of hosts occupying habitats with differing numbers of bovid species.

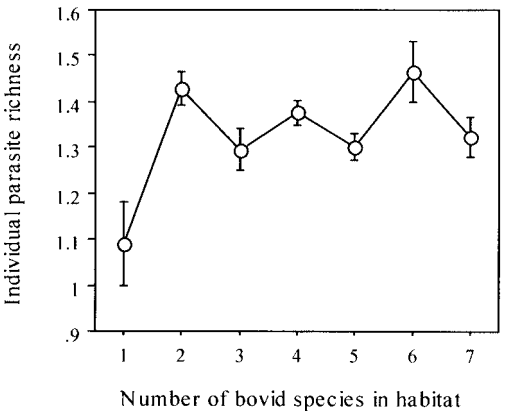

Fig. 3. Individual parasite richness±S.E. of hosts living in habitats with differing numbers of bovid species.

coefficient=0·41, $P=0·07$), but this relationship disappeared in the independent contrasts analysis ($n=10$, standardized regression coefficient=0·12, $P=0·16$).

DISCUSSION

All of the bovid species in this study were infected with gastrointestinal parasites and levels of infection

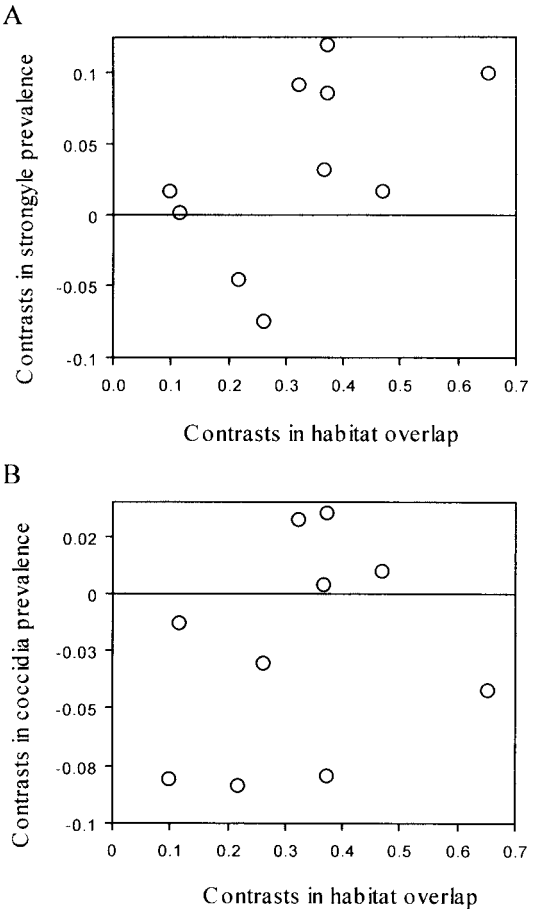

Fig. 4. Relationship between contrasts in species habitat overlap score and arcsine transformed strongyle prevalence (A) and coccidian prevalence (B).

varied across species. Strongyle nematodes and coccidia were the most commonly observed parasites, and like most macroparasites (Shaw & Dobson, 1995; Shaw *et al.* 1998), both were highly overdispersed across study populations reflecting differences in host exposure and susceptibility to these parasites. Indirect cross-species contact through habitat overlap was documented widely throughout the study area and contributed to differences in strongyle infection rates at both the individual and species levels. Many studies have demonstrated that sympatric bovids harbour common strongyle parasites (e.g. Sachs & Sachs, 1968; Bindernagel, 1970; Waruiru *et al.* 1995; Zaffaroni *et al.* 2000), and similarly in this study over 50% of strongyle species recovered at necropsy infected more than 1 host species. Assuming that these parasites are transmitted as well as carried by multiple host species, it is no surprise that increasing habitat overlap among species was associated with increased strongyle abundance; or that across taxa, strongyle prevalence was positively correlated with the degree of species overlap. These differences in strongyle infection rates probably reflect heterogeneity in parasite contamination levels across habitats. Because strongyle infective stages are fecally dispersed and accumulate

in the soil and on vegetation over time (Durie, 1961; Stromberg, 1997), contacts between susceptible hosts (of any species) and generalist parasites probably occur at a higher frequency in habitats supporting larger numbers of host species. Hosts spending more time in diverse habitats (=habitats with a high number of related species) are therefore more likely to acquire generalist parasites as a result of increased exposure.

From a 1 host – 1 parasite perspective, a similar argument explains why increasing host density is often associated with increased parasite abundance and prevalence (e.g. Arneberg *et al*. 1998; Morand & Poulin, 1998; Morand *et al*. 2000; Arneberg, 2001). Epidemiological theory predicts that as host density increases, individuals are more likely to come in contact with parasite infective stages resulting in increased transmission rates (Anderson & May, 1978; May & Anderson, 1978). Extending this idea to a multi-host species parasite system where all host species contribute to parasite dispersal, an increase in contact among host species should also lead to an increase in parasite transmission. This prediction is supported empirically by the results of this study, and furthermore habitat overlap emerges as a good measure of cross-species contact rates. While host density and group size serve as good surrogates for within species contact rates in many population-level and comparative studies (e.g. Brown & Brown, 1986; Poulin, 1991; Côté & Poulin, 1995; Arneberg *et al*. 1998; Arneberg, 2001), these traits may not accurately reflect rates of contact between species. For example, the extent to which a species comes into contact with other species can be influenced by factors such as home range size, social structure, mating system and habitat requirements, but none of these traits is reflected in simple measures of host density. Thus for community level studies, measuring levels of habitat overlap among host species may be a better means of quantifying contact rates depending on the transmission mode of the parasite of interest.

Unlike strongyles, coccidian parasites are relatively host specific and transmission of these parasites across host species is extremely rare (Levine & Ivens, 1986). It is therefore unlikely that cross-species transmission plays any role in the dynamics of coccidian infections in the study populations and, as such it was predicted that there would be no correlation between coccidia infection rates and habitat overlap. While coccidia prevalence was not correlated with habitat overlap across taxa, at the individual level, increasing overlap among species was associated with decreasing fecal oocyst counts (coccidia abundance). Furthermore, the probability of becoming infected with coccidia declined for individuals with higher habitat overlap scores. This negative relationship between coccidian infection rates and degree of habitat overlap may be an indicator of competitive interactions among parasites. If as suggested above, strongyle abundance levels were higher among hosts in species rich habitats, then individuals in these habitats should support large strongyle communities potentially leading to the competitive exclusion of dissimilar parasite taxa (Roberts *et al*. 2002). Heavy gastrointestinal parasite burdens in ruminants also trigger host immune responses creating indirect competition among parasites. Immune defences can reduce parasite fecundity and limit the establishment of new parasites (Balic, Bowles & Meeusen, 2000; Claerebout & Vercruysse, 2000). Since defences against coccidian parasites are particularly effective in controlling re-infection (Cox, 1993), this may have contributed to the decline in coccidia abundance among individuals inhabiting diverse habitats.

In addition to the strongyle parasites found in this study, some of the other parasites such as *Strongyloides* spp., *Moniezia* spp., and *Trichuris* spp. may also infect multiple host species. If this is the case, then like strongyle abundance and prevalence, parasite richness should also increase with increasing levels of habitat overlap among species. More generally, parasite richness should increase in species rich habitats because inter-specific transmission opportunities are highest in these areas. Also, in habitats where closely related potential hosts have high levels of direct or indirect contact, parasite host switching may be more common, further increasing host parasite richness. Study results show that individuals occupying habitats with more host species had higher parasite taxa richness. While this suggests that cross-species contact has an important influence on patterns of parasite richness in ecological time, the lack of any correlation between phylogenetic contrasts in richness and contrasts in habitat overlap implies that other factors predominate in determining patterns of parasite colonization over evolutionary time. On the other hand, because the parasite richness scores used in this study were based on parasite identifications made at taxonomic levels higher than species, there may have been insufficient variability in parasite richness estimates across hosts to detect a correlation between habitat overlap and richness. However, Watve & Sukumar (1995) also tested a similar hypothesis comparatively across 12 mammalian species in India and found no relationship between the number of related species present in the study area and host parasite (helminth and/or protozoa) diversity, which supports the idea that inter-specific interactions are not important predictors of parasite richness across taxa. Among mammals, traits that have been positively associated with parasite richness include host body size and density (Poulin, 1995; Gregory *et al*. 1996; Morand & Poulin, 1998), but body size relationships tend not to hold up when phylogeny is incorporated into the analyses. At this juncture, more work is needed to fully understand what factors determine patterns of

parasite richness across host populations and communities.

The inherent complexities of studying parasite transmission dynamics in natural multi-host systems have limited our understanding of host–parasite community ecology. Despite the difficulties, attempts are being made to understand these systems (e.g. Dobson, 1995; Krasnov *et al*. 1997). This study demonstrates that in communities comprised of very closely related species, cross-species contact is an important determinant of generalist parasite infection risk and should be considered when evaluating patterns of infection even within single-host populations. Further implications of these results are that hosts living in diverse habitats may be more susceptible to parasite 'spill-over' than other hosts. Since generalist parasites can pose a significant threat to endangered and threatened wildlife species (Begon & Bowers, 1995; McCallum & Dobson, 1995), adequately quantifying cross-species contact rates in natural systems may have important consequences for species conservation. Finally, given the regulatory effects parasites can have on host populations (Gulland, 1992; Hudson, Newborn & Dobson, 1998), insights into the role cross-species contact plays in the transmission of certain parasites will contribute to a better understanding of how parasites impact host community structure.

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