

PATTERNS OF ASSOCIATION, NESTEDNESS, AND SPECIES CO-OCCURRENCE OF HELMINTH PARASITES IN THE GREATER KUDU, *TRAGELAPHUS STREPSICEROS*, IN THE KRUGER NATIONAL PARK, SOUTH AFRICA, AND THE ETOSHA NATIONAL PARK, NAMIBIA

K. Joel Fellis, N. J. Negovetich, G. W. Esch, I. G. Horak*, and J. Boomker*

Department of Biology, Wake Forest University, Winston-Salem, North Carolina 27109. e-mail: fellk01g@wfu.edu

ABSTRACT: The helminth parasites of the greater kudu from the Kruger National Park (KNP), South Africa, and the Etosha National Park (ENP), Namibia, were examined to determine the major patterns of spatial and demographic variation in community structure and to evaluate nonrandomness in parasite community assembly. Nonmetric multidimensional scaling ordination procedures were used to test for differences in parasite community composition between hosts of the 2 parks and between hosts of different demographic groups within KNP. Infracommunities within KNP were also examined for patterns of nonrandomness using 2 null models, i.e., nestedness and species co-occurrence. Infracommunities of KNP and ENP were significantly different from each other, as were infracommunities of different host demographic groups within KNP. Parasite species in the greater kudu from KNP displayed significant levels of nestedness and were found to co-occur less frequently than expected by chance; however, this lack of co-occurrence was significant only when all demographic groups were considered. When restricted to any particular age class, co-occurrence patterns could not be distinguished from random. Overall, these data suggest that biogeography and host demographics are important factors in determining community organization of helminth parasites in the greater kudu.

One of the key concerns of community ecology is to establish whether species assemblages are structured entities or stochastic groupings and, if structured, what mechanisms are responsible for their organization (Gotelli and McCabe, 2002; Janovy, 2002). A common way to conclude whether an assemblage of species is a structured or ordered community is to determine whether specific groupings of species are associated with a particular habitat or biogeographic area (Brown and Lomolino, 1998), i.e., whether there are observable patterns in the distribution of species (Roberts et al., 2002). Within the context of host–parasite systems, the combination of species assemblages with habitat can be further subdivided by testing for associations among hosts of different genders and age classes. Structured communities can also be delineated by a departure from randomness, where an assemblage of species is significantly more ordered than would be expected by chance. To test whether communities are significantly structured, pattern-based null models are often formulated. These null models are pattern-generating methods that intentionally exclude a mechanism of interest to determine whether a specific pattern can be produced by a stochastic process (Gotelli, 2000, 2001). Two useful null models that have been used to assess community structure are species nestedness (Atmar and Patterson, 1993) and species co-occurrence (Gotelli and McCabe, 2002).

Community nestedness represents a Russian doll-like pattern in which species-poor communities are an ordered subset of more diverse communities (Atmar and Patterson, 1993). Nestedness has been well documented for both free-living (Patterson and Atmar, 1986; Fernandez-Juricic, 2002) and parasitic taxa (Poulin and Valtonen, 2001; Šimková et al., 2001) and has been used extensively to test for nonrandom patterns among species assemblages. Nested patterns were originally thought to develop through ordered extinction (Patterson and Atmar, 1986) but have subsequently been shown to arise through colonization as well (Simberloff and Martin, 1991). Although nestedness can

evolve through both colonization and extinction processes, it suggests a higher-level order that renders community structure predictable.

Species co-occurrence models are largely built upon Diamond's (1975) community assembly rules, i.e., forbidden species combinations, checkerboard distributions, and incidence functions (Gotelli and McCabe, 2002), where species are predicted to co-occur less frequently than would be expected by chance alone owing to competitive interactions. Many of Diamond's (1975) original assembly rules have been converted to measurable co-occurrence indices and have been used to determine whether communities lack certain species combinations. One of the more powerful co-occurrence indices is Stone and Roberts' (1990) C-score metric, which is used to measure the average number of "checkerboard" units in a species presence–absence matrix. A checkerboard pattern refers to the case where species A is present in a host while species B is absent, combined with the presence of species B in another host where species A is absent. Such a pattern is thought to arise when competitive interactions are important in structuring a community (Diamond, 1975; Gotelli and McCabe, 2002).

The parasites of a wide range of African ruminants have been the subject of extensive surveys (Mönnig, 1932; Boomker, 1982, 1991; Horak et al., 1983; Boomker et al., 1991, 1997). These studies have culminated into several substantial checklists detailing the species present, levels of abundance and prevalence, and insights into seasonal fluctuations (Boomker et al., 1986, 1989). Despite the considerable progress that has been made, there is a dearth of detailed community studies from this region.

To this end, we examined an exceedingly diverse and abundant assemblage of helminths from 119 greater kudus (*Tragelaphus strepsiceros*) from 2 localities in southern Africa. The effort was designed to determine whether (1) parasite communities differ between geographic locations, (2) parasite communities differ between hosts of different age classes or gender, (3) parasite infracommunities form nested subsets, and (4) helminth communities in the greater kudu exhibit evidence of competitive exclusion.

Received 3 February 2003; revised 23 June 2003; accepted 23 June 2003.

* Department of Veterinary and Tropical Diseases, University of Pretoria, Private Bag X04, Onderstepoort 0110, Pretoria, South Africa.

METHODS

Study areas

Kudus were collected from the southern part of the Kruger National Park (KNP) in South Africa and the Etosha National Park (ENP) in Namibia. The KNP is a 19,485-km² park located in the northeast portion of South Africa. The vegetation in the southern region of KNP is relatively diverse, consisting of 4 veld types (Boomker et al., 1989). The climate varies from warm or hot summers to mild winters, with an annual rainfall between 600 and 700 mm. The ENP is a 22,269-km² reserve located in the northern region of Namibia. The ENP is centered on the Etosha salt pan in a semiarid habitat with an annual rainfall around 389 ± 118 mm (Simmons, 1996). Vegetation consists largely of desert scrub and mopane forests.

Study animals

The greater kudu, *T. strepsiceros*, is a large antelope, reaching upwards of 315 kg, and is distributed widely throughout southern and eastern Africa. Kudus are consummate browsers, feeding primarily on flowers, fruits, seeds, pods, leaves, and twigs of a variety of plants, but they seldom consume grass (Owen-Smith and Cooper, 1987; Boomker et al., 1989). Social organization is based on the cow social unit, where a closed matriarchal kinship group consisting of several cows and their offspring is formed. Calves stay concealed for the first 3 mo of their lives before joining the maternal group (Boomker et al., 1989). Males leave the maternal group at approximately 2 yr of age and form temporary associations with peers. Adult bulls show a tendency to become increasingly solitary with age and form transient associations with cows during the breeding season.

Data collection

A total of 119 kudus were collected from KNP and ENP. Ninety-six kudus were taken from KNP between April 1981 and March 1983 as part of a previous survey (Boomker et al., 1989). In brief, monthly collections from KNP included 1 adult male, 1 adult female, 1 young adult male, and 1 juvenile or calf of either sex. Full-body necropsies of these animals were performed, and all helminths were identified and counted. Twenty-three kudus were culled from ENP on a bimonthly basis from June 1983 to April 1984. Two adult males and 2 adult females were taken on each occasion. Necropsies were performed using the same procedures as those used in KNP.

Data analysis

Nonmetric multidimensional scaling (NMDS) was used to elucidate differences in community structure between KNP and ENP. NMDS has been used extensively in free-living ecology to examine the associations of species assemblages with different habitats (Bailey and Whitham, 2002), and it has also been used to examine differences in parasite communities along a stream gradient in Appalachian fishes (Barger and Esch, 2001). Ordinations were performed using 2 separate distance matrices, one constructed from quantitative abundance data using the Sorenson distance measure and the other created from presence-absence data also using Sorenson distance. Sorenson distance was used for distance matrices because it is well suited for both quantitative data and presence-absence data (McCune and Medford, 1999). Differences in community composition between KNP and ENP were analyzed using multiresponse permutation procedures (MRPP). An indicator species analysis that calculates species indicator values (IV) was used to determine which species differed between the 2 parks. This analysis was used because it combines both abundance and prevalence data to determine whether a particular species is indicative of a given habitat (McCune and Medford, 1999). Ordination procedures, MRPP, and indicator species analyses were all performed using PC-ORD software (McCune and Medford, 1999).

Differences in parasite community composition among hosts of different age classes and genders were examined using NMDS, MRPP, and indicator species analyses. No difference was detected between male and female hosts and between juvenile and adult hosts. Subsequently, male and female hosts and adults and juveniles were lumped together for all the remaining analyses. A Kruskal-Wallis test was performed to test for differences in species richness among different age-class hosts.

The presence of nested communities was examined using Nested Cal-

culator software (Atmar and Patterson, 1995) to compare the degree of nestedness in kudu infracommunities from KNP, with the level of nestedness from 1,000 randomly generated communities based on presence-absence data from KNP. The level of significance was determined by calculating the frequency of randomly generated communities that contained greater levels of nestedness.

A co-occurrence module developed by Gotelli and Entsminger (1999) was used to determine whether parasite species co-occurred less frequently than expected by chance. This module was performed using the C-score index of Stone and Roberts (1990), which measures the average number of checkerboard units among all possible combinations of species and has been shown to be resistant to type I error (Gotelli, 2002). This model was run 4 different times using data from KNP for the following scenarios: (1) for all helminths of all kudus, (2) for all helminths of adults only, (3) for enteric nematodes of all kudus, and (4) for enteric nematodes of adults only. Each of the observed C-score values was compared with C-score values for 5,000 randomly generated matrices to establish significance.

RESULTS

Twenty-two species of helminths were recovered from 96 kudus in KNP. Of these, 16 species were nematodes, 4 cestodes, and 2 trematodes (Tables I–III). Eleven of the 16 species of nematodes were trichostrongylids. Four of the 16 nematode species were common, infecting more than 50% of the hosts. Three were of intermediate prevalence, infecting more than 10% of the hosts but less than 50%, whereas the remaining 9 nematode species were rare, infecting less than 10% of the kudus from KNP. The 2 trematodes from KNP, *Schistosoma mattheei* and *Calicophoron* sp., had intermediate levels of prevalence, whereas 3 of the 4 cestode species infected less than 10% of the hosts; *Taenia* sp. infected 11% of the kudus from KNP.

Thirteen species of helminths were recovered from 23 kudus in ENP, including 11 species of nematodes and 2 cestodes (Tables IV, V). Nine of the 11 nematode species were trichostrongylids. Only 2 species from ENP, *Cooperia neitzi* and *Haemonchus vegliai*, infected more than 50% of the hosts. Five species were intermediate in abundance, whereas the remaining 6 (including the 2 cestode species) were rare, infecting <10% of the hosts.

Quantitative abundance ordination of kudu infracommunities from both KNP and ENP explained 79% of the variation in these data (axis 1 = 48%, axis 2 = 31%, stress = 0.11) and displayed a high level of segregation in ordination space between hosts from different geographic locations (Fig. 1A). A 2-dimensional ordination solution based on presence-absence data revealed similar results, explaining 84% of the variation among infracommunities (stress = 0.20) and suggesting even greater levels of infracommunity segregation between KNP and ENP with almost no overlap in ordination space (Fig. 1B). MRPP were performed to test the hypothesis that there is no difference in parasite community composition between KNP and ENP. This hypothesis was rejected for both quantitative ($P < 0.0001$; $A = 0.08$) and presence-absence data ($P < 0.0001$; $A = 0.06$). Further examination of the 2 component communities showed significant differences in the indicator values (a metric of abundance and prevalence combined) of 10 species between the 2 parks (Table VI). Six parasite species were found to be more commonly associated with kudus from KNP, whereas 4 species were more indicative of kudus from ENP. The indicator value for *S. mattheei*, which occurs only in KNP, was not statistically significant ($P = 0.07$; $IV = 20.8$); however, the

TABLE I. Mean abundance (\pm SE), prevalence, and trait matrix for nematode species recovered from 96 kudus from the Kruger National Park.

Nematodes	Abundance	Prevalence	Transmission	Site	Family
<i>Haemonchus vegliai</i> *	122.5 \pm 137.5	88	Ingestion	GI tract†	Trichostrongylidae
<i>Cooperia neitzi</i> *	502.8 \pm 578.7	83	Ingestion	GI tract	Trichostrongylidae
<i>C. acutispiculum</i> *	120.9 \pm 144.2	77	Ingestion	GI tract	Trichostrongylidae
<i>Elaeophora sagittus</i> *	10.8 \pm 21.6	68	Vector	PA and CBV‡	Onchocercidae
<i>Trichostrongylus deflexus</i> *	106.3 \pm 254.6	44	Ingestion	GI tract	Trichostrongylidae
<i>Agriostomum gorgonis</i> §	9.3 \pm 25.5	28	Penetration, vertical	GI tract	Chabertiidae
<i>Impalalia tuberculata</i> §	21.5 \pm 82.9	22	Ingestion	GI tract	Trichostrongylidae
<i>T. falculatus</i>	4.7 \pm 15.9	10	Ingestion	GI tract	Trichostrongylidae
<i>C. hungi</i>	6.8 \pm 29.6	8	Ingestion	GI tract	Trichostrongylidae
<i>Strongyloides papillosus</i>	46.8 \pm 283.1	6	Penetration, vertical	GI tract	Strongyloididae
<i>Trichuris</i> sp.	1.3 \pm 5.6	5	Ingestion	GI tract	Trichuridae
<i>C. fuelleborni</i>	1.6 \pm 9.5	4	Ingestion	GI tract	Trichostrongylidae
<i>Paracooperia devossi</i>	0 \pm 0.1	2	Ingestion	GI tract	Trichostrongylidae
<i>Setaria</i> sp.	0 \pm 0.1	2	Vector	Body cavity	Onchocercidae
<i>C. yoshidaï</i>	0.5 \pm 5.1	1	Ingestion	GI tract	Trichostrongylidae
<i>Parabronema</i> sp.	0 \pm 0.1	1	Vector	GI tract	Habronematidae

* Common species infecting more than 50% of the host population.
 † Gastrointestinal tract.
 ‡ Pulmonary artery and coronary blood vessels.
 § Occasional species infecting more than 10% but less than 50% of the host population.
 || Rare species infecting less than 10% of the host population.

parasite was found to be statistically more prevalent in KNP ($\chi^2 = 0.99$; $P < 0.001$).

An MRPP analysis of hosts from different age classes within KNP revealed significant differences in community composition between calves and adults ($P < 0.0001$; $A = 0.06$) and between calves and juveniles ($P = 0.0003$; $A = 0.07$); however, there was no significant difference between adults and juveniles ($P = 0.15$; $A = 0.007$). These differences are readily apparent in ordination space based on quantitative (stress = 0.11) (Fig. 2A) and presence-absence (stress = 0.17) (Fig. 2B) matrices. Both quantitative and presence-absence ordination solutions show a high level of segregation for parasites in calves from those in adults and juveniles, whereas those in adults and juveniles largely cluster together. Because there was no detectable difference in parasite community composition between adults and juveniles, these 2 age classes were lumped together, and a species indicator analysis was performed to test for associations between individual species and specific age-class hosts. Twelve species, all nematodes, were found to be indicative of a particular age-class host (Table VII). Six species were more commonly associated with adults and juveniles, and 6 species were more commonly associated with calves. Furthermore, a Kruskal-Wallis test was performed to determine whether there were differences in parasite species richness among different age-class hosts. This analysis returned a significant P value ($P = 0.01$), with adult kudus harboring the greatest number of spe-

cies, juveniles the second greatest number of species, and calves the least number of species.

An examination of 2 community null models revealed highly nonrandom patterns of parasite infracommunity structure within KNP kudus. Kudu infracommunities were significantly nested ($P < 0.0001$; Fig. 3), demonstrating that rare species primarily occur in more diverse infracommunities. A comparison of observed C-score indices with C-score values from randomly generated communities exposed a lack of species co-occurrence for all helminths ($P = 0$; C-score = 92.1) and for enteric nematodes ($P = 0$; C-score = 109.6) when all kudus from KNP were examined (Table VIII). When this co-occurrence null model was restricted to a specific age class, including adults from ENP, parasite species were distributed randomly with respect to co-occurrence patterns (Table VIII).

DISCUSSION

The greater kudu parasite communities from KNP and ENP are species rich and abundant. Both communities are largely composed of enteric nematodes primarily from the Trichostrongylidae. *Haemonchus veglia*, *C. neitzi*, and *C. acutispiculum* were the 3 most abundant helminths in both KNP and ENP. It is unclear why these worms are more common than other helminths in this system. However, Horak (1980) and Boomker et al. (1989) have suggested that kudus in KNP serve as the pri-

TABLE II. Mean abundance (\pm SE), prevalence, and trait matrix for trematode species recovered from 96 kudus from the Kruger National Park.

Trematodes	Abundance	Prevalence	Transmission	Site	Family
<i>Calicophoron</i> sp.*	31.8 \pm 92.7	32	Ingestion	GI tract†	Paramphistomatidae
<i>Schistosoma mattheei</i> *	3.9 \pm 11.3	20	Penetration	Blood vascular system	Schistosomatidae

* Occasional species infecting more than 10% of the host population.
 † Gastrointestinal tract.

TABLE III. Mean abundance (\pm SE), prevalence, and trait matrix for cestode species recovered from 96 kudus from the Kruger National Park.

Cestodes	Abundance	Prevalence	Transmission	Site	Family
<i>Taenia</i> sp*	0.2 \pm 0.9	11	Ingestion	Muscle	Taeniidae
<i>Moniezia benedeni</i> *	0.2 \pm 0.7	10	Ingestion	GI tract†	Anoplocephalidae
<i>Avitellina</i> sp*	0.1 \pm 0.7	3	Ingestion	GI tract	Anoplocephalidae
<i>Echinococcus</i> sp.*	0 \pm 0.1	1	Ingestion	Liver	Taeniidae

* Rare species infecting less than 10% of the host population.

† Gastrointestinal tract.

mary definitive host for these worms along with *Trichostrongylus deflexus*. Many of the other species found in this study are probably maintained commonly in other ungulate, or herbivorous, hosts, only occasionally or rarely infecting kudus.

The segregation of kudu infracommunities of different geographic locations in ordination space suggests strong differences in component parasite community structure between kudus from the 2 parks. This contention is further supported by the MRPP results, which revealed that kudu infracommunities of KNP and ENP were compositionally distinct, i.e., parasite communities within a park are more similar to each other than to parasite communities from the other park. These data also confirm the results demonstrated by Goüy de Bellocq et al. (2002), who examined parasite communities of 16 species of mammals and found parasites to be a reliable biogeographic marker. It is likely that these disparities stem from major differences in climate and vegetation between the 2 parks, as well as slight differences in the ungulate fauna and the absence of the required intermediate snail hosts in ENP. Thus, ENP is generally considered as semiarid, and the vegetation consists largely of desert scrub in the south and mopane forests in the north. KNP tends to be a wetter region of southern Africa, with an annual rainfall of 600–700 mm/yr and a more diverse flora (Boomker et al., 1989). The ungulate faunas of the 2 parks are relatively similar, although there are some slight differences. For example, springbok and gemsbok are not present in KNP but occur in ENP, whereas, buffalo, oribi, and grysbok are absent from ENP but present in KNP. It is possible that the presence or absence of

these potential host species could influence the transmission dynamics for a number of the generalist parasites.

Another important difference between the 2 parks is the absence of *Bulinus globosus* in ENP (K. de Kock, pers. comm.). The absence of this snail explains the lack of *S. mattheei* in ENP. Even though 2 closely related species, *B. forskali* and *B. angolensis*, both occur in Etosha, there is no report of natural infection of *S. mattheei* in ENP. The absence of *Onchocerca* sp. in KNP is perplexing because the vectors for this parasite, *Simulium* spp., are abundant in the park (E. Nevill, pers. comm.). It is possible that *Onchocerca* sp. could be absent from KNP because of historical factors; however, it seems reasonable that it could easily spread throughout the range of *Simulium* spp. in Africa, and thus it is likely that there are unknown abiotic factors preventing the transmission of *Onchocerca* sp. in KNP. Further studies are needed to establish the factors limiting the range of *Onchocerca* sp. in southern Africa.

Within KNP, host demographics appear to be a reliable predictor of infracommunity structure. Both quantitative and presence-absence ordination solutions displayed a strong separation of calf infracommunities from juvenile and adult infracommunities. This segregation of calves from juvenile and adult infracommunities in ordination space was confirmed using an MRPP analysis, demonstrating that calf infracommunities are compositionally distinct from those of adults and juveniles. The factor driving this difference in community composition is not solely an accumulation of parasites associated with age but rather that 6 species are more commonly associated with calves and 6

TABLE IV. Mean abundance (\pm SE), prevalence, and trait matrix for nematode species recovered from 23 kudus from the Etosha National Park.

Nematodes	Abundance	Prevalence	Transmission	Site	Family
<i>Cooperia neitzi</i> *	88 \pm 113.8	68.4	Ingestion	GI tract†	Trichostrongylidae
<i>Haemonchus vegliai</i> *	26 \pm 29.4	63.2	Ingestion	GI tract	Trichostrongylidae
<i>C. acutispiculum</i> ‡	63 \pm 120.3	47.4	Ingestion	GI tract	Trichostrongylidae
<i>Onchocerca</i> sp.‡	1 \pm 1.7	47.4	Vector	Conn. tissue§	Onchocercidae
<i>Cooperiodes hamiltoni</i> ‡	8 \pm 18.7	21.1	Ingestion	GI tract	Trichostrongylidae
<i>Impalaia nudicollis</i> ‡	9 \pm 22.4	15.8	Ingestion	GI tract	Trichostrongylidae
<i>Trichostrongylus thomasi</i> ‡	4 \pm 12.5	10.5	Ingestion	GI tract	Trichostrongylidae
<i>Paracooperia devossi</i>	11 \pm 45.9	5.3	Ingestion	GI tract	Trichostrongylidae
<i>Elaeophora sagittus</i>	0 \pm 0.5	5.3	Vector	PA and CBV#	Onchocercidae
<i>I. tuberculata</i>	3 \pm 11.5	5.3	Ingestion	GI tract	Trichostrongylidae
<i>T. falculatus</i>	1 \pm 5.7	5.3	Ingestion	GI tract	Trichostrongylidae

* Common species infecting more than 50% of the host population.

† Gastrointestinal tract.

‡ Occasional species infecting more than 10% but less than 50%, of the host population.

§ Connective tissue.

|| Rare species infecting less than 10% of the host population.

Pulmonary artery and coronary blood vessels.

TABLE V. Abundance (\pm SE), prevalence, and trait matrix for cestode species recovered from 23 kudus from the Etosha National Park.

Cestode	Abundance	Prevalence	Transmission	Site	Family
<i>Moniezia expansa</i> *	0 \pm 0.2	5.3	Ingestion	GI tract†	Anoplocephalidae
<i>Thysaniezia giardi</i> *	0 \pm 0.2	5.3	Ingestion	GI tract	Anoplocephalidae

* Rare species infecting less than 10% of the host population.

† Gastrointestinal tract.

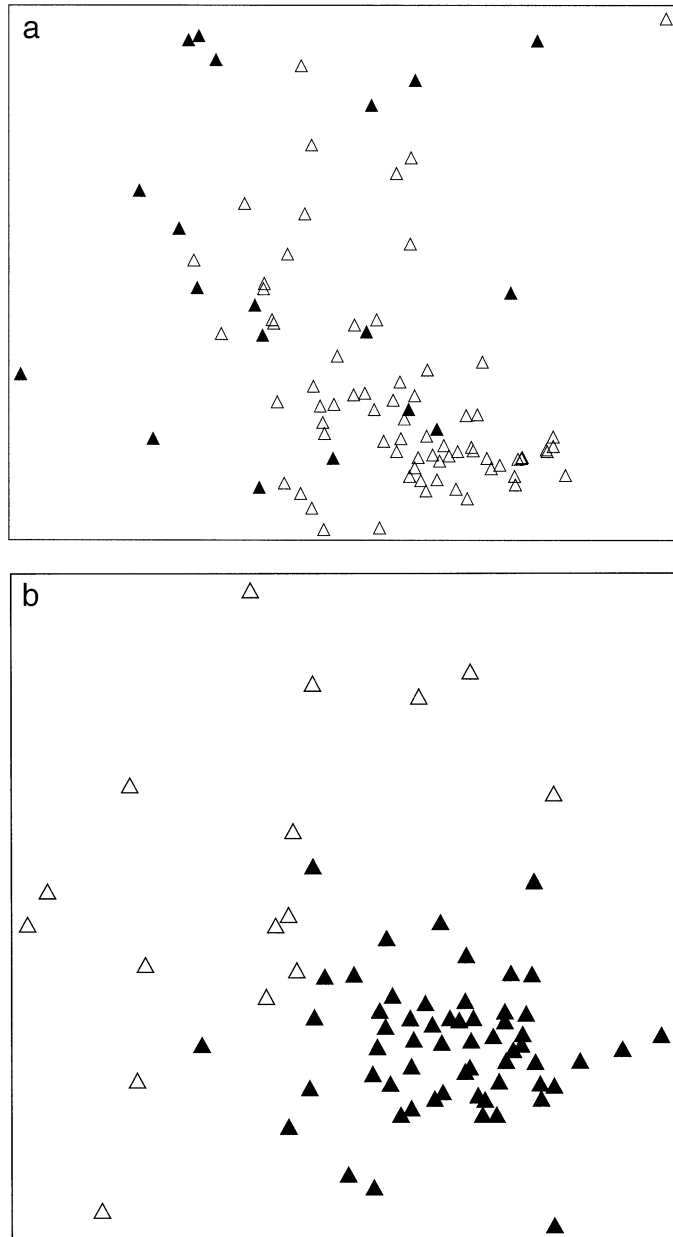


FIGURE 1. Nonmetric multidimensional solutions for kudu infracommunities from Kruger and Etosha National Parks (KNP and ENP, respectively) based on (A) quantitative abundance data (axis 1 = 48%, axis 2 = 31%, stress = 0.11) and (B) presence-absence data (axis 1 = 34%, axis 2 = 50%, stress = 0.20). Δ and \blacktriangle = infracommunities from KNP and ENP National Parks, respectively.

other species are more common in adult or juvenile hosts. Five trichostrongylids, as well as *Strongyloides papillosus*, were found to be significantly more indicative of calf hosts than of any other demographic group. Several explanations are possible for the increased “association” with calves. Calves are still undergoing an experimental learning period, when they are likely to eat any vegetation that is present, including grass, whereas adults are consummate browsers, rarely grazing on grass. Because transmission of these trichostrongylid species requires the ingestion of grass to which infective larvae adhere, calves would have a greater exposure and, therefore, opportunity to recruit larval parasites. Density-dependent mechanisms, such as acquired immunity and parasite-induced host mortality, are also potential factors that could be important in generating the differences between calf infracommunities and those of adults and juveniles. Explanatory models elucidating the aggregation of trichostrongylid infections in ruminant hosts have attributed similar patterns to the density-dependent effects of acquired immunity and parasite-induced host mortality (Grenfell et al., 1995). Acquired host resistance has been well documented for several trichostrongylid species (Reinecke, 1983), and, as such, many of these infections may be maintained through immunologically naive hosts. The greater occurrence and abundance of *S. papillosus* in calves may be due to the vertical transmission of the parasite, even though this parasite may also be acquired via a percutaneous route or by direct ingestion of L3 stages. Because *S. papillosus* may be transmitted by the transmammary route (Moncol and Grice, 1974), an infected mother could pass the parasite infection to all her offspring.

The greater association of the 6 parasite species in adult hosts can be attributed to differences in behavior as well as increased exposure of parasites over time. Presumably, adult kudus have greater overall energy demands and spend more time feeding. Further, calves remain hidden from the maternal group for the first few months of their lives, resulting in a differential exposure to parasites. Finally, by chance alone, adults are likely to be exposed to a wider array of parasites over time and will likely accumulate new, but rare, parasite species throughout their lives. This pattern has been well documented in many other host-parasite systems (Esch and Fernandez, 1993). Similarly, Poulin (1997) has reviewed major patterns of parasite species richness and has documented a positive correlation between parasite species richness and host geographic range for several rodent species, suggesting that vagile species will tend to acquire more parasites and parasite species. Because adult kudus are more mobile than calves, they will be exposed to more parasites not only as a function of time but also as a function of space.

Nested analyses of kudu data from KNP displayed a highly ordered distribution of parasite species among kudu infracom-

TABLE VI. Parasite species indicative of Kruger and Etosha National Parks (KNP and ENP, respectively).

Species	KNP		Species	ENP	
	IV†	P value		IV†	P value
<i>Cooperia acutispiculum</i> *	65.9	0.001	<i>Cooperiodes hamiltoni</i>	21.1	0.003
<i>C. neitzi</i> *	80.3	0.001	<i>Impalaia nudicollis</i>	15.8	0.009
<i>Elaeophora sagitta</i> *	86.9	0.001	<i>Onchocerca</i> sp.	47.4	0.001
<i>Haemonchus vegliai</i> *	79.2	0.001	<i>Trichostrongylus thomasi</i>	10.5	0.033
<i>T. deflexus</i>	33.3	0.022			
<i>Calicophoron</i> sp.	40.3	0.015			

* Parasite species recovered in both KNP and ENP.

† IV = observed species indicator value.

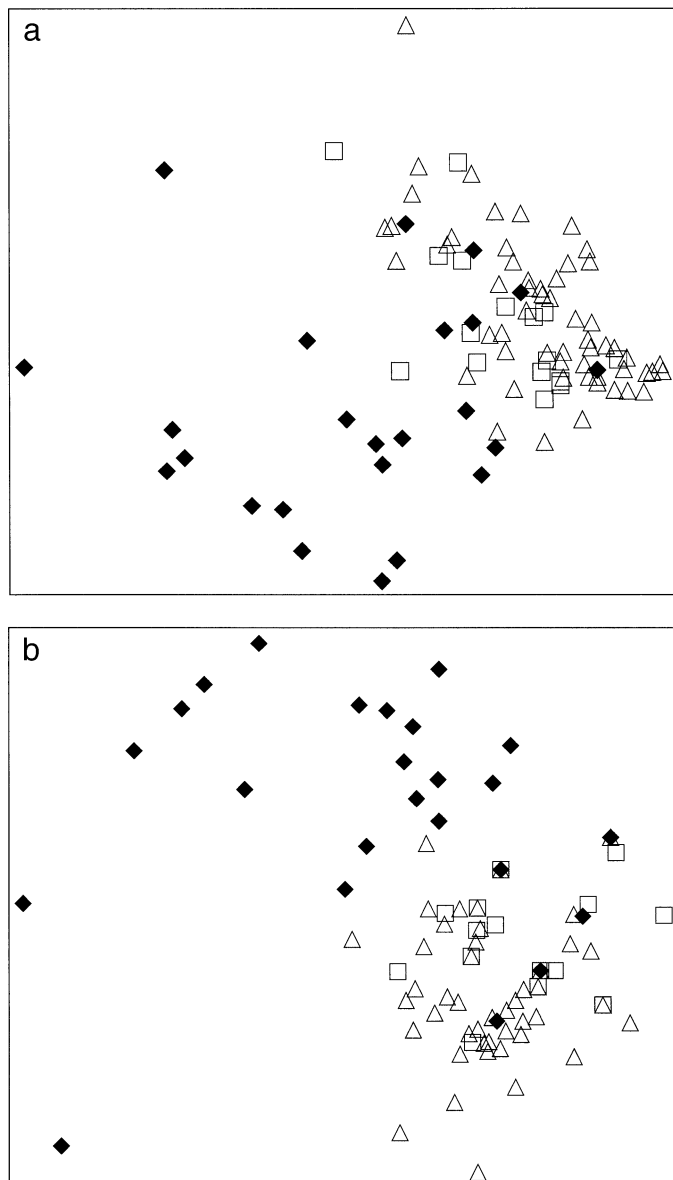


FIGURE 2. Nonmetric multidimensional solutions for adult and calf kudu infracommunities based on (A) quantitative data (axis 1 = 44%, axis 2 = 27%, stress = 0.11) and (B) presence-absence data (axis 1 = 59%, axis 2 = 30%, stress = 0.17). Δ = adult infracommunities, \square = juvenile infracommunities, \blacklozenge = calf infracommunities.

communities. A nested pattern implies a hierarchical community structure, where species-poor infracommunities represent an ordered subset of more diverse communities. Moreover, nestedness suggests that rare species are likely to be found in only the most diverse communities. Several explanations have been proposed for nested patterns for free-living organisms (Atmar and Patterson, 1993) as well as for parasites (Poulin and Valtonen, 2001). An ordered extinction of species due to low population density of species-poor patches has been proposed for nestedness among insular mammal communities, but it is not a feasible explanation for most parasites because of varied indirect life cycles and metapopulation dynamics (Guégan and Hugué, 1994). Other hypotheses that have been put forth to explain nested subsets include (1) positive interactions, where the presence of one species facilitates the presence of another, either through suppression of the host's immune response or through an alteration of the host-parasite in such a way as to make recruitment of another species more conducive; (2) increased habitat heterogeneity, where there is a positive association between niche diversification and host size or age; and (3) passive sampling of parasites by the host, where hosts are exposed to a greater diversity of species over time by chance alone (Guégan and Hugué, 1994). Although these hypotheses are not necessarily mutually exclusive and are difficult, if not impossible, to distinguish from each other by observation alone, the passive sampling hypothesis appears to be the most parsimonious explanation. A comparison of species richness values between different age classes is consistent with this hypothesis, where adult kudus were found to harbor the greatest number of species, juveniles the second greatest number of species, and calves the least number of species. Whereas experimental studies are needed to tease apart the various hypotheses generating nestedness in this system, the fact that kudu infracommunities form a nested pattern is central to understanding the patterns for commonness and rarity among ungulate parasites.

The lack of co-occurrence observed among all helminth species, and among species of enteric nematodes in KNP, is likely the result of age-related differences in hosts and not of competitive exclusion. Patterns of species co-occurrence, i.e., checkerboard distributions, are often regarded as evidence for competitive exclusion (Diamond, 1975; Gotelli and McCabe, 2002); however, in the present study, significant C-score values were obtained only when hosts of all age classes were examined. When these analyses were restricted to any particular age group, they were found to occur randomly with regard to com-

TABLE VII. Parasite species indicative of adult or calf hosts.

Species	Adults		Species	Calves	
	IV*	P value		IV*	P value
<i>Agriostomum gorgonis</i>	36.0	0.006	<i>Cooperia fuelleborni</i>	16.7	0.003
<i>C. acutispiculum</i>	80.0	0.001	<i>C. hungi</i>	28.8	0.001
<i>C. neitzi</i>	75.2	0.001	<i>Impalaia tuberculata</i>	32.7	0.006
<i>Elaeophora sagitta</i>	85.7	0.001	<i>Strongyloides papillosus</i>	20.8	0.001
<i>Haemonchus vegliai</i>	73.4	0.001	<i>Trichostrongylus deflexus</i>	64.0	0.001
<i>Calicophoron</i> sp.	35.1	0.001	<i>T. falculatus</i>	22.2	0.004

* IV = observed species indicator value.

petitive exclusion. Similarly, when the data matrix of kudus from ENP, which contained only adults, was examined for checkerboard distributions, the lack of co-occurrence was not detected. These results support the findings of Gotelli and Rohde (2002), who examined checkerboard patterns in the ectoparasite communities of marine fishes and found largely random co-occurrence patterns. They surmised that the life history characteristics of many parasites, i.e., small size and limited vagility, have prevented the saturation of ecological niches, and as a consequence, the interspecific interaction of parasites remains a rare phenomenon.

Although the nonrandom co-occurrence patterns found in this study are unlikely to be the result of competitive exclusion, this does not diminish their importance but rather serves to illustrate that parasite species in the greater kudu from KNP are segregated in ecological time. D. P. Pielou and E. C. Pielou (1968)

and Gotelli and Rohde (2002) noted that nonrandom co-occurrence patterns can arise in the absence of competition if there exists a level of site–host heterogeneity. These authors also warned that it is difficult, and often impossible, to distinguish between these 2 alternative hypotheses; however, the examination of co-occurrence patterns within, and among, different age-class hosts allows for a distinction between these 2 hypotheses. In the present study, it has been demonstrated that calf infracommunities harbor parasite assemblages that are compositionally distinct from those of adults and juveniles. It is therefore reasonable to suspect that the checkerboard distribution of parasites among all age classes is the result of differential associations of parasites with specific age-class hosts and not of a competitively structured community.

Fisher and Lindemayer (2002) have recently warned that blindly relying on *P*-values generated by null models in general and the nestedness temperature calculator in particular may lead to false conclusions. Their point is well taken and has been foreshadowed for several decades as the heart of 1 of the longest debates in community ecology (Lewin, 1983; Gotelli, 2000). Statistical significance acquired from null models does not necessarily equate with ecological significance and should not be used without a thorough understanding of the biology of a given system and the assumptions and limitations of the model. However, null models, like inferential statistics, are powerful tools, which can be used to gain insight that would be otherwise unavailable. Fisher and Lindemayer (2002) demonstrated that the nestedness temperature calculator may be susceptible to type I error with some data sets and thus may not be appropriate for communities composed primarily of ubiquitous and rare species or where statistical significance approaches the desired α -level. Despite the limitations of the nestedness temperature calculator, Fisher and Lindemayer (2002) acknowledge its usefulness as an analytical tool.

On the basis of this analysis, it can be concluded that the helminth parasites of the greater kudu from southern Africa show significant levels of association with hosts of a different geographic location and demography. As a result, parasite communities from these various groups can readily be distinguished from each other and lend a level of predictability to community patterns. Null model analyses displayed high levels of nonrandomness among infracommunities of KNP and suggest a higher-level order that can be attributed to both the accumulation of species over time and the segregation of species among different age-class hosts.

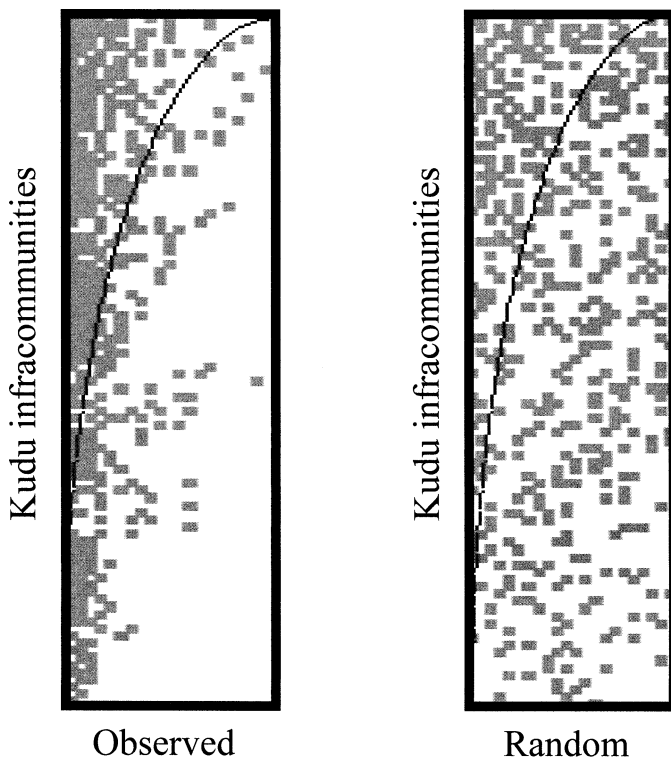


FIGURE 3. Maximally packed presence–absence matrices for observed kudu infracommunities from the Kruger National Park and 1 randomly generated community based on observed data.

TABLE VIII. Species co-occurrence summary for all helminths and enteric nematodes from Kruger and Etosha National Parks (C-obs = observed C-score value, C-sim = average C-score from randomized communities).

	All worms present			Enteric nematodes		
	C-obs	C-sim	P value	C-obs	C-sim	P value
KNP						
All kudu	92.1	83.6	0*	109.6	89.5	0*
Adults and juveniles	28.35	28.22	0.39	25.68	24.6	0.15
Calves	8.9	8.7	0.28	11.29	11.1	0.23
ENP						
Adults	28.35	28.22	0.39	6.04	6.33	0.9

* None of the C-score values from the 5,000 randomized communities was greater than the observed C-score value.

LITERATURE CITED

- ATMAR, W., AND B. D. PATTERSON. 1993. The measure of order and disorder in the distribution of species in fragmented habitat. *Oecologia* **96**: 373–382.
- , AND ———. 1995. Nested temperature calculator: A visual basic program, including 294 presence absence matrices. AICS Research, University Park, NM and The Field Museum Chicago, Illinois.
- BAILEY, J. K., AND T. G. WHITHAM. 2002. Interactions among fire, aspen, and elk affect insect diversity: Reversal of a community response. *Ecology* **83**: 1701–1712.
- BARGER, M. A., AND G. W. ESCH. 2001. Downstream changes in the composition of fishes in an Appalachian stream. *Journal of Parasitology* **87**: 250–255.
- BOOMKER, J. 1982. *Cooperia acutispiculum* n. sp. (Nematoda: Trichostrongylidae) from the kudu, *Tragelaphus strepsiceros* (Pallas, 1766). *Onderstepoort Journal of Veterinary Research* **49**: 95–97.
- . 1991. A comparative study of the helminth fauna of browsing antelope of South Africa. D.V.Sc. Thesis. Medical University of Southern Africa, Pretoria, South Africa, 297 p.
- , I. G. HORAK, AND D. G. BOOYSE. 1997. Parasites of South African wildlife. XV. Helminths of scrub hares, *Lepus saxatilis* in the Kruger National Park. *Onderstepoort Journal of Veterinary Research* **64**: 285–290.
- , ———, AND V. DE VOS. 1986. The helminth parasites of various artiodactylids from some South African nature reserves. *Onderstepoort Journal of Veterinary Research* **53**: 21–24.
- , ———, AND ———. 1989. Parasites of South African wildlife. IV. Helminths of kudu, *Tragelaphus strepsiceros*, in the Kruger National Park. *Onderstepoort Journal of Veterinary Research* **56**: 111–121.
- , ———, AND M. M. KNIGHT. 1991. Parasites of South African wildlife. IX. Helminths of kudu, *Tragelaphus strepsiceros*, in the eastern Cape Province. *Onderstepoort Journal of Veterinary Research* **58**: 203–204.
- BROWN, J. H., AND M. V. LOMILINO. 1998. *Biogeography*, 2nd ed. Sinauer Associates, Sunderland, Massachusetts, 691 p.
- DIAMOND, J. 1975. Assembly of species communities. In *Ecology and evolution of communities*, M. L. Cody and J. M. Diamond (eds.). Harvard University Press, Cambridge, Massachusetts, p. 342–444.
- ESCH, G. W., AND J. C. FERNANDEZ. 1993. A functional biology of parasitism: Ecological and evolutionary implications. Chapman and Hall, New York, 337 p.
- FERNANDEZ-JURICIC, E. 2002. Can human disturbance promote nestedness? A case study with breeding birds in urban habitat fragments. *Oecologia* **131**: 269–278.
- FISHER, J., AND D. B. LINDEMAYER. 2002. Treating the nestedness temperature calculator as a “black box” can lead to false conclusions. *Oikos* **99**: 193–199.
- GOTELLI, N. J. 2000. Null model analysis of species co-occurrence patterns. *Ecology* **81**: 2606–2621.
- . 2001. Research frontiers in null model analysis. *Global ecology and biogeography* **10**: 337–343.
- , AND G. L. ENTSMINGER. 1999. EcoSim: Null model software for ecology, version 4.0. Acquired Intelligence and Keesey-Bear.
- , AND D. J. MCCABE. 2002. Species co-occurrence: A meta-analysis of J.M. Diamond’s assembly rules model. *Ecology* **83**: 2091–2096.
- , AND K. ROHDE. 2002. Co-occurrence of ectoparasites of marine fishes: A null model analysis. *Ecology Letters* **5**: 86–94.
- GOÛY DE BELLOCQ, J., S. MORAND, AND C. FELIU. 2002. Patterns of parasite species richness of Western Palaearctic micro-mammals: Island effects. *Ecography* **25**: 173–183.
- GRENFELL, B. T., K. WILSON, V. S. ISHAM, H. E. G. BOYD, AND K. DIETZ. 1995. Modelling patterns of parasite aggregation in natural populations: Trichostrongylid nematode-ruminant interactions as a case study. *Parasitology (Suppl.)* **111**: S135–S151.
- GUÉGAN, J. F., AND B. HUGUENY. 1994. A nested parasite species subset pattern in tropical fish: Host as major determinant of parasite infracommunity structure. *Oecologia* **100**: 184–189.
- HORAK, I. G. 1980. The incidence of helminths in pigs, sheep, cattle, impala and blesbok in the Transvaal. Ph.D. Thesis. University of Natal, Durban, South Africa, 201 p.
- , V. DE VOS, AND M. R. BROWN. 1983. Parasites of domestic and wild animals in South Africa. XVI. Helminth and arthropod parasites of blue and black wildebeest (*Connochaetes taurinus* and *Connochaetes gnou*). *Onderstepoort Journal of Veterinary Research* **50**: 243–255.
- JANOVY, J. JR. 2002. Concurrent infections and the community ecology of helminth parasites. *Journal of Parasitology* **88**: 440–445.
- LEWIN, R. 1983. Santa Rosalia was a goat. *Science* **221**: 636–639.
- MCCUNE, B., AND M. J. MEDFORD. 1999. PC-ORD. Multivariate analysis of ecological data, version 4. MJM Software Design, Glendale Beach, Oregon, 237 p.
- MONCOL, D. J., AND M. J. GRICE. 1974. Transmammary passage of *Strongyloides papillosus* in the goat and sheep. *Proceedings of the Helminthological Society of Washington* **41**: 1–4.
- MÖNNIG, H. O. 1932. Wild antelope as carriers of nematode parasites of vertebrates. Part II. 18th report of the Director of Veterinary Services and Animal Industry. Department of Agriculture, Pretoria, South Africa, p. 153–172.
- OWEN-SMITH, N., AND S. M. COOPER. 1987. Palatability of woody plants to browsing ruminants in a South African savannah. *Ecology* **68**: 319–331.
- PATTERSON, B. D., AND W. ATMAR. 1986. Nested subsets and the structure of insular mammalian faunas and archipelagos. *Biological Journal of the Linnean Society* **28**: 65–82.
- PIELOU, D. P., AND E. C. PIELOU. 1968. Association among species of infrequent occurrence: The insect and spider fauna of *Polyporus betulinus* (Bulliard) Fries. *Journal of Theoretical Biology* **21**: 202–216.
- POULIN, R. 1997. Species richness of parasite assemblages: Evolution and patterns. *Annual Review of Ecology and Systematics* **28**: 341–358.
- , AND E. T. VALTONEN. 2001. Nested assemblages resulting from

- host size variation: The case of the endoparasite communities in fish hosts. *International Journal for Parasitology* **31**: 1194–1204.
- REINECKE, R. K. 1983. *Veterinary helminthology*. Butterworths, Durban, South Africa, 392 p.
- ROBERTS, M. G., A. P. DOBSON, P. ARENBERG, G. A. DE LEO, R. C. KRECK, M. T. MANFREDI, P. LANFRANCHI, AND E. ZAFFARONI. 2002. Parasite community ecology and biodiversity. *In* *The ecology of wildlife diseases*, P. J. Hudson, A. Rizzoli, B. T. Grenfell, H. Heesterbeek, A. P. Dobson (eds.). Oxford University Press, New York, p. 63–82.
- SIMBERLOFF, D., AND J. L. MARTIN. 1991. Nestedness of insular avifaunas: Simple summary statistics masking complex species patterns. *Ornis Fennica* **68**: 178–192.
- ŠIMKOVÁ, A., M. GELNAR, AND S. MORAND. 2001. Order and disorder in ectoparasite communities: The case of congeneric gill monogeneans (*Dactylogyrus* spp.). *International Journal for Parasitology* **31**: 1205–1210.
- SIMMONS, R. E. 1996. Population declines, viable breeding areas, and management options for flamingos in southern Africa. *Conservation Biology* **10**: 504–514.
- STONE, L., AND A. ROBERTS. 1990. The checkerboard score and species distributions. *Oecologia* **85**: 74–79.