A comparison of the helminth communities in *Anas undulata*, *Anas erythrorhyncha*, *Anas capensis* and *Anas smithii* at Barberspan, South Africa

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ABSTRACT

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Examination of the helminth communities in 25 yellow-billed ducks (*Anas undulata)*, 21 red-billed ducks (*Anas erythrorhyncha)*, ten Cape teal (*Anas capensis*) and seven Cape shovellers (*Anas smithii)* that had overwintered at Barberspan, revealed differences in community structure. Infracommunities in yellow-billed and red-billed ducks were characterized by low diversity and high eveness, and generally consisted of less than 100 helminths per duck. Similarity values (mean percent similarity and mean Jaccard's coefficients) were low. In contrast, infracommunities in Cape teal and Cape shovellers were more diverse, displayed low eveness values and consisted of far greater numbers of helminths. Mean similarity values for the infracommunities in Cape teal and Cape shovellers were much higher than those in yellow-billed or red-billed ducks. The component communities in all four duck hosts were species rich. Those in yellow-billed and red-billed ducks, however, consisted predominantly of satellite species and no core species were present, whereas those in Cape teal and Cape shoveller included several core species. Cape teal and Cape shovellers each had a group of recurrent species but there was not much of a tendency for species to co-occur in yellow-billed and red-billed ducks. Multivariate analysis revealed a greater similarity between the communities in Cape teal and Cape shovellers than between the latter and the communities in yellow-billed or red-billed ducks. Communities in Cape teal and Cape shovellers could be distinguished from each other by the presence or absence of particular cestode species. The communities in these two species could be distinguished from those in yellow-billed or red-billed ducks by a suite of cestode species that was absent in the latter two. Two recurrent groups, consisting of eight and two species, were identified in the compound community. Each group consisted of species found predominantly in Cape teal and Cape shovellers. Patterns seen in the helminth communities of the various hosts reflected differences in diet, but other factors, including feeding behaviour, spatial segregation and host specificity, may also have had an effect.

Keywords: *Anas*, Barberspan, *capensis*, *erythrorhyncha*, helminth, *smithii*, *undulata*

INTRODUCTION

During the past decade, several studies have been conducted to examine the structure of helminth communities in aquatic birds. In general, helminth communities of aquatic birds are species rich and consist of large numbers of individuals (Bush, Aho & Kennedy 1990). Although most studies address helminth communities within a single host species, two have been conducted on the helminth communities in sympatric species. Stock & Holmes (1987) found that different species of grebes have distinctive communities, and concluded that host specificity and food habits play significant roles in defining and maintaining the communities in these birds. Fedynich, Pence & Bergan (1996) also found differences in the helminth communities in two species of whistling ducks and suggested that feeding behaviour was the important

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factor in determining the pattern and structure of helminth communities in these hosts. While several factors may contribute to the structure of helminth communities in different host species, feeding behaviour and diet seem to have the greatest influence.

Wetlands are shared by a variety of waterfowl species and, despite mechanisms that reduce competition, temporal, spatial and dietary overlaps occur. Contamination of a wetland by one host species results in exposure of others, providing an opportunity for exchange of helminths among hosts (cf. Nerassen & Holmes 1975; Stock & Holmes 1987). Most helminths that infect waterfowl require crustacean or molluscan intermediate hosts for transmission (cf. McDonald 1969), and both the diversity of the helminth community and the magnitude of the infections in a particular host species depend to a large extent on the kind and quantity of animal matter present in the diet. However, the composition of the host community is also important (Nerassen & Holmes 1975; Edwards & Bush 1989). The compound community (i.e. the local populations of potential definitive and intermediate hosts) has an important influence on the community patterns in a particular species because of the mix of helminth communities it supports (Edwards & Bush 1989).

Barberspan is an important moulting and wintering site for waterfowl in the North West (Skead & Dean 1977). Fifteen species have been reported from Barberspan, with peak numbers occurring during the dry winter season (Milstein 1975; Skead & Dean 1977). Eight species, including the yellow-billed duck (*Anas undulata)*, red-billed duck (*A. erythrorhyncha*), Cape teal (*A. capensis*), Cape shoveller (*A. smithii*), South African shelduck (*Tadorna cana*), southern pachard (*Netta erythrophthalma*), Egyptian goose (*Alopochen aegyptiacus*) and spur-winged goose (*Plectropterus gambensis),* concentrate in varying numbers at Barberspan during this period; seven other species occur as vagrants (Milstein 1975; Skead & Dean 1977). Most data on helminth communities are from hosts collected in the northern temperate regions (Bush *et al.* 1990), and the concentration of waterfowl at Barberspan afforded a unique opportunity to examine the helminth communities in anatid species from a single wetland complex in the Southern hemisphere.

We selected yellow-billed ducks, red-billed ducks, Cape teal and Cape shovellers for study because, taxomonically and ecologically, they are more closely related to each other than to the other species at Barberspan, and because their local distribution and food habits have been documented (Milstein 1975; Skead & Dean 1977; Mitchell 1983; Skead & Mitchell 1983; Skead, unpublished data).

In this study we examined the helminth communities of each species in detail, as well as the impact of each host on the helminth communities of the others. Details of the helminth infections in each species and pertinent host and geographic records have been presented elsewhere (Alexander & McLaughlin 1997).

MATERIALS AND METHODS

Twenty-five yellow-billed ducks, 21 red-billed ducks, ten Cape teal and seven Cape shovellers were collected at Barberspan and adjacent Leeuwpan in November and December, 1979. The ducks were collected in numbers proportional to their local abundance. Most of the yellow-billed and red-billed ducks were collected at Barberspan, but a few individuals were collected at Leeuwpan. Cape teal and Cape shoveller, which occur in much smaller numbers, were collected only at Leeuwpan. Details of the collection, preservation and identification proceedures used in this study can be found in Alexander & McLaughlin (1997).

All the helminths present in yellow-billed and red-billed ducks were collected at necropsy and fixed individually for subsequent identification and counting. Owing to the large numbers of small cestodes present in Cape teal and Cape shovellers, only a sample from each bird was fixed specifically for taxonomic work. The remaining specimens, still in the gut contents, were fixed for counting. On completion of the taxonomic sample, the larger species were removed from the preserved gut contents and identified. The gut contents, which contained the remainder of the smaller species, were measured volumetrically and three 1-mℓ subsamples were taken. All the helminths in each subsample were stained, identified and counted. The mean number of each species in the three subsamples was then used to estimate the total number of each species present in the host. Although the numbers of the smaller species in these hosts are estimates, they are a reasonable reflection of the numbers in each bird.

The terms prevalence, abundance and intensity follow Margolis, Esch, Holmes, Kuris & Schad (1982). The terms infracommunity, component community and compound community follow Holmes & Price (1986). Infracommunity refers to the helminth community within an individual host, component community refers to the infracommunities within a host population and compound community refers to the helminth communities within the community of hosts.

Brillouin's index and an eveness index (J) were calculated for each individual and averaged over the sample of each host species. Mean percent similarity and mean Jaccard's coefficients were calculated for all pairwise combinations of host individuals to compare the similarity of helminth communities within and between host species (Bush 1990).

Hanski (1982) introduced the concept of core and satellite species. Core species are common, locally abundant and well distributed in niche space, whereas satellite species are not. Bush & Holmes (1986) applied this concept to helminth communities and identified a third category, which they designated as secondary species, that had characteristics intermediate between those of core and satellite species. Following Bush & Holmes (1986), species with prevalences of 70% were considered core species, those with prevalences of < 40% as satellite species and those with intermediate prevalences (≥ 40% but < 70 %) as secondary species.

Recurrent group analysis (RGA) (Fager 1957; Fager & McGowan 1963), corrected for sample size (Hayes 1978), was performed on the component communities in each host species and on the entire data set. Briefly, an affinity index is calculated on the proportion of joint occurrences of a species pair corrected for sample size. This can be used to identify groups of species that regularly co-occur in the same birds (Stock & Holmes 1987). Species pairs with indices of ≥ 0,5 are considered to demonstrate affinity, while those below this value are not. The dichotomy permits definition of the largest group within which all possible pairs of species show affinity (i.e. the recurrent group). More than one recurrent group is possible (Fager & McGowan 1963). Applications of RGA in the analysis helminth communities can be found in Custer & Pence (1981), Stock & Holmes (1987) and Radomski & Pence (1993). Following Stock & Holmes (1987), species that were positively associated with some, but not all, of the recurrent group members were designated as associate species.

As we were interested in the presence or absence of species in the different hosts, we performed hierarchical cluster analysis on binary transformed data. The abundance data for most species were strongly overdispersed and attempts to normalize the data met with limited success. Rank transformations provided the best approximations of univariate and multivariate normality. Principle-components analysis (PCA) was performed on the covariance matrix of the rank-transformed data in an attempt to detect any underlying patterns in the abundance data.

RESULTS

The helminth species encountered, their status (core, secondary or satellite), their occurrence in recurrent groups in the component community of each host species, their occurrence in the recurrent groups in the compound community and their factor loadings from the principal-components analyses are presented in Table 1. Overall, the component communities in each host were species rich, ranging from 13–20 species (Tables 1 and 2).

The general characteristics of the infracommunities in each host species are summarized in Table 2 and in Fig. 1–3. Infracommunities in yellow-billed and red-billed ducks differed fundamentally from those in Cape teal and Cape shoveller. Those in yellow-billed and red-billed ducks were less diverse (lower mean Brillouin's indices) and had higher mean eveness indices than those in Cape teal or Cape shovellers (Table 2). Yellow-billed and red-billed ducks had significantly fewer species and significantly fewer individuals per bird than Cape teal or Cape shovellers (Table 2, Fig. 1 and 2). Cape shovellers and Cape teal had comparable numbers of helminths per bird, but Cape teal had significantly more species.

Frequency distributions of the number of species and of the total number of helminths in each host species are shown in Fig. 1 and 2. All the red-billed ducks and about two-thirds of the yellow-billed ducks were infected by six or fewer species, whereas Cape teal and Cape shovellers had at least six species per bird (Table 2, Fig. 1). Yellow-billed and red-billed ducks typically had fewer than 100 helminths per bird. The number of helminths in individual Cape shovellers was more variable. However, three of the shovellers and all but one of the Cape teal had in excess of 1 000 worms (Fig. 2).

The mean percent similarity and the mean Jaccard's coefficients were lower for yellow-billed and red-billed ducks than for Cape teal and Cape shovellers (Fig. 3). Comparison of the mean percent similarities and mean Jaccard's coefficients between pairs of host species revealed little overall similarity between the communities in yellow-billed and red-billed ducks and even less similarity between the communities in either of these species and those in Cape teal or Cape shovellers. In contrast, the mean scores for the teal-shoveller comparisons were much higher, indicating a greater number of shared species. Curiously, the mean scores for the yellow-billed versus red-billed duck comparisons were slightly greater than the mean within scores for yellow-billed ducks.

The frequency distributions of the prevalences of helminth species in each host species were bimodal (Fig. 4) and there was a significant, positive correlation between prevalence and intensity of infection in each host species (Kendall's rank correlation; $P < 0,05$ for yellow-billed ducks, $P < 0,005$ for red-billed ducks and Cape shovellers, and $P < 0,0005$ for Cape teal). Both assumptions of Hanski's (1982) core-satellite hypothesis were therefore met. The component communities of yellow-billed and red-billed ducks consisted almost entirely of satellite species; there were no core species, and only four and five secondary species, respectively, were present (Table 1, Fig. 4). Ten of 18 species in Cape teal and eight of 13 species in Cape shovellers were core species. Cape teal and Cape shoveller had six and five satellite species, respectively; Cape teal also had two secondary species (Table 1, Fig. 4).

TABLE 1 Summary of associations of helminths found in *Anas undulata, Anas erythrorhyncha, Anas capensis and Anas smithii* collected at Barberspan, South Africa

Associations of helminths	*Anas undulata*	*Anas erythro-rhyncha*	*Anas capensis*	*Anas smithii*	Recurrent group	Factor loading	
						PC 1	*PC 2*
Digenea							
Apatemon minor	2	2 a				–0,52	0,40
Echinoparyphium elegans	S	S	S			–0,18	0,29
Catatropis orientalis		S	S	S		0,23	–0,16
Hypoderaeum conoideum	S					0,43	0,04
Zygocotyle lunata	S					–0,08	0,08
Cestoda							
Platyscolex ciliata	S					–0,18	0,36
Cloacotaenia megalops	2	2 r	C a	C r	Rs,a	0,44	–0,49
Dicranotaenia coronula	S		S a			0,19	0,51
Diorchis flavescens	S		C r	S	Rl	0,72	0,30
Diorchis (23)*			C r	S	Rl	0,81	0,35
Diorchis (43)*			S			0,11	0,07
Diorchis (60)*	S	S				–0,20	0,34
Diorchis (68)*	S	S				–0,26	0,20
Echinocotyle capensis			C r	C r	Rl	0,97	0,04
E. clerci			C r	C r	Rl	0,94	0.01
E. rosseteri			C r		Rl	0,76	0,36
Echinocotyle (36)*				C r		0,46	–0,40
Fimbriaria fasciolaris		S				–0,07	0,04
Fimbriasacculus africanensis	S	S	2 a			0,40	0,31
Gastrotaenia cygni	S	2	C r	C r	a	0,72	–0,13
Microsomacanthus macrotesticulata	S a	S				–0,16	0,32
M. spiralicirrata	S a	S	C r	C r	Rl	0,79	0,33
M. teresoides		S				–0,08	–0,14
Microsomacanth us (25)*	S					–0,18	0,32
Skrjabinoparaxis tatianae		S	C r	C	Rl	0,95	–0,01
Sobolevicanthus gracilis	S a	S				–0,35	0,43
S. transvaalensis			C r		Rl	0,77	0,37
dilepid sp.				S		0,24	–0,15
Nematoda							
Amidostomum acutum	S					–0,19	0,37
Epomidiostomum uncinatum	2 a	2	S	S		–0,35	0,41
Tetrameres crami	2					–0,46	–0,10
T. ryjikovi		2 r	2 r	C r	Rs	0,70	–0,01
Tetrameres sp.	S					–0,15	0,22
Capillaria contorta		S	S			0,08	–0,15

* Numbers following generic names of cestodes refer to the lengths of the rostellar hooks

Abbreviations: C = core species
2 = secondary species
S = satellite species
Rl = member of the large recurrent group in the compound community
Rs = member of the small recurrent group in the compound community
r = recurrent group member in component community
a = associate species

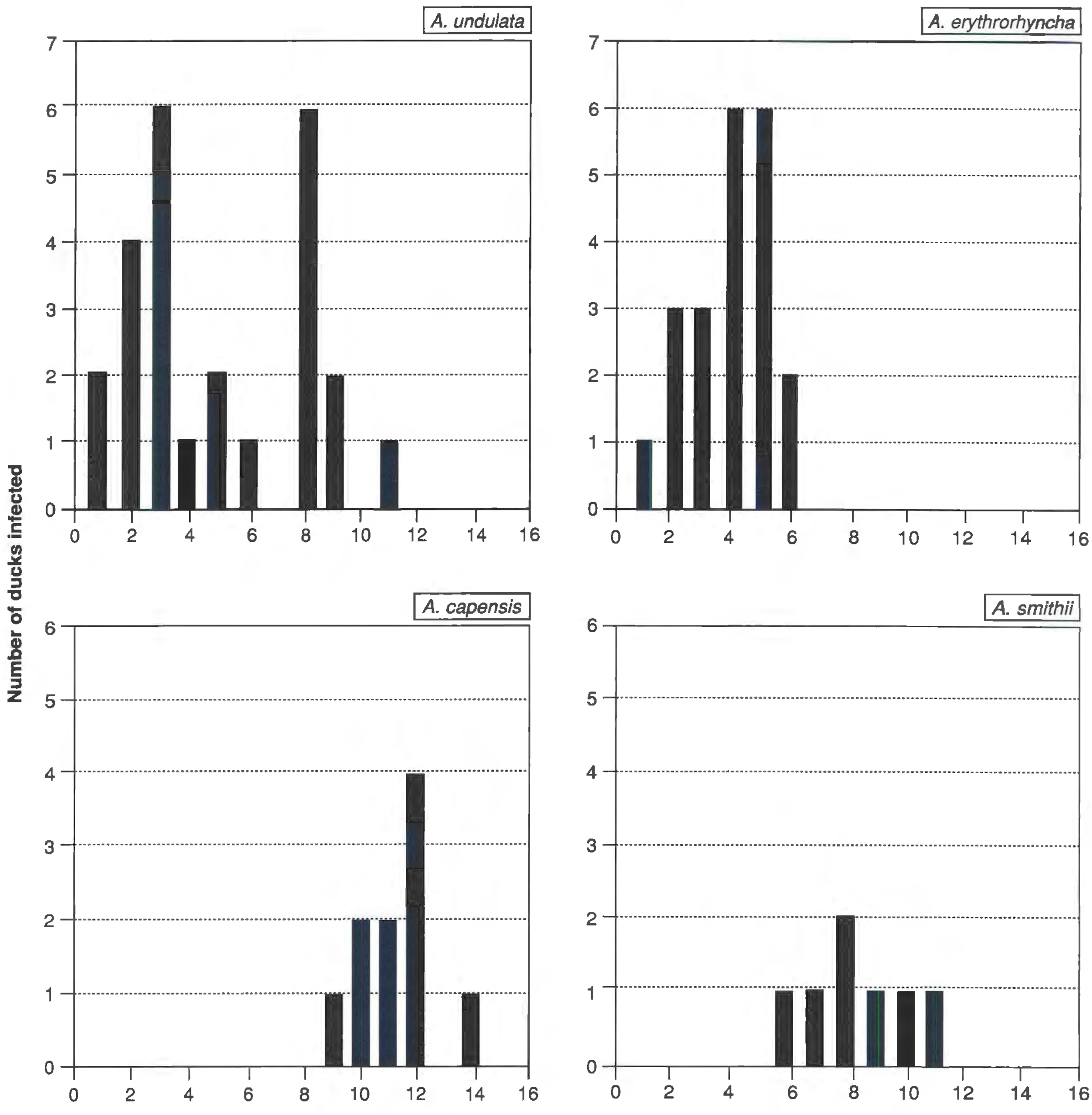

FIG. 1 Frequency distributions of the total number of helminth species found in individual ducks at Barberspan. The vertical bars indicate the number of individuals in the sample infected by a particular number of helminth species

Recurrent groups were identified in Cape teal, Cape shoveller and red-billed ducks. The largest recurrent group occurred in Cape teal and consisted of ten species (nine core and one secondary species). Three associate species (including one core, one secondary and one satellite species) were also identified in Cape teal (Table 1). Cape shovellers and red-billed ducks had smaller recurrent groups consisting of seven and two species, respectively (Table 1). All the recurrent species in shovellers were core species, and those in red-billed ducks were secondary species. There was no recurrent group in yellow-billed ducks, but five associate species were identified (Table 1).

Hierarchical cluster analysis performed on presence-absence data for the entire sample confirmed differences in the species composition of the infracommunities suggested by the mean Jaccard's coefficients. The infracommunities in Cape teal and Cape shovellers differed from each other and from those in

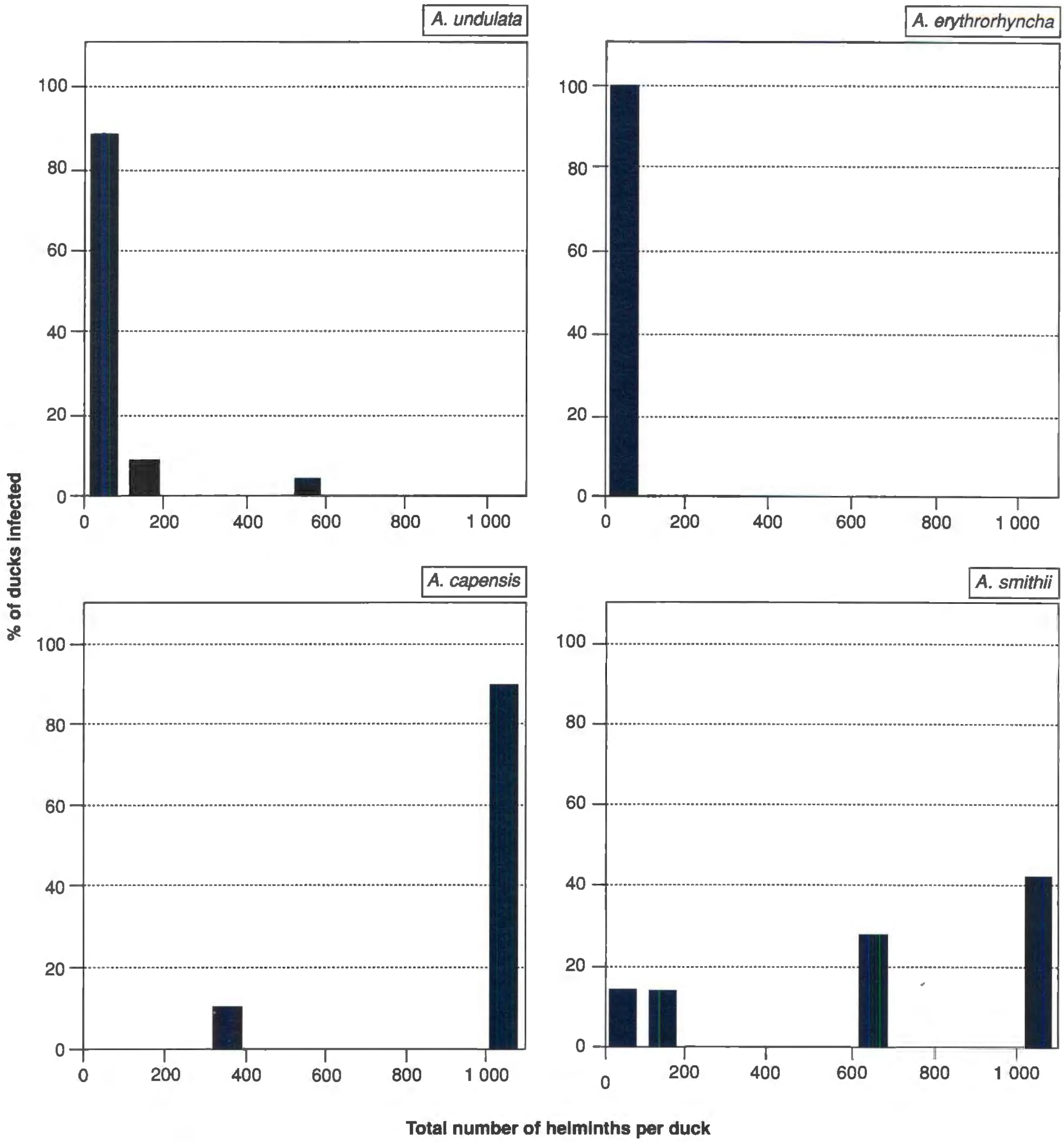

FIG. 2 Frequency distributions of the total number of helminths (digeneans, cestodes and nematodes) in individual ducks at Barberspan. The x axis displays the total helminth load by class size (0–100, 101–200, etc. to 1 000+ helminths per duck). The y axis represents the percentage of individuals within each sample with helminth loads within a particular size class

yellow-billed ducks and red-billed ducks (Fig. 5) (cophenetic correlation coefficient = 0,86). The infracommunities of the latter two species could not be resolved into distinct groups.

Yellow-billed ducks and red-billed ducks shared 11 species. Three, *Cloacotaenia megalops, Apatemon minor* and *Epomidiostomum uncinatum*, were secondary species in both hosts; *Gastrotaenia cygni* was a secondary species in red-billed ducks. The remaining seven species were satellite species. Eleven of the 13 species in Cape shovellers also occurred in Cape teal and six of these were core species in both host species. Cape teal shared ten species with red-billed ducks and eight species with yellow-billed ducks. Five of the species shared with each host were core species in Cape teal. Cape shovellers shared seven species with red-billed ducks and five species with yellow-billed ducks. Five and three species, respectively, were core species in Cape shovellers.

Principal-component analyses revealed that the infracommunities in Cape teal and Cape shovellers could be distinguished from each other and from those in yellow-billed and red-billed ducks, but that the infracommmunities in the latter two species overlapped extensively (Fig. 6). The first three components accounted for 54% (37, 9 and 8%, respectively) of the variance in the covariance matrix.

The factor loadings for each species on PC1 and PC2 are shown in Table 1. PC1 separated the helminth communities of yellow-billed ducks and red-billed ducks from those in Cape teal and Cape shovellers. Helminths with heavy positive loadings on PC1 (> 0,7; n = 10) were parasites of Cape teal or Cape shovellers. *Diorchis* (23), *Echinocotyle capensis* and *E. clerci* were present in both species; *E. rosseteri* and *Sobolevicanthus transvaalensis* occurred exclusively in Cape teal.

Five other species; *Diorchis flavescens*, *G. cygni*, *Microsomacanthus spiralicirrata*, *Skrjabinoparaksis*

Mean % similarity (± SE)

	Au	Ae	Ac	As
Au	17,8 (0,9) / 0,19 (0,01)	20,3 (0,8)	4,1 (0,4)	5,3 (0,5)
Ae	0,21 (0,01)	29,9 (1,6) / 0,27 (0,01)	2,3 (0,3)	5,6 (0,6)
Ac	0,09 (0,01)	0,11 (< 0,01)	55,7 (2,7) / 0,72 (0,02)	30,4 (1,8)
As	0,11 (0,01)	0,14 (0,01)	0,47 (0,01)	42,1 (3,8) / 0,69 (0,08)

Mean Jaccard's (± SE)

FIG. 3 Mean percent similarity and mean Jaccard's coefficients (± SE) for helminth infracommunities of four species of ducks at Barberspan. Values above the diagonal are mean percent similarities; values below the diagonal are mean Jaccard's coefficients. Intraspecific comparisons are shown in the boxes on the diagonal; interspecific comparisons shown in the boxes above (mean percent similarity) and below (mean Jaccard's coefficient) the diagonal

Abbreviations: Au, Ae, Ac and As represent *Anas undulata*, *A. erythrorhyncha*, *A. capensis* and *A. smithii*, respectively

tatianiae and *Tetrameres ryjikovi*, which were predominantly parasites of Cape teal and Cape shovellers, were occasional parasites of yellow-billed and red-billed ducks (Table 1). Twelve of 15 species with negative loadings were parasites of yellow-billed or red-billed ducks. The other three species (*Echinoparyphium elegans*, *Microsomacanthus macrotesticulata* and *Epomidiostomum uncinatum*) were also occasional parasites of Cape teal or Cape shovellers.

The interpretation of PC2 is more tenuous. PC2 seems to separate the communities in Cape teal and Cape shoveller. Among the species with the higher positive loadings (> 0,3; n = 14) on PC2 were three that infected Cape teal but not Cape shovellers (*Dicranotaenia coronula*, *Echinocotyle rosseteri*, and *Sobolevicanthus transvaalensis*) and three that were predominantly parasites of Cape teal but occasionally infected other hosts (*Diorchis* 23, *D. flavescens* and *Fimbriasacculus africanensis*). The remaining species with positive loadings were predominantly parasites of yellow-billed or red-billed ducks. Two species with heavier negative loadings on PC2 also appeared to contribute to the separation of the communities in Cape teal and Cape shovellers. *Echinocotyle* 36 occurred only in Cape shovellers. *C. megalops* infected all four duck species, but was three to ten times more abundant in Cape shovellers than in the others (Alexander & McLaughlin 1997), and it is evident that shovellers are the predominant host of this cestode. PC3 failed to provide any further resolution and was excluded.

Results of the RGA for the total sample are presented in Fig. 7. Two recurrent groups, consisting of eight and two species, were identified. All the members of the larger recurrent group were core species in Cape teal and four were core species in Cape shovellers (Table 1). Three of the species in this group also occurred as satellite species in yellow-billed or red-billed ducks. The smaller recurrent group consisted of *C. megalops*, a core species in Cape teal and Cape shovellers and a secondary species in the others, and *T. ryjikovi*, a core species in Cape shovellers and a secondary species in red-billed ducks and Cape teal. *C. megalops* was an associate species of *S. tatianae* and *M. spiralicirrata* in the larger recurrent group. *G. cygni*, a core species in Cape teal and Cape shovellers and a secondary and satellite species in red-billed and yellow-billed ducks, respectively, was an associate of the four core species shared by Cape teal and Cape shoveller in the larger recurrent group.

DISCUSSION

Helminth communities in aquatic birds are species rich and typically consist of large numbers of individuals (Bush *et al.* 1990). Although the component communities in all four ducks were species rich, those in

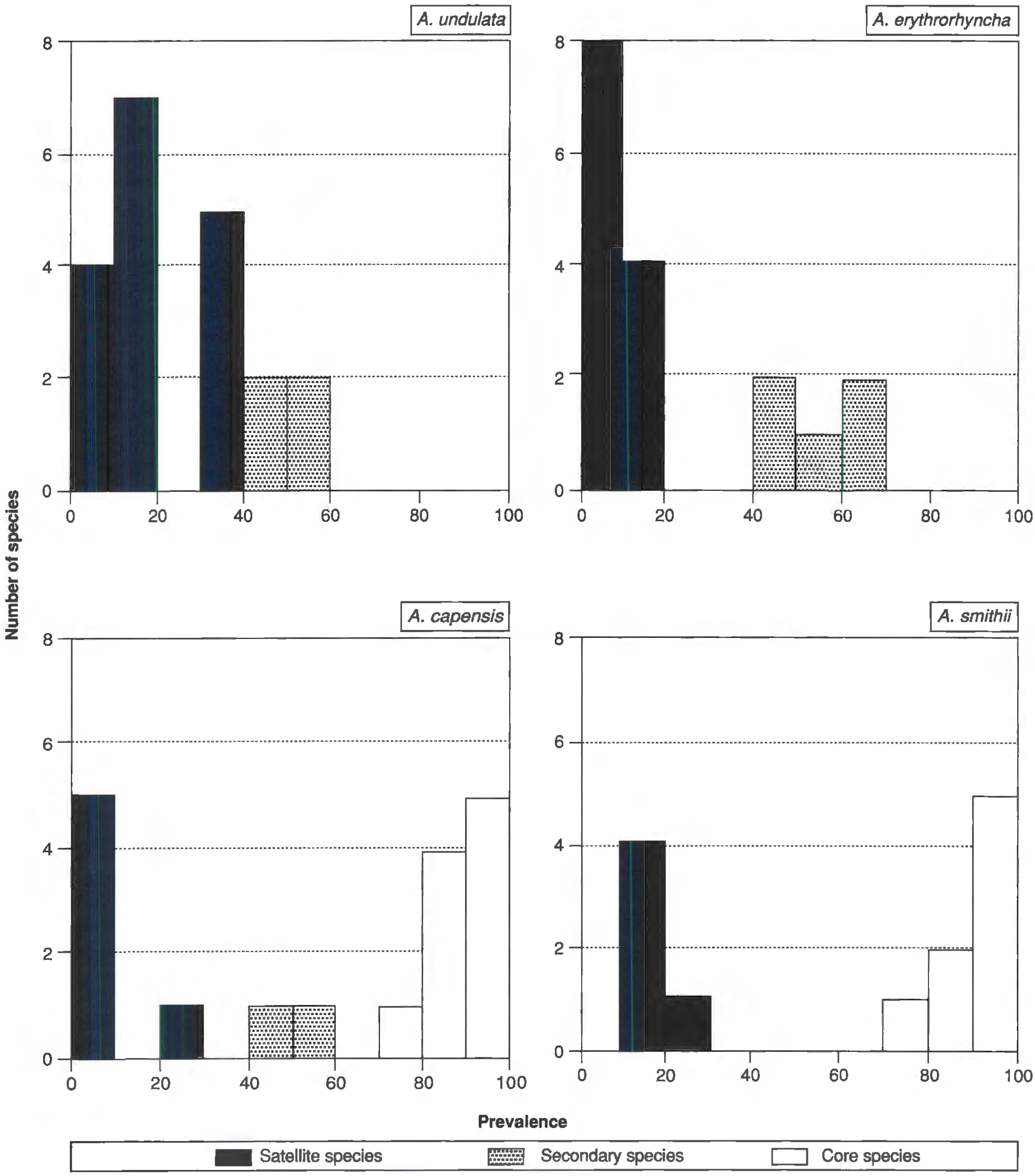

FIG. 4 Frequency distributions of prevalences of gastrointestinal helminth species in four species of ducks at Barberspan

yellow-billed and red-billed ducks differed qualitatively and quantitatively from those in Cape teal and Cape shovellers. The component communities in yellow-billed and red-billed ducks were dominated by satellite species and no core species were present, whereas approximately half of the species present in Cape teal and in Cape shovellers were core species. Recurrent groups of helminth species were present in Cape teal and Cape shovellers but there was little tendency for species in yellow-billed or red-billed ducks to co-occur.

Infracommunities in yellow-billed and red-billed ducks were characterized by lower diversity, higher eveness

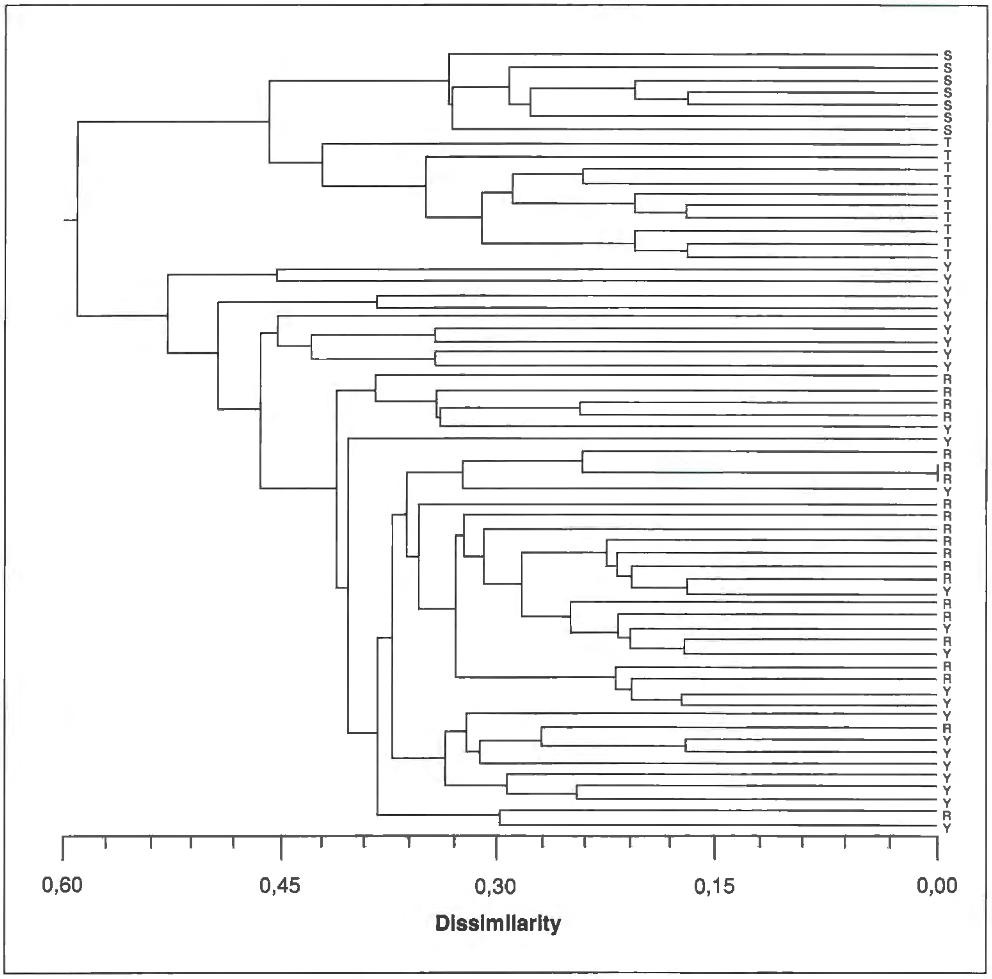

FIG. 5 Hierarchical cluster analysis of the presence-absence data of helminth species found in four species of ducks at Barberspan

Abbreviations: Y, R, T and S represent *Anas undulata*, *A. erythrorhyncha*, *A. capensis* and *A. smithii*, respectively

TABLE 2 Comparison of helminth infections found in *Anas undulata, Anas erythrorhyncha, Anas capensis and Anas smithii* from Barberspan, South Africa

Details compared	*Anas undulata*	*Anas erythro-rhyncha*	*Anas capensis*	*Anas smithii*
Number examined	25	21	10	7
Total number of species	20	17	18	14
Mean number of species (SD)	5,0 (3,00)^{a}	3,9 (1,40)^{9}	11,3 (1,40)^{9}	8,4 (1,70)^{9}
Range in species number	1–11	1–6	9–14	6–11
In mean number of helminths (SD)	4,0 (4,80)^{9}	2,9 (2,90)^{9}	8,5 (8,20)^{9}	8,3 (8,50)^{9}
Range in helminth number	3–581	2–79	372–10,396	92–13,052
Brillouin's Index (SD)	0,37 (0,22)	0,33 (0,13)	0,54 (0,11)	0,61 (0,07)
Evenness (SD)	0,71 (0,31)	0,74 (0,24)	0,52 (0,09)	0,68 (0,11)

Note: Values with different superscripts within each row differ significantly (ANOVA $P \leq 0,05$)

and small numbers of helminths. Similarity values (mean percent similarity and mean Jaccard's coefficients) were low. In contrast, infracommunities in Cape teal and Cape shoveller were more diverse, displayed lower eveness values and far greater numbers of helminths. Mean similarity values for the infracommunities in each species were much higher than in either yellow-billed or red-billed ducks. Overall, Cape

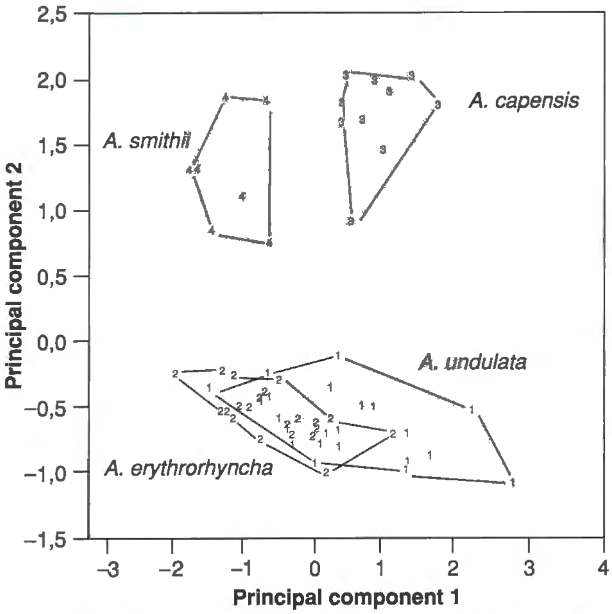

FIG. 6 Plot of the PC1 and PC2 scores of 63 ducks collected at Barberspan. Numerals: 1, 2, 3 and 4 represent infracommunities in *Anas undulata*, *A. erythrorhyncha*, *A. capensis* and *A. smithii*, respectively. PC1 and PC2 account for 37% and 9% of the variance in the covariance matrix

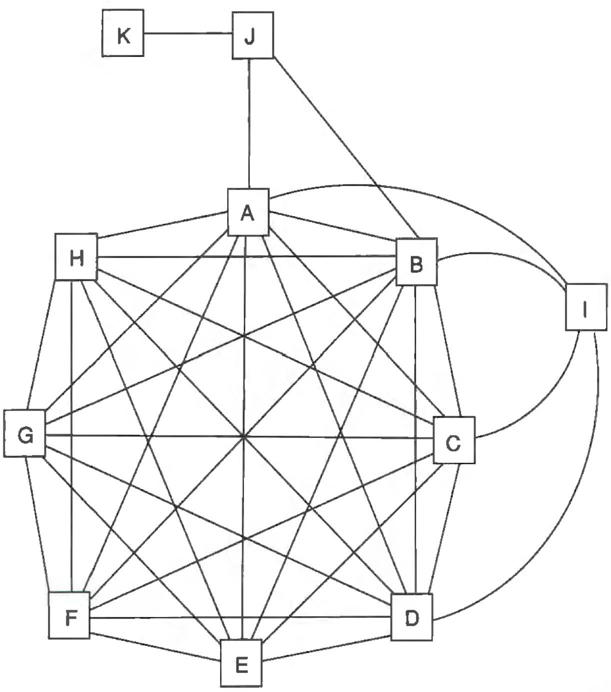

FIG. 7 Recurrent group analysis of the helminth species in 63 ducks (four species) collected at Barberspan. Recurrent group members are connected by thick lines; associate species (i.e. species associated with only some of the recurrent group members) are connected to those species by thin lines

Abbreviations: A, *S. tatianae*; B, *M. spiralicirrata*; C, *E. clerci*; D, *E. capensis*; E, *E. rosseteri*; F, *Diorchis* 23; G, *D. flavescens*; H, *S. transvaalensis*; I, *G. cygni*; J, *C. megalops*, K, *T. ryjikovi*

teal and Cape shovellers that had overwintered at Barberspan had predictable communities consisting of a group of core species that infected most hosts, usually in large numbers. This was not the case for yellow-billed or red-billed ducks. Whether changes occur in the communities of these hosts over the course of the summer, remains an open question.

Kennedy, Bush & Aho (1986) and Price (1990) discussed a number of factors essential for the production of diverse helminth-community patterns. Three of these, host vagility, host diet and selective feeding on potential intermediate hosts, are of significance here.

The vagility of a host may influence the component communities because species that move about sample more environments and are exposed to more sources of parasites than sedentary species (Price 1990). Cape teal and Cape shovellers were permanent residents of Leeuwpan and were rarely seen elsewhere during this study, whereas yellow-billed and red-billed ducks were widely distributed and evidently moved regularly from Barberspan to Leeuwpan and other local pans. The disparity in digenean infections between the two host groups seems to reflect greater movement by yellow-billed and red-billed ducks. Snails are absent at Barberspan but are present in nearby wetlands (Milstein 1975) which apparently served as infection foci for the more vagile duck species (Alexander & McLaughlin 1997).

Although host vagility can influence helminth communities to some degree, diet and feeding behaviour ultimately determine the extent of exposure to helminth larvae and are known to influence community patterns in sympatric hosts (Stock & Holmes 1987; Feydnych *et al.* 1996). Yellow-billed and red-billed ducks are generalist feeders that consume a variety of plant and animal foods at Barberspan (Mitchell 1983; Skead & Mitchell 1983; Skead, unpublished data). The animal component consists primarily of insects (Mitchell 1983; Skead, unpublished data) which are of little importance in the transmission of waterfowl helminths (McDonald 1969). Nevertheless, infection by a variety of digeneans, cestodes and nematodes, albeit lightly, is consistent with the view that species with varied diets have diverse communities (Kennedy *et al.* 1990; Price 1990). However, infracommunities in these host species had low diversity and few individuals. It appears that the same dietary variation that produces the diversity in the helminth community at the species level, limits both the probability and frequency of encounters with parasites at the individual level. Neither host specializes on any particular prey species, thus further limiting exposure to helminth larvae. This is reflected in the generally low prevalences and intensities seen for most helminth species (Alexander & McLaughlin 1997), the large proportion of satellite species and the lack of recurrent groups in these hosts.

Cape teal and Cape shovellers are carnivorous and much of their diet consists of entomostracans (ostracods and copepods); the rest consists mainly of aquatic insects (Mitchell 1983). Ordinarily, a restricted or specialized diet should reduce species richness (Price 1990). However, the number of component species in each of the four host species was the same, despite differences in sample size. This was due to the fact that Cape teal and Cape shovellers specialize on prey that serve as intermediate hosts of the hymenolepidid cestodes (McDonald 1969) that dominated the component communities in both host species (Alexander & McLaughlin 1997).

Cape teal and Cape shovellers had fewer digenean and nematode species than did yellow-billed or red-billed ducks, and these accounted for only a minute proportion of the total helminth loads found in these hosts (Alexander & McLaughlin 1997). Their presence in some individuals, usually in small numbers, suggests that ecological factors such as the more specialized diet and the more sedentary behaviour of these hosts limited exposure to these helminths.

Most core species in Cape teal and Cape shovellers were present in large numbers. Bush & Holmes (1986) found that lesser scaup (*Aythya affinis*) also had large populations of core species. Most of these were hymenolepidid cestodes that require amphipod intermediate hosts. Scaup are amphipod specialists (Bush & Holmes 1986) and naturally infected amphipods may support up to 250 cysticercoids (Podesta & Holmes 1970). Although not present in the numbers reported from scaup, most core species in Cape teal and Cape shovellers also occurred in large numbers. Copepods and ostracods were the only crustacean intermediate hosts available at Barberspan and Leeuwpan. Neither can support the numbers of cysticercoids reported for amphipods and consumption of enormous numbers of these crustaceans would be necessary to produce the helminth populations seen in some hosts.

Although specialization on a particular prey species increases the probability of exposure to particular parasites, feeding behaviour can also influence the frequency of contact with the infective pool and, ultimately, the magnitude of the infections that develop. Bush (1990) found that willets (*Catoptrophorus semipalmatus*; Charadriiformes) feeding on restricted beaches or on small sloughs where foraging space was limited, had heavier infections than did willets foraging in more open areas. Willets feeding on restricted beaches foraged back and forth over the same area, while those on open beaches did not. He concluded that repeated foraging in a restricted area would result in heavy exposure of the intermediate host populations to helminth eggs deposited by birds, and in heavier infections in birds, owing to increased exposure to infected intermediate hosts.

Cape teal and Cape shovellers spend more time feeding than other species do (Skead 1977), presumably because of the low energetic value of individual entomostracans. Feeding activity at Leeuwpan would be most intense in patches where entomostracans were abundant. Cape shovellers are known to feed cooperatively by "circle swimming" (Forbush 1925 in Siegfried 1965) during which they forage intensively (and repeatedly) in open water over a food patch. Cape teal feed in open water but also feed extensively around mud flats (Mitchell 1983) which could also restrict the feeding zone, perhaps increasing contact with infected crustaceans. Concentration of feeding activities in areas where prey is abundant would, as suggested by Bush (1990), ensure heavy contamination of the site, heavy infection of the intermediate host populations and, ultimately, more frequent exposure and heavier helminth loads in the definitive hosts.

Although yellow-billed and red-billed ducks shared 11 helminth species, the mean similarity values between their helminth communities were low. Most of the helminths shared were satellite species and the comparatively light infections preluded any significant impact of one host species on the helminth community of the other. Eleven of the 13 species found in Cape shovellers also infected Cape teal. Most of those shared were core or secondary species in both hosts. The overlap in diet and feeding zones at Leeuwpan, and the sedentary behaviour of these hosts, all contributed to a greater similarity in the helminth communities in these species. Each species contributed extensively to the infective pools at Leeuwpan and, through them, to the helminth communities of the other.

Despite the number of species shared by Cape teal and Cape shovellers, there were differences between the communities that reflected the presence of cestodes unique to one host or the other (*E. rosseteri, Echinocotyle 36, F. africanensis* and *S. transvaalensis*). While we acknowledge that, owing to the methods used, we may have failed to detect some of the smaller *Echinocotyle* spp. in some hosts, the consistent failure to recover them in the samples from a particular species suggests that they were indeed absent. Both *F. africanensis* and *S. transvaalensis*, however, are large, easily recognized species, and we are confident that neither was present in Cape shovellers. Because Cape teal and Cape shovellers share the majority of their cestode species, the presence of a species in one host but not the other, is noteworthy. Such species are either highly host specific or there is some ecological barrier to transmission. Approximately 33 and 15% of the diets of Cape teal and Cape shovellers consist of ostracods, while copepods make up about 3 and 40%, respectively (Mitchell 1983). The possibility of partial or complete partitioning of a parasite population exists if that species uses intermediate hosts that are either unavailable to different definitive hosts, or are consumed in different quantities by these hosts. This apparently occurred with *D. flavescens* and *Diorchis* 23, two core species in Cape teal, also found in one and two Cape shovellers, respectively (Alexander & McLaughlin 1997). While it is impossible to rule out host specificity, ecological explanations for the absence of *F. africanensis* and *S. transvaalensis* in Cape shovellers are possible. *Echinocotyle rosseteri*, found only in Cape teal in this study, infects other species of shovellers (McDonald 1969) and we are at a loss to explain its absence here.

Although Cape teal and Cape shovellers live in close proximity to, and interact to some extent with, yellow-billed and red-billed ducks, only 13 of the 34 species were shared between them. Of these species, six in yellow-billed and red-billed ducks or in Cape teal and Cape shovellers infected single individuals in the other host group (Alexander & McLaughlin 1997). Species that were shared more evenly between the two groups (*C. megalops*, *D. flavescens*, *M. spiralicirrata*, *S. tatianae*, *T. ryjikovi* and *G. cygni*) were core or secondary species in Cape teal or Cape shovellers. All but *G. cygni* were members of the recurrent groups in the compound community that were dominated by species characteristically found in Cape teal and Cape shovellers.

While dietary differences were a significant factor in defining the helminth communities in the two host groups, spatial factors may also have played a role. The two groups of ducks were, to some degree segregated spatially at Barberspan and Leeuwpan, and it follows that their infective pools were segregated as well. The greater vagility of yellow-billed and red-billed ducks would bring them into more frequent contact with infective pools at Leeuwpan than would have been the case for Cape teal and Cape shovellers at Barberspan. While yellow-billed ducks and red-billed ducks probably acquired parasites from various foci, both species probably acquired at least some of their infections at Leeuwpan. The data suggest that infective pools produced by Cape teal and Cape shovellers at Leeuwpan may be important sources for a small number of species found in yellow-billed and red-billed ducks, but otherwise have little impact on their helminth communities. Yellow-billed and red-billed ducks seem to have a negligible impact on the helminth communities of Cape teal and Cape shovellers.

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