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A Study of the Structure and Organization of Intestinal Helminth Communities in Ten Species of Waterfowl (Anatinae)

by

Eric Wynn Butterworth

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled A Study of the Structure and Organization of Intestinal Helminth Communities in Ten Species of Waterfowl (Anatinae) submitted by Eric Wynn Butterworth in partial fulfilment of the requirements for the degree of DOCTOR OF PHILOSOPHY.

J. Holmes

Supervisor

W. M. Samuel

External Examiner

Date February 9, 1982

ABSTRACT

The intestinal helminth communities of 97 birds representing 10 species of ducks (widgeon, Anas americana, gadwall, Anas strepera, mallard, Anas platyrhynchos, blue-winged teal, Anas discors, ruddy, Oxyura jamaicensis, canvasback, Aythya valisineria, ring-necked duck, Aythya collaris, lesser scaup, Aythya affinis, bufflehead, Bucephala albeola, white-winged scoter, Melanitta fusca) were compared along two resource axes: host (habitat) and intestine (microhabitat).

Parasite communities in duck species (i.e., widgeon) which eat a small proportion of animal foods had few species and individuals and showed little similarity between communities of birds of the same duck species. Parasite communities in duck species (i.e., scoter) which eat a high proportion of animal foods had a large number of species and individuals and showed high similarity between communities in birds of the same duck species. The parasite communities of the latter group are composed of three components (or groups of parasites). Characteristic species are frequent, usually abundant and mature exclusively or primarily in one host species. Other common species were either host generalists or specialists in other hosts. The characteristic and common parasite species provide most of the similarity and predictability between birds of the same duck species. The third group of parasites were infrequent in occurrence and are random elements in the parasite

communities.

For parasite communities in hosts with characteristic species cluster analyses indicated that the host species was the most important level of habitat. For parasite communities without characteristic species the multispecies host populations were the important habitat level.

The structure of the parasite communities along the second resource axis was investigated using the linear distributional features of the parasite species within the intestines of individual birds. Most parasite species occupied predictable and restricted locations within the intestine. Parasite species which occurred in more than one duck species generally occupied similar locations. In addition to the predictable locations occupied by the parasites, their sequence of occurrence along the gut was highly predictable. The arrangement of these locations was more uniform than expected by chance. Some parasite species were observed to occupy the entire intestine within individual birds while the average range occupied across all hosts infected was usually much less.

Realized niches were measured by distributions of helminth species in individual birds. Fundamental niches were estimated by distributions of helminth species in all individuals birds summed. For several pairs of parasite species realized niche overlaps (average overlaps) were reduced from the fundamental overlaps (summed overlaps). These significant reductions in realized niche overlap are

interpreted as evidence for interactions. The characteristic parasite species overlapped each other significantly less than the average overlap between other parasite species. This reduced overlap occurred despite the fact that characteristic species had significantly larger ranges than the other species. The characteristic species showed evidence for interactions when they overlapped. These parasites appeared to form a coadapted unit in their respective host species.

Infrequent parasite species occurred rarely in host species and can be considered a random component within the parasite communities. Parasite communities in host species with few parasites were mainly composed of infrequent species.

In summary, the low number of parasites and lack of a characteristic species group in some hosts suggests these parasite communities are primarily chance aggregations of helminth species. In other host species the presence of a group of characteristic parasite species, with reduced niche overlap between these species, suggests a highly predictable coadapted complex of parasite species co-occurring in association with less predictable complex of parasite species.

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I thank all members of all my supervisory committees, each provided encouragement, advice and help through all phases of my programme, no matter how brief their tenure. Members of my final committee provided generously of their time and experience. Dr. Boag never allowed the biology of the waterfowl to slip in its importance and at the end compensated for my ability to push deadlines past their limit. John Addicott always provided challenging ideas for discussion and his expertise at integrating computing facilities with data was invaluable. Bill Samuel, who was always enthusiastic, provided me with the opportunity to teach in his courses and has forever instilled in my memory the importance of providing basic information for those who follow us.

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I believe the acknowledgement section of a thesis allows a reader to gain an insight into the author and the environment in which the individual has worked. John Holmes, my supervisor, more than anyone reflected and provided the environment in which I was able to develop my own ideas and who at all times was a source of encouragement and challenge to my own abilities as a scientist and a human being. I extend my heartfelt thanks to John for the open exchange of his ideas of teaching and research and his ability to allow one to explore their own potential.

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microhabitat specificity of parasite species within host individuals. The evidence for microhabitat specificity for helminths is based primarily on data in reviews by Crompton (1973) and Holmes (1973). More recently, Hair and Holmes (1975), Hair (1975) and Bush (1980) have all demonstrated that the common helminth species within the intestine of lesser scaup (Aythya affinis) occupy predictable, restricted loacations. Avery (1969) has shown a similar situation for helminth species within the intestine of mallards (Anas platyrhynchos). In contrast, some parasites such as Hymenolepis diminuta in rodents (Cannon and Mettrick, 1970) and Schizorchis caballeroi in pika (Hobbs, 1980) are capable of occupying most of the small intestine. In addition, some species (eg., Schistocephalus solidus) are known to occupy different locations in different host species (McCaig and Hopkins, 1963). Shifts in location in response to the presence of other parasites have been noted for some species. H. diminuta has been shown to shift locaton in the presence of Moniliformis dubius (Holmes, 1961, 1962) and Trichinella spiralis (Silver et al. 1981). Tetrabothrius procerus has been shown to occupy a more posterior location when a related species T. minor extends its distribution posteriorly with increased population sizes within the intestine of fulmar (Fulmarus glacialis) (Riley and Owen, 1975). This latter group of examples suggests that parasite species may not be obligate microhabitat specialists, and may be capable of occupying more extensive ranges within the host individual than they normally occupy.

In an examination of the literature, Price (1980) concluded such examples of interactions were rare. Because individual hosts are distributed in a patchy and discontinuous fashion, Price (1980) considered that the chance of colonization would be low for any single parasite species. Therefore, the potential for co-occurrence of several species would be low and the communities should be existing under non-equilibrium conditions in which interactions should be unimportant. Price (1980) suggested that the restricted microhabitat distributions are a result of pressures other than competition but did not indicate what pressures might be responsible. Rohde (1979) has suggested a noninteractive mechanism by which microhabitats are restricted as a result of selective pressures on individuals to mate in sparse populations. Individuals have a higher probability of making contact with other indivduals in sparse populations if they restrict their microhabitat on or within a host. In contrast to the ideas of Price (1980) and Rohde (1979), Holmes (1973) proposed that microhabitat specificity in parasite communities was a response to past competition (interaction) with other parasite species. Another interactive explanation has been proposed by Sogandares-Bernal (1959) and Martin (1969) whereby parasites are restricted in their microhabitat distributions as a mechanism to prevent hybridization. A critical feature to distinguish between the noninteractive and interactive views of parasite community organization is whether the host is a patchy and ephemeral resource for parasites as suggested by Price (1980). For interactions between parasite species to be important in determining community structure, parasite species must co-occur regularly.

Kuris et al. (1980) have suggested three levels at which hosts may be regarded as habitats (or patches) for parasites. The first and most important is the host individual. Interactions between parasite species can occur only within the host individual. The second level of habitat is that of the local host population. The importance of interactions at the host individual level can only be measured by their regularity of occurrence in host populations. For parasites which are able to use different host species all potential host species populations in a community may be regarded as a single multispecies population. The third level of habitat is that of the host species. The importance of interactions in the evolutionary development of the parasite community can be closely related to the evolutionary relationships of the host species within a community. The latter two boundaries of habitats can only be defined by the distribution of the parasites, not the study. Individual hosts are the only unequivocal habitats for parasite species (Kuris et al. 1980). In part, the co-occurrence of parasite species will depend on at what level different species recognize habitat boundaries.

The importance of both noninteractive and interactive forces in organizing communities of freeliving organisms has long been recognized (Whittaker, 1975). Wilson (1969) has integrated the two concepts, and their importance in his theory of community development. The initial phase is noninteractive, in which species are rapidly colonizing a new community, resources are plentiful and interactions are unimportant. The second phase is interactive, in which populations of individual species are large enough that species interactions are important. The third assortative phase is also interactive, in which colonization and extinction are still occurring but some species are able to persist longer by either being better adapted to the local environment or by being able to coexist with specific groups of other species. The final evolutionary phase is noninteractive, in which species have adapted to coexist with other species and the environment.

In a discussion of the importance of noninteractive and interactive forces in structuring parasite communities Holmes and Price (1980) have aligned their contrasting views with the first and last of Wilson's phases. Price's (1980) proposal that parasite communities are young is equated to the initial noninterative phase, whereas Holmes's (1973) suggestion that parasite communities are mature is equated to the final evolutionary phase. Holmes and Price (1980) have proposed a set of predictions for parasite communities in the initial noninteractive phase, in which interactions are unimportant, or the evolutionary phase, in which interactions are reduced after having been through the interactive and assortative phases of community development.

Bush (1980) has examined these two opposing views with reference to the intestinal helminth communities of lesser scaup. He demonstrated there were two components within the intestinal communities of scaup: a deterministic component consisting of common or frequently co-occurring species and a stochastic component consisting of infrequent or rare species. Comparison of realized niche overlap based on the observed distributions within individual birds with fundamental niche overlap based on the summed distributions across all individual birds indicated that interactions may be important in maintaining the structure of the deterministic component but not the stochastic. Bush (1980) concluded that both of the opposing views (noninteractive and interactive) were applicable, but to the different components in the intestinal helminth community of scaup.

Studies by Cornwell and Cowan (1963), Graham (1966), Hair (1975) and Bush (1980) suggest that the waterfowl host-parasite system is an excellent one for studies of parasite community organization. Individual birds provide discrete, recognizable boundaries separating communities of parasites in one individual host from another. In addition, host species and multispecies waterfowl communities provide other recognizable boundaries. The ease of identification of boundaries for the parasite communities within individual hosts is a situation not often encountered in freeliving communities. Twenty-four of North America's 45 species of waterfowl (Anseriformes) reproduce in the three major biomes of northwestern North America. This large number of waterfowl species provides a diverse and abundant source of hosts in which to compare parasite community structure. Waterfowl species are seasonal residents on the breeding grounds in western Canada during which assemblages of several waterfowl species co-occur together locally on single waterbodies.

Reviews by LaPage (1961) and MacDonald (1969), plus the studies cited above indicate waterfowl have a large number of individuals and species of parasites. The combination of different and abundant species of both waterfowl (hosts) and parasites allows one to examine the community structure in replicate habitats. The replicate habitats enables one to examine the potential importance of interactions in organizing community structure.

It is my intention in this study to examine the structure of parasite communities in ten waterfowl species, first examining structure across individual birds (Part II), then within individual birds (Part III). Finally in Part IV, I will examine the hypothesis that parasites of waterfowl are specialists, then compare the community structures to the two opposing views proposed by Price (1980) and Holmes (1973), using the set of predictions outlined in their joint paper (Holmes and Price, 1981).

II.

STRUCTURE AND ORGANIZATION OF INTESTINAL HELMINTH COMMUNITIES ACROSS INDIVIDUAL BIRDS

INTRODUCTION

Price (1980) proposed that most parasite species show a high degree of host specificity and are therefore, host specialists. In contrast, studies on parasite composition in more than one duck species indicate a high degree of overlap in parasite species between hosts (Beverley-Burton, 1972; McLaughlin and Burt, 1979; Shaw and Kocan, 1980). These studies indicate host generalists are not uncommon on the waterfowl-host parasite system. In a study on a single host species, lesser scaup, Bush (1980) concluded that the intestinal helminth community of scaup had two components. The first was a regularly co-occurring (recurrent) group of both host specialists (in lesser scaup) and host generalists (in waterfowl). He found that the recurrent group of helminth species contributed most of the similarity between host individuals. In addition, all of the recurrent group have been reported in all three studies of the helminth fauna of lesser scaup over a 16 year period in Alberta (Graham, 1966; Hair, 1975; Bush, 1980). Bush (1980) has suggested these species represent a highly coevolved unit. The second was a stochastic component, made up of parasites which were specialists in other host species. Thus, there appear to be three components in scaup: host specialists in scaup, host generalists and specialists from other host species. The latter two components may be providing the overlap in faunal composition seen in most host surveys. The first group provides a distinct component.

The presence of these three components in the helminth fauna of waterfowl raises the question as to what level(s) of habitat above the individual host (i.e., host species; host populations; multispecies populations (Kuris et al. 1980)) reflects the structure of the parasite communities. If each host has a distinct parasite composition made up of host specialists, (as suggested by Bush, 1980) these host specialists will provide a high degree of similarity between individuals of the same duck species. Individual birds of that host species will, therefore, be more similar to each other than to individuals of other species. Under these conditions, the host species will be the habitat level best reflecting the parasite community.

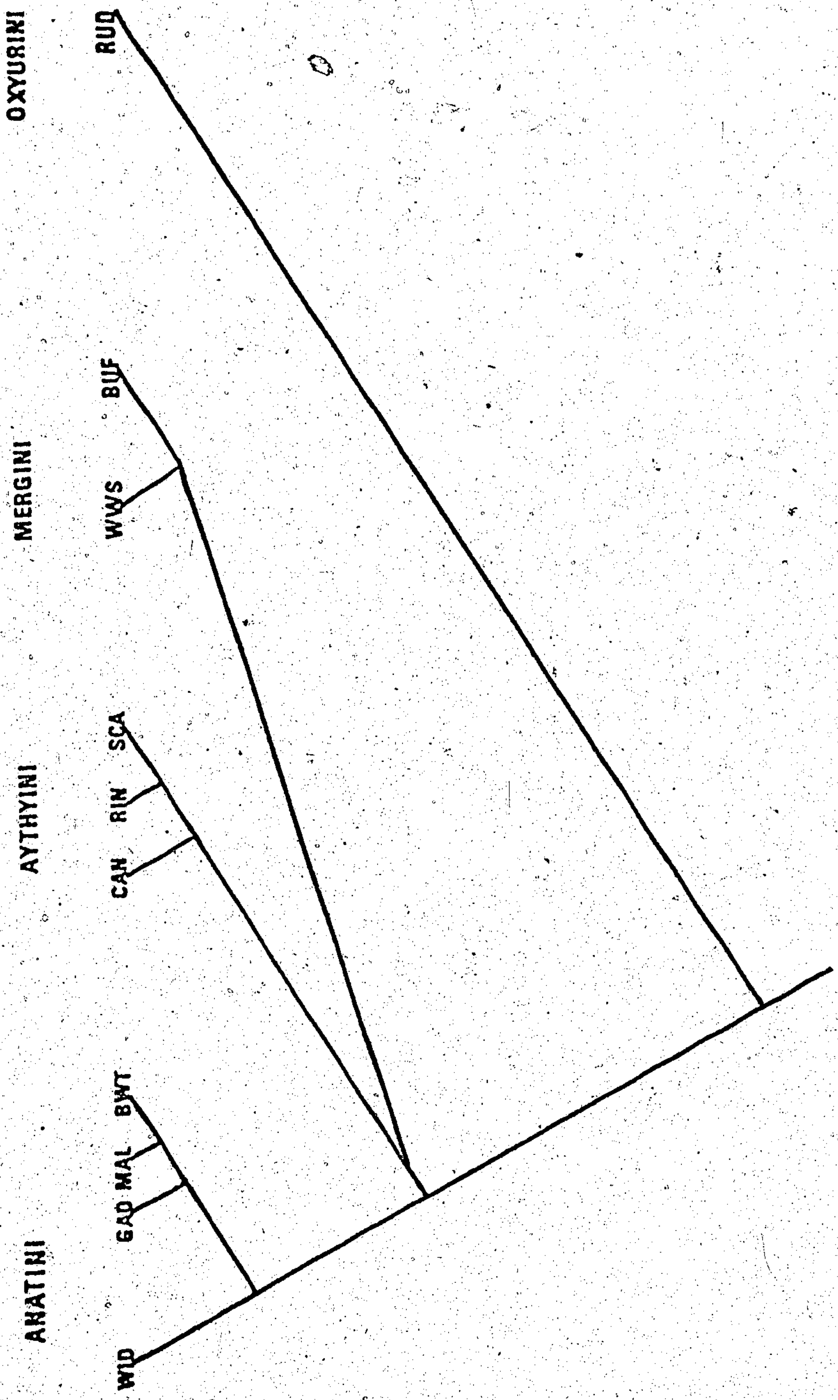
If host species do not have a distinct parasite composition, but one consisting of host generalists and parasite species exchanged with other hosts, then individuals of one species may be just as similar to individuals of other species as to other individuals of the same species. Under these conditions, the host populations or multispecies populations will be the habitat level best reflecting the parasite community. Two factors become important at the host or multispecies population level: 1) phylogenetic relationships of host species and 2) ecological relationships (in terms of diet or numerical abundance) between host species.

Three hypotheses have been proposed to explain patterns in helminth communities above the host species level:

1. Host specificity, or the phylogenetic hypothesis (Kotecki, 1970; Brooks, 1979)
2. Diet, or the food hypothesis (Dogiel, 1964)
3. Density and composition of host populations, or the numerical dominance hypothesis (Sulgostoska, 1963; Neraasen and Holmes, 1975)

The phylogenetic hypothesis, as proposed for the Anseriformes by Kotecki (1970), states that the parasite fauna is specific at the host tribe level (i.e., Anatini, Aythyini). Johnsgard (1960, 1961, 1964) (Fig. 1) has proposed that the Mergini are more closely related to the Aythyini than to the Anatini. The Oxyurini are considered to have separated prior to the Aythyini and Mergini (Delacour and Mayr, 1945; Woolfenden, 1961). Thus, one could predict that the Oxyurini (represented in this study by ruddy duck, _Oxyura jamaicensis_) would show the least similarity to the other tribes. The greatest similarity should be between the Mergini (represented by white-winged scoter, _Melanitta fusca_, and the bufflehead, _Bucephala albeola_) and the Aythyini (represented by canvasback, _Aythya valisineria_,

Figure 1. Phylogenetic relationships of ten species of waterfowl as proposed by Johnsgard (1961) and Woolfenden (1961). (WID - Widgeon, GAD - Gadwall, MAL - Mallard, BWT - Blue-winged teal, CAN - Canvasback, RIN - Ring-necked duck, SCA - Scaup, WWS - White-winged scoter, BUF - Bufflehead, RUD - Ruddy.)


ANATINI
WID
GAD
MAL
BWT
AYTHYINI
CAN
RIN
SCA
MERGINI
WWS
BUF
OXYURINI
RUD

ring-necked duck, Aythya collaris and lesser scaup, Aythya affinis). All of the duck species (within the above three tribes) are referred to as 'divers'.

Within the tribes with multiple representatives (Anatini, Aythyini) the relationship between individual species (Johnsgard, 1961) can be used to predict the similarity in their parasites. Within the Anatini, gadwall, Anas strepera, mallard, Anas platyrhynchos, and blue-winged teal, Anas discors, should be similar to each other, whereas widgeon, Anas americana, should be more distinct (Fig. 1). The duck species within the Anatini are referred to as 'dabblers'. Within the Aythyini, Johnsgard's evolutionary relationships would predict the canvasback and ring-necked duck would be more similar to one another than either is to lesser scaup.

The food hypothesis proposes that species with similar food habits should have similar parasites. Since the majority of parasites are transmitted by intermediate hosts it is possible to predict the type of faunal similarity one might expect to see if diet was the major influencing factor of helminth community structure. Unfortunately, most studies on food habits and dietary overlap in waterfowl have been done on different species combinations or on single species at different times in different locations (see summary in Swanson and Meyer, 1973). In addition, dietary differences have been noted between male and female birds for canvasback, blue-winged teal, gadwall, and scaup. In other studies, data from male and female birds have not been separated. Since sample sizes are small (n=6) for most species in this study comparisons of helminths between sexes is not possible. Therefore, data on food habits of the two sexes are combined. In addition, some studies classify food items to a "finer" taxonomic level than do others. The importance of this is minor since parasites tend to be non-specific at the intermediate host level. Few detailed studies of life cycles in western North America are available, most of the life cycles have to be extrapolated from information on life cycle studies from Eurasia or eastern North America, often involving related species of parasites. Therefore, only the general groups of invertebrates will be considered (Table 1). All of the studies on food habits used in the following analysis were done in western North America, except for that on ring-necked duck (eastern North America; Mendall, 1958). Ring-necked ducks were collected only on Cow Lake, which occurs in the boreal forest biome of Alberta, a similar type of habitat to that studied by Mendall (1958). Most studies on the food habits of waterfowl from the western breeding grounds were conducted on sloughs and ponds rather than lakes. However, while the resource availability may differ,

Table 1. Percent (by volume) of animal matter in the diet of ten duck species.

Duck Species	% Animal Matter	% Crustacea	(Amphipoda)*	% Insecta	(Chironimidae)**	% Gastropoda
Ring-necked duck[1]	14	0	(0)	2	(1)	6
Widgeon[2]	31	7	(7)	25	(22)	0
Gadwall[3]	46	30	(1)	16	(9)	1
Canvasback[4]	46	1	(1)	16	(2)	33
Mallard[5]	50	1	(1)	52	(1)	1
Blue-winged teal[3]	74	4	(4)	6	(1)	33
Bufflehead	84	6	(3)	72	(8)	1
Scaup[7]	91	60	(52)	23	(10)	1
Ruddy[8]	94	5	(2)	75	(72)	21

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* (Amphipoda) - Percent by volume of animal matter consisting of Amphipoda.

** (Chironimidae) - Percent by volume of animal matter consisting of Chironimidae.

[1] Mendall (1958)

[2] Bartonek (1972)

[3] Swanson and Meter (1973)

[4] Bartonek and Hickey (1969)

[5] Perret (1962)

[6] Erskine (1972)

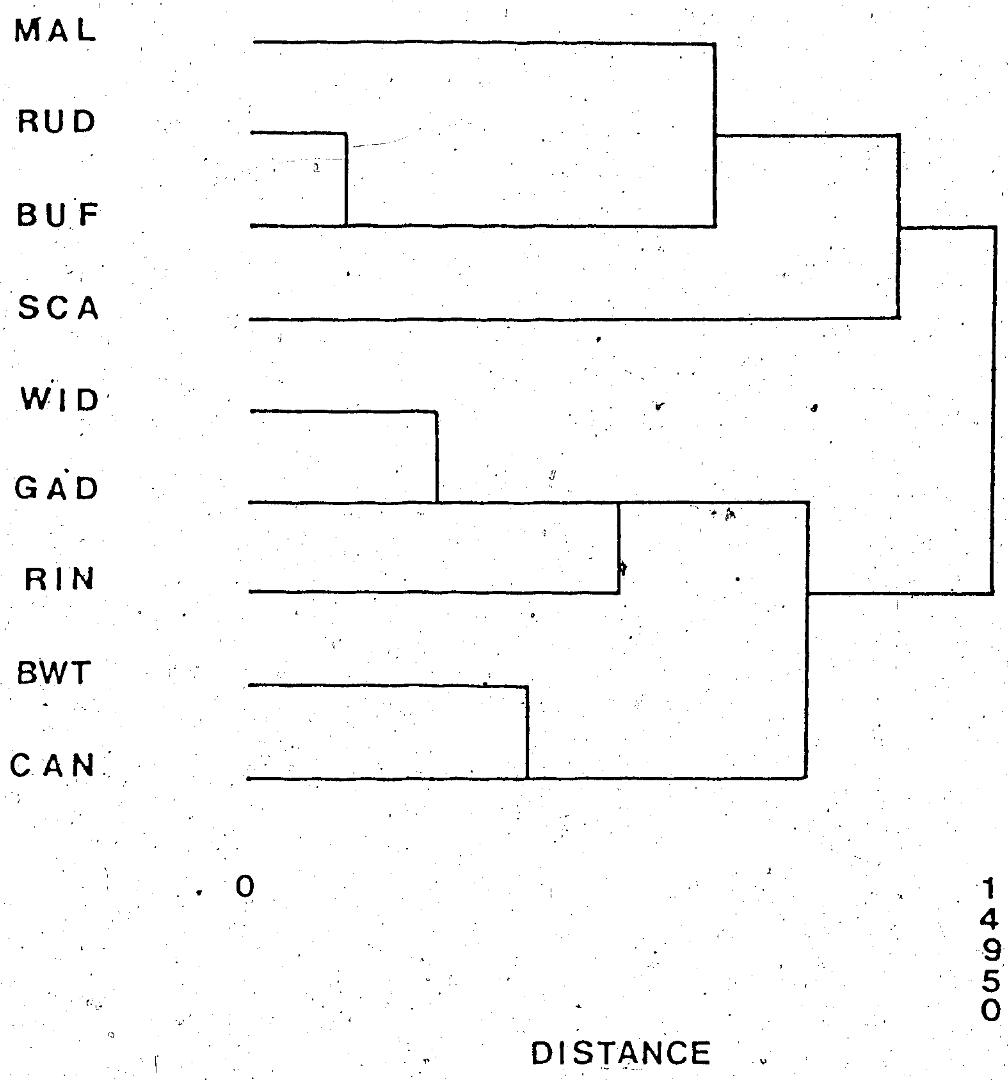
[7] Rogers and Korschgen (1966)

[8] Siegfried (1973)

the types of organisms in sloughs and lakes, particularly, the known major intermediate hosts (Amphipoda, Copepoda, Ostracoda), will overlap. I am unaware of any study on the food habits of white-winged scoter from freshwater habitats therefore, they are omitted from the diet analysis. Personal observation indicates scoter eat amphipods, insects (Chironimidae) and sphaerids most frequently.

There are major differences in the food habits between waterfowl species, both in the proportion of plant and animal matter consumed and in the proportion of major invertebrate classes consumed (Table 1). Widgeon and ring-necked ducks consumed the smallest proportions of animal matter followed by gadwall, canvasbacks and mallards. Blue-winged teal, bufflehead, scaup and ruddy all consumed a high proportion of animal matter. Gadwall and scaup consumed a higher proportion of crustaceans than the other species, while mallard, ruddy and bufflehead all consumed a high proportion of insects. Blue-winged teal and canvasback consumed a high proportion of gastropods. The species are listed in Table 1 on the basis of the proportion of animal matter consumed. Cluster analysis (see below for discussion of cluster analysis) using Euclidean distance and minimum variance algorithm was applied to the four variables (%animal matter, %Crustacea, %Insecta, %Gastropoda) (Fig. 2).

Figure 2. Cluster analysis comparing nine species of waterfowl with respect to the kind and percent of animal matter (percent of animal matter, percent of Crustacea, percent of Insecta, and percent of Gastropoda,) consumed by each species. Vertical axis represents Euclidian distance as a measure of similarity. (MAL - Mallard, RUD - Ruddy, BUF - Bufflehead, SCA - Scaup, WID - Widgeon, GAD - Gadwall, RIN - Ring-necked duck, BWT - Blue-winged teal, CAN - Canvasback.)


MAL
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Two patterns of similarity in helminth communities between the nine duck species (scoter not included) can be predicted. The first is based entirely on the percent of animal matter consumed; blue-winged teal, bufflehead, scaup, and ruddy should have larger and more complex parasite communities. The second is based on the similarity illustrated by the cluster analysis of the four variables. That analysis would predict similar parasites in ruddy and bufflehead, widgeon and gadwall, and blue-winged teal and canvasback.

The information used to predict the pattern of parasite community organization under the phylogenetic and diet hypotheses overlap. Anatomy is used to distinguish and classify species and is related to the mode of feeding behaviour in waterfowl. It is important therefore to indicate whether or not they can be distinguished. The major difference between the two hypotheses is the separation of the three species of Aythyini in the diet hypothesis compared to their similarity in the phylogenetic hypothesis. All three species of Aythyini are more similar to species of different tribes than to each other under the diet hypothesis (Figs. 1 and 2).

The numerical dominance hypothesis was proposed by Sulgostowska (1963) who found that the trematode fauna in a group of waterfowl species on a single lake was primarily determined by the fauna of the numerically dominant host species. Leong and Holmes (1981) showed that within groups of related fish species the parasites of the most abundant hosts spread to the less abundant hosts. The present study was originally designed to test this hypothesis by examining helminth communities on three lakes with very different waterfowl assemblages. However, censuses of the birds on these lakes indicated that the relative numbers of different species of birds changed throughout the breeding season and between years. As a result the data obtained are inadequate to test this hypothesis directly. In a few instances the hypothesis can be examined indirectly from the point of species exchange (spreading of parasites from one host to another).

METHODS AND MATERIALS

Field Methods

Prior to any collecting of birds at each lake, the waterfowl populations were censused. Techniques of the censuses are presented in Bush (1980). Initially, in 1979 three lakes were selected on the basis of a different composition of waterfowl (based on bird censuses from 1977 and 1978; see Bush, 1980). Once it was realized the waterfowl assemblages on the lakes had changed from previous years and continued to change throughout the summer, birds were chosen from an additional nine lakes to increase sample sizes of birds from the initial three lakes (Appendix 1). During 1977 and 1978 the six numerically dominant waterfowl species at each lake were collected. During 1979 the ten numerically dominant bird species were collected. During 1980, the five numerically dominant waterfowl were collected. Immediately after each bird was collected, it was weighed, the intestine tied off, removed and placed in an enamel pan. Absolute alcohol cooled to -70 C with dry ice was poured over the gut completely freezing it in a few seconds. The gut was then labelled, placed in a plastic bag and stored in a cooler of dry ice . The intestine remained frozen until examination in the laboratory. The rapid freezing prevents the chance of postmortem movement by the parasites and enhances ease of identification of specimens.

Laboratory Methods

A total of 97 birds have been examined from the collections of 1977-1980. Fifteen of the 16 scaup were examined by A.Bush (1980) and 11 of the 16 mallards and 2 of the 11 widgeon were examined by K.M.Nielsen.

In the laboratory the intestines were partially thawed, straightened and the small intestine cut into twenty equal sections. The large intestine was examined as one unit. The caeca were thawed, straightened and divided into 4 equal sections. Each section was stored in a separate vial in the freezer until examined . At the time of examination, the section was placed in a petri dish with saline and allowed to thaw. The section was cut longitudinally and flooded gently with saline. This washed any loose parasites into the dish. The gut section was then turned over and the serosal side scraped. This technique removed those parasites which had remained in contact with the intestinal wall with little damage to the specimens. The intestinal wall was then examined for any remaining parasites.

All parasites were then counted. Large numbers of helminths in scoter and scaup necessitated the use of a dilution technique. When more than 500 helminths were located in a section all large or heavy bodied worms were removed and the remaining specimens placed in a 100 ml graduated cylinder. The contents were mixed thoroughly, two ten ml aliquots were poured off, the worms identified and counted. Counts were summed (if within 10%, otherwise a third count was made) and multiplied by 5 to estimate the total number of worms present.

Helminths were identified in temporary water mounts. Where the numbers of worms permitted, representative specimens were stained and mounted using standard techniques. Nematodes and acanthocephalans were identified in temporary mounts after being cleared in a 1:1 solution of lactophenol and beechwood creosote.

Analytical Methods

In general, the parasites from each individual bird were treated as comprising a separate community (infracommunity). Where more inclusive community levels were considered individual birds were used as replicates, and means and standard deviations were used to quantify the species of parasites. The data were transformed, using a ln (x+1) transformation, but not standardized. All statistical analyses were done using the programs in Midas (Fox and Guire, 1976).

Evenness was calculated using the common measure 'J', which is the Shannon Weaver diversity index divided by the natural logarithm of the total number of species in each sample (Pielou, 1975). The values range from 0.0 (only one species abundant, others represented by single individuals) to 1.0 (equal abundances of all species).

Qualitative similarity of parasite species between host individuals was measured by Jaccard's coefficent of similarity (formula 11 of Janson and Vegelius, 1981). The value of the coefficent ranges from 0.0 to 1.0 (low to high similarity) such that a 0.5 value indicates 50% of the total number of species are shared between the paired samples. Jaccard's coefficent is considered to be one of the most reliable and interpretable coefficents of species association (Janson and Vegelius, 1981). Jaccard's coefficent of similarity uses presence or absence data only, measures co-occurrence of parasite species between pairs of host individuals, and does not use cases in which parasite species are absent from both individuals.

Quantitative similarity between pairs of host individuals was measured by Euclidean distance. This measure is based on differences between numbers of individuals of each species found in at least one of the pairs of hosts (Clifford and Stephenson, 1975). Euclidean distance tends to weight the dominant species more heavily (Whittaker, 1975).

Cluster analysis was used to examine patterns of similarity (see Wishart, 1978 for discussion of clustering techniques). Jaccard's coefficent was used with the average distance algorithm (Wishart, 1978). Euclidean distance was used with the minimum variance algorithm (Wishart, 1978). Two methods of examining patterns of similarity in communities are clustering of helminth species groupings (or 'inverse' classification) and duck groups (or 'normal' analysis). The former method groups parasite species by the similarity of their sites of occurrences (i.e., the birds they are found in) the latter groups birds by the similarity of the parasite species occurring in them (Clifford and Stephenson, 1975). Clusters from the inverse analysis were compared to the clusters of the normal analysis by the following matrix method developed by Stephenson et. al. (1972). Host groups were used as columns, parasite groups as rows. The cells were the number of occurrences (Jaccard analysis) or the number of individuals (Euclidean distance analysis) of the appropriate species group in the given host group standardized by dividing by by the number of hosts in each duck group. These standardized cell values were then analyzed in two ways. Each value was divided by the appropriate row sum to give a measure of the concentration of the parasite group in that host group, then by the appropriate colum[illegible]m to give a measure of the importance of that parasite group in that host group. A value of 20 percent was considered to be a significant proportion of individuals in one cell. All values above 20 percent were chosen as the level of concentration or importance.

RESULTS

Species Composition and Distribution

I examined 97 birds belonging to 10 species of waterfowl. The number, sex and weight of each bird and the lake and date of its collection are listed in Appendix 1.

One hundred and eighteen taxa of parasites (species or if the material was unidentifiable to species, recognizable types of immature worms) were found (Appendix 2). These included 100 taxa of cestodes, 11 of trematodes, 4 acanthocephalans and 3 nematodes. Fifty-one taxa were types of immature worms which could not be positively identified to species (characteristics of these taxa are given in Appendix 3). Forty-three taxa occurred in only one or two individual birds; all of these taxa were found in small numbers, except for one (Parvula?-mean=209). These taxa were eliminated from most analyses, leaving a data set of 75 species (Table 2). Sixty-three of the 118 taxa were represented by mature individuals (with shelled eggs). These were treated separately in some analyses.

Composition and Similarity of the Helminth Communities within Duck Species

Several summary indices were used to compare community structure between host species (Table 3).

Table 2. The number of birds infected and intensity of infection of seventy-five helminth taxa in ten species of ducks.

Parasite Species	Widgeon	Gadwall	Mallard	Blue-winged teal	Ruddy	Canvasback	Ring-necked duck	Scaup	Bufflehead	White-winged scoter	B'a	B'a (mat)
TREMATODA												
Echinoparyphium recurvatum	2/11*^{A} 2±1.4^{B}	1/7 25	8/16* 59±113.1	7/10* 20±2.9	1/6 27	5/6* 376±507.4	4/6* 15±18.0	2/16* 20±23.3	2/6* 23±31.8		.06	.10
Echinostoma revolutum	4/11* 4±21.7		3/16* 5±5.2		1/6* 2		1/6 5		1/6 11		.35	.22
Echino?		2/7 1±0.0	3/16 28±44.5	3/10 1±00		2/6 4±4.9	1/6 2		1/6 4		.20	-
Hypoderaeum conoideum			1/16 1	1/10* 1		1/6* 3					.09	0.06
Apatemon gracilis	5/11* 11±14.4	4/7 4±2.1	11/16* 59±127.6	6/10* 18±23.8	5/6* 39±22.1	4/6* 27±29.4	4/6* 69±108.3	11/16* 29±25.0	1/6* 1	7/13 37±87.4	.66	.57
Cotylurus flabelliformes			6/16* 6±3.3				2/6* 2±0.7			1/13* 1	.15	.18
Cotylurus hebraicus	1/11* 4			1/10* 2	4/6* 10±13.0	1/6* 4		7/16* 11±9.5		1/13* 3	.22	.21
PP			2/16 109±153.4	2/10 1.5±0.7	3/6 2±0.6	3/6 5±3.6	3/6 77±50.8		2/6 178±181.0	1/13 1	.16	-
Notocotylus attenuatus	1/11* 57	3/7 17±13.0	5/16* 5±7.5	3/10 2±1.5	2/6* 2±0.7			1/16 1	3/6* 4±4.4	3/13* 6±4.6	.36	.34

	Widgeon	Gadwall	Mallard	Blue-winged teal	Ruddy	Canvasback	Ring-necked duck	Scaup	Bufflehead	White-winged scoter	B'a	B'a (mat)
Zygocotyle lunata	3/11* 2±1.0	3/7 4±4.9	3/16* 2±2.3			4/6* 10±15.5	1/6 1	2/16* 3±1.4	1/6 1		.14	.35
Microphallus sp.										3/13* 150±256.6	.08	-
CESTODA												
Unciunia n.sp		1/7* 37	1/16 1	3/10 8±3.5		3/6* 181±302.8	2/6 6±6.4	4/16* 136±191.3	3/6* 1.0±0.6		.15	.01
Lateriporus clerci										4/13 7±10.8		
Lateriporus mathevossianae										12/13* 111±205.9	.08	.11
Lateriporus skrjabini				2/10 1±0.0				9/16* 16±25.5	2/6 5±4.2	9/13 307±151.6	.09	.11
Fimbraria fasciolaris	5/11 2±1.7	3/17* 11±10.8	8/16* 23±21.2	3/10 3±2.1	6/6 16±13.0	6/6 26±26.1	3/6* 1±0.6	15/16* 45±47.3		13/13 214±354.2	.21	0.36
Aploparaksis fucigera	3/11* 1±0.6										.05	.05
P										9/13 12±13.4	.07	-
Diorchis danutae	5/11* 4±4.7	3/7* 4±2.6				2/6 1±0.0					.15	.09

	Widgeon	Gadwall	Mallard	Blue-winged teal	Ruddy	Canvasback	Ring-necked duck	Scaup	Bufflehead	White-winged scoter	B'a	B'a (mat)
Diorchis elisae			1/16 1	3/10* 17±14.0		2/6 1±0.0	1/6 1	2/16 87±119.5			.22	.04
Diorchis excentricus					6/6 150±217.6	1/16 1		1/16 13 1			.01	.00
Diorchis spinata	2/11* 9±1.4	6/7* 19±24.2		1/10 1							.04	.02
Diorchis n. sp. TT						6/6* 24±22.0	3/6 2±1.2	3/16 105±122.3			.17	.00
Diorchis AD			2/16 6±7.8	1/10 3	2/6 16±17.7			1/16 1			.08	-
Dicranotaenia coronula			10/16* 5±5.6			4/6 3±1.0		10/16* 16±9.5			.25	.24
Retinometra cyrtoides					6/6* 1460±867.3	2/6* 37±33.5		4/16 86±119.6			.07	.001
Retinometra pittaluci						3/6 8±6.0		12/16* 50±63.2			.12	.11
Retinometra macroacanthos		1/7 1	7/16 17±14.7			5/6 25±10.0	1/6 3	1/16 5	2/6 28±17.7	1/13 6	.28	-
X			1/16 9			2/6 36±7.1	1/6 3		5/6 106±162.6	2/13 49±46.7	.05	-

	Widgeon	Gadwall	Mallard	Blue-winged teal	Ruddy	Canvasback	Ring-necked duck	Scaup	Bufflehead	White-winged scoter	$B'a$	$B'a_*$(mat)
Sobolevicanthus gracilis			3/16 3±0.6			1/6 1		2/16 28±32.5				
Sobolevicanthus kenaiensis						2/6 21±27.5		2/16* 46±57.2			.17	.11
Sobolevicanthus octacantha				6/10 37±36.9							.04	-
TTT	1/11 1	1/7 1		2/10 1±0.0							.21	-
Hymenolepis AB		1/7 3		3/16* 5±2.5	6/10* 684±849.7	1/6 2	1/6 1			11/13* 7498±9551.4	0.09	
AB?					3/10 33±51.1	1/6 2				8/13* 302±383.5	.09	.10
Hymenolepis abortiva			1/16 1			2/6* 22±6.4		15/16* 9712±13332.5		7/13 109±165.7	.11	-
Abort?				4/10 7±5.7				1/16 965		10/13 1526±1968.1	.09	-
Hymenolepis arcuata						1/6 1		3/16 61±98.4			.11	-
Hymenopelis albertensis										13/13* 5449±5110.4	.07	.03
Hymenolepis compressa			3/16* 5±6.1			1/6* 57					.04	.01
RR			3/16 2±1.0			1/6 5		4/16 14±2.2			.26	-

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	Widgeon	Gadwall	Mallard	Blue-winged teal	Ruddy	Canvasback	Ring-necked duck	Scaup	Bufflehead	White-winged scoter	B'a	B'a (mat)
Hymenolepis fausti[a]			11/16 34±30.9	1/10 6		4/6* 96±104.3		3/16* 33±16.9			.17	.21
Hymenolepis formosoides								4/16 136±191.3		7/13 58±91.1	.07	.07
Hymenolepis hopkinsi	5/11* 11±5.0	3/7* 4±2.9	12/16* 63±72.5	2/10 21±26.1	1/6 2	3/6* 5±5.9	2/6* 3±2.1	2/16 5±5.6	1/6 3	11/13* 31±21.6	.29	.16
Hymenolepis microskrjabini			2/16* 10±4.9			1/6 1	4/16* 111±170.9			5/13* 13.55±1250.6	.11	.10
Micro?			1/16 1						1/6 1	2/13* 701±722.6	.08	-
Hymenolepis melanittae										10/13* 670±753.8	.07	.08
Hymenolepis GCC			2/16 10+12.0			1/6* 12					.16	.00
Hymenolepis paracompressa			1/16* 40 40			2/6* 40±50.2		2/16* 4±4.2			.09	.02
Hymenolepis parvula			2/16* 91±103.2				4/6* 43±78.3				.13	.01
Hymenolepis pusilla						3/6* 56±90.4		15/16* 5044±6742.9		4/13 38±66.3	.11	.11
Pusilla?										3/13 123±130.4	.08	-
Hymenolepis recurvata						1/6* 79		9/16* 172±332.5	1/6 2		.13	.11

	Widgeon	Gadwall	Mallard	Blue-winged teal	Ruddy	Canvasback	Ring-necked duck	Scaup	Bufflehead	White-winged scoter	B'a	B'a (mat)
Hymenolepis spinocirrosa			2/16 22±29.7			4/6* 253±129.5		15/16* 8228±10553.0		6/13* 18585±31357.2	.25	.14
Spino?			1/6 6	2/10 10±11.3		1/6 1		1/16 999	1/6 2	11/13 4162±7869.8	.08	-
Hymenolepis spiralibursata			1/6 2					1/16* 3		13/13* 562±943.3	.08	.08
Hymenolepis tuvensis						2/6* 4±3.5		15/16* 1010±1286.1		2/13 13±42	.11	.11
Hymenolepis tuv?								7/16 687±737.2		2/13 143±173.2	.12	-
Hymenolepis tuvAB?										4/13 157±128.9	.07	-
D								3/16 4±3.5			.11	-
Hymenolepis WWW		7/7* 32±33.3									.01	.01
Hymenolepis XXX		3/7 3±2.0									.01	-
Anatinella spinulosa			1/16 1			4/6* 6±5.7					.01	.00
Echinocotyle rosseteri				10/10* 359±940.1							.04	.04
Echinocotyle QQQ	2/11* 5±1.4	6/7* 4±4.1		4/10* 1±0.5							.11	.07

	Widgeon	Gadwall	Mallard	Blue-winged teal	Ruddy	Canvasback	Ring-necked duck	Scaup	Bufflehead	White-winged scoter	B'a	B'a (mat)
<u>Echinocotyle</u> NNN		7/7 32±33.3		7/10* 8±8.2							.04	.04
<u>Diploposthe laevis</u>						5/6* 3±5.4	6/6* 2±0.4				.06	.01
<u>Oligorchis</u> n.sp.								3/16 20±15.5			.11	-
Acanthocephala												
<u>Polymorphus contortus</u>	8/11* 55±89.2	7/7* 16±31.8	8/16* 26±25.1		2/6* 3±2.1	3/6* 27±15.0	1/6 1		2/6 2±2.1	5/13* 3±3.6	.25	.32
<u>Polymorphus marilis</u>	1/11* 2		2/16* 4±4.2	1/10 2	2/6* 3±2.8	4/6* 16±16.7		15/16* 26±56.0	4/16* 10±11.1	11/13* 50±54.8	.30	.16
<u>Polymorphus paradoxus</u>			4/16* 28±31.4	2/10 2.0±0.7					1/6 2 2	8/13* 8±8.5	.25	.23
<u>Corynosoma constrictum</u>	5/11* 4±1.6	3/7* 2±1.5	10/16* 8±11.3	10/10* 8±6.5	3/6* 2±1.5	4/6 4±3.2		4/16* 2±1.0	2/6 2±1.4	9/13* 6±10.2	.52	.35
Nematoda												
<u>Capillaria anatis</u>	4/11* 1±0.5	1/7 1	5/16* 1±0.5	1/10* 2	1/6 1		2/6* 3±1.4	3/16* 2±2.3	3/6* 5±6.9		.33	.34
<u>Capillaria obsignata</u>						2/6* 1±0.0	2/6* 3±2.1	4/16* 3±2.4		7/13 58±91.2	.22	.20
<u>Capillaria nyrocinarium</u>										6/13* 6±7.4	.08	.08

* - Hosts in which the helminth species matured as indicated by the presence of shelled eggs.
A - Number of birds infected / number of birds examined.
B - Mean number of parasites per infected bird ± one standard deviation.
B' - Niche breadth values.
B' (mat) - Niche breadth values for hosts in which the parasite matured (mat).

Table 3. Number of helminth species, individuals, evenness, mature species and common species in each duck species.

	N	N_{TOT}	S	I	E	M	C(n)
Widgeon	11	17	5 ± 3.3*	85 ± 92.8	.347 ± .217	15	6 (1)
Ruddy	6	19	9 ± 1.9	1680 ± 1001.0	.257 ± .020	11	26 (5)
Ring-necked duck	6	20	7 ± 3.6	134 ± 148.6	.219 ± .170	10	20 (4)
Bufflehead	6	22	7 ± 3.3	180 ± 171.8	.296 ± .130	6	4 (1)
Gadwall	7	24	10 ± 4.5	197 ± 168.3	.136 ± .060	13	25 (6)
Blue-winged teal	10	31	10 ± 4.5	854 ± 1467.0	.210 ± .110	11	23 (7)
White-winged scoter	13	43	19 ± 6.2	28087 ± 33574.0	.131 ± .060	21	42 (18)
Mallard	16	47	10 ± 5.1	266 ± 301.0	.155 ± .090	22	13 (6)
Canvasback	6	48	20 ± 9.7	917 ± 613.9	.092 ± .050	27	23 (11)
Lesser Scaup	16	48	14 ± 4.8	23076 ± 29227.0	.108 ± .040	23	23 (11)

N = sample size

N_{TOT} = cumulative total number of species

S = mean number of Species

I = mean number of individuals

E = mean evenness

M = number of mature species

C(n) = percent of common species(number of common species)

*mean ± 1 standard deviation

Total number of helminth species in each bird species varied from 17 (widgeon) to 48 (canvasback, scaup). The mean number of species varied from 5 (widgeon; range=1-10) to 20 (canvasbacks; range=9-30). Although all birds were infected one mallard and one widgeon had only one helminth species each. The proportion of common helminths (>50% of the birds infected) in each host species varied from 4% (bufflehead) to 42% (scoter) in each duck species (Table 3).

Widgeon had the lowest number of individuals (85; range=3-304), white-winged scoter had the highest (28,087; range=1,082-128,660). The effect of the number of birds sampled on the total number of parasite species within each host was examined by plotting the cumulative number of species recovered with increasing numbers of individuals sampled. Birds were arranged randomly (random numbers table). Mallard, gadwall, bufflehead, canvasback and scaup all appear to continue to increase numbers of parasite species with increased number of hosts examined (Fig. 3). Blue-winged teal, ring-necked duck, scoter and possibly widgeon and ruddy, all appear to reach an asymptote in species accumulation (Fig. 4). Most species had accumulated 50% of the final total species number by the third bird. The only exception was scaup which required 5 birds to accumulate 50%. Mallard, widgeon, gadwall and bufflehead required more than 50% of the birds sampled to accumulate 75% of the helminth species. Blue-winged teal and ruddy required

Figure 3. Cumulative number of intestinal helminth species in the number of birds examined of each duck species. (GAD - Gadwall, BUF - Bufflehead, CAN - Canvasback, SCA - Scaup, MAL - Mallard.)

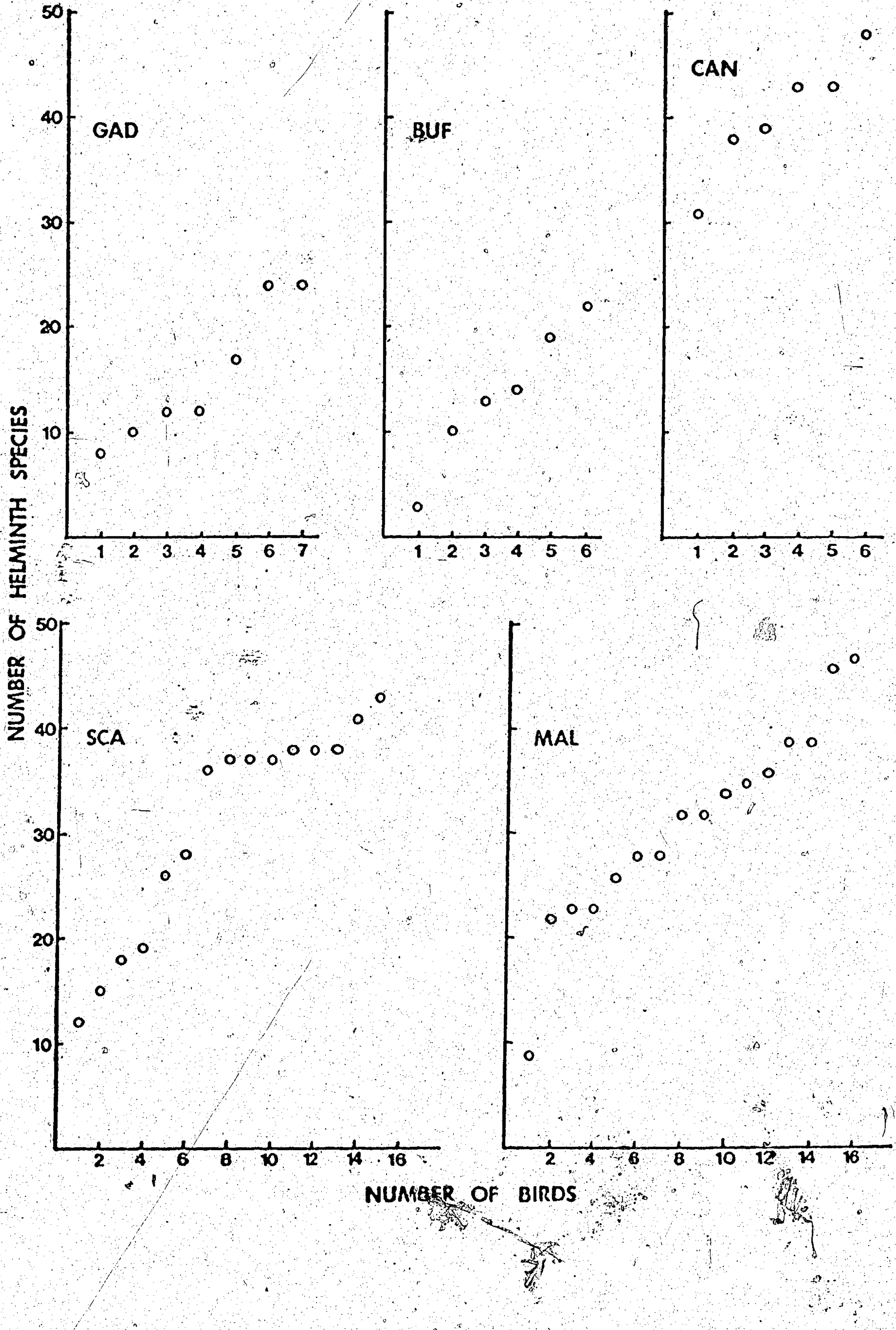
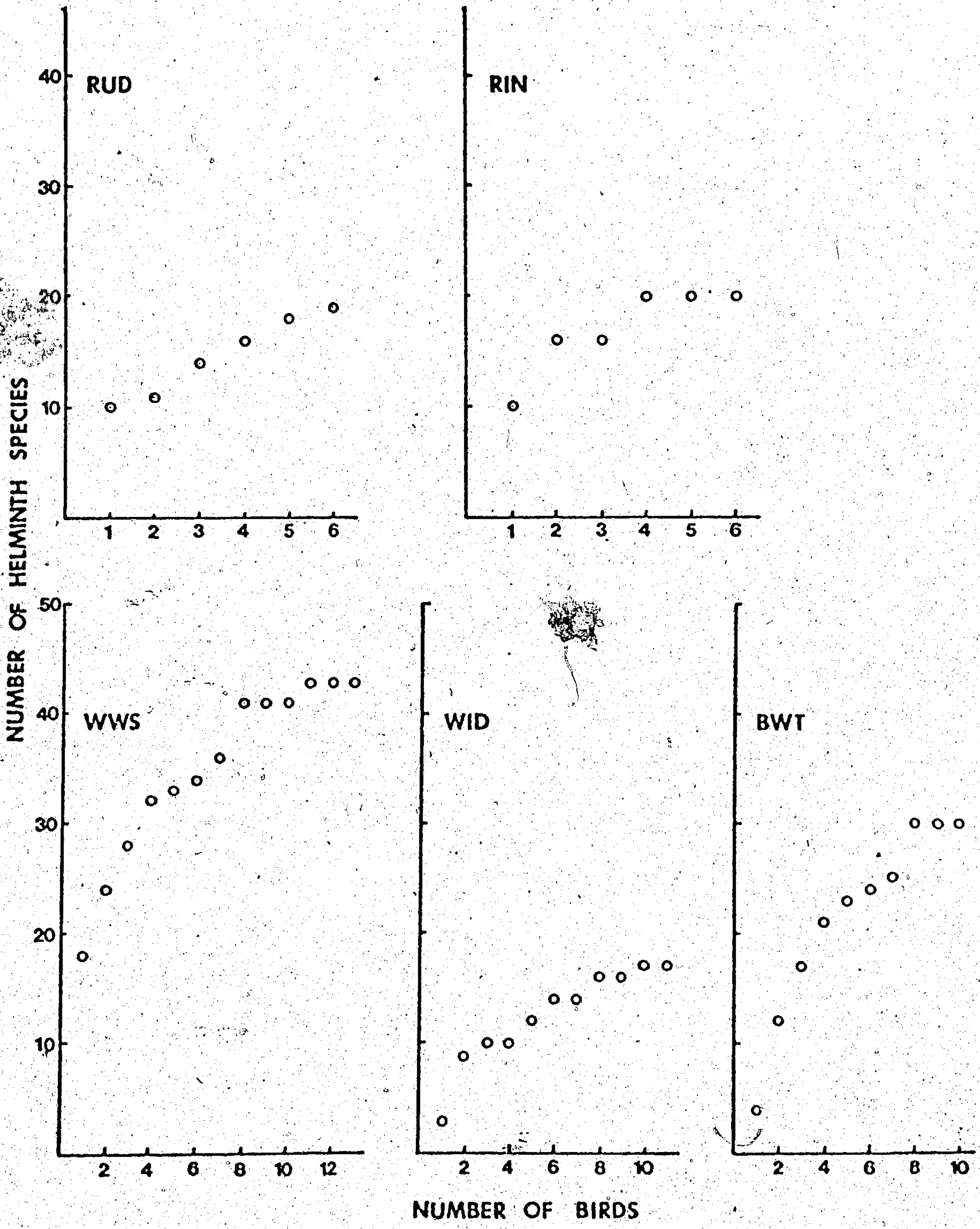

GAD
BUF
CAN
SCA
MAL
NUMBER OF HELMINTH SPECIES
NUMBER OF BIRDS
10
20
30
40
50
1
2
3
4
5
6
7
8
10
12
14
16

Figure 4. Cumulative number of intestinal helminth species in the number of birds examined of each duck species. (RUD - Ruddy, RIN - Ring-necked duck, WWS - White-winged scoter, WID - Widgeon, BWT - Blue-winged teal.)


RUD
RIN
WWS
WID
BWT
NUMBER OF HELMINTH SPECIES
NUMBER OF BIRDS
10
20
30
40
50
1
2
3
4
5
6
8
10
12

half of their samples to accumulate 75%, while canvasback, ring-necked duck, scoter and scaup required less than 50%

The number of lakes from which birds were examined may have an important effect upon the total number of parasite species found in each host species. For example, the number of helminth species in widgeon from three lakes (Rattlesnake, Charron, Bellshill) was 4, 11 and 13, respectively. Each lake had species not found in birds from the other lakes (Rattlesnake-1, Charron-3, Bellshill-4). Rank correlation (Spearman's) was used to examine the effects of sample size of birds and number of lakes examined on the number of parasite species, in each species of host. Neither the number of helminth species nor the mean number of helminth species in each host species was correlated with either number of birds or number of lakes sampled (Rho=0.38;0.33;0.44;0.35, respectively). The number of mature parasite species per duck species was correlated with both total numbers and mean numbers of helminth species (Rho=0.73;0.70, respectively).

Similarity between individuals of the same duck species were compared using the Jaccard coefficent of similarity. Mallards, widgeon, buffleheads and ring-necked ducks all had low similarity between individuals (Table 4).

Table 4. Proportion of similarity values (Jaccard's Coefficient) of helminth species between pairs of individual birds of each duck species and mean similarity of each duck species.

Range of Similarity (%) Values	Proportion of pairs with given similarity values									
	BUF*	RIN	MAL	WID	CAN	BWT	GAD	RUD	SCA	WWS
0 - 25	93	60	58	71	40	29	14	0	13	14
26 - 50	7	40	42	22	53	69	76	87	63	44
51 - 75				7	7	2	10	13	24	41
76 - 100										1
Mean	.14	.25	.22	.20	.29	.32	.38	.40	.41	.46
± 1 S.D.**	±.07	±.08	±.12	±.17	±.11	±.10	±.12	±.10	±.14	±.16

*BUF - Bufflehead; RIN - Ring-necked duck; MAL - Mallard; WID - Widgeon; CAN - Canvasback; BWT - Blue-winged teal; GAD - Gadwall; RUD - Ruddy; SCA - Scaup; WWS - White-winged scoter.

**± 1 standard deviation.

Approximately 50% of the pairs within this group had 0 to 25% similarity. Gadwall, blue-winged teal, ruddy, canvasback, scoter and scaup all had the majority (>50%) of individuals with 26 to 50% similarity. Only scoter and scaup had a large proportion of pairs with similarity values greater than 50%. Mean similarity varied from a low of 14% in bufflehead to a high of 46% in scoter.

Several of the measures of community structure were significantly correlated (Fig. 5). Of special interest were the positive intercorrelations between the proportion of common species, the mean similarity, and the mean number of individuals. Duck species with a large number of individuals have a high number of common species and a high similarity.

Similarly, the total number of species, the mean number of species and the number of mature species were positively intercorrelated. Each of these three measures was negatively correlated with evenness (J). This pattern differs markedly from that normally reported in the literature on freeliving communities, in which the number of species and evenness are either unrelated, or commonly, positively correlated (McNaughton and Wolf, 1979). In this study the opposite occurred, as species numbers increased the equitability in species abundances decreased (approached 0.0).

The only significant correlation between these two groups of measures (mature species, evenness, mean number of species and mean number of individuals, number of common species, similarity)

Figure 5. Significant intercorrelations between seven measures of community structure (S- total number of species; S_m- total number of mature species; E- evenness; $\bar{S}$- mean number of species; I- mean number of individual worms; N_c- number of common species; SIM- mean similarity within each duck species (Jaccard's Coefficient)).

	S	S_m	E	$\overline{S}$	I	N_c	SIM
S		+	−	+			
S_m			−	+			
E				−			
$\overline{S}$					+		
I						+	+
N_c							+
SIM							

was a positive correlation between the mean number of species and the number of individuals. These patterns of intercorrelation suggest that differences in the community structure of the parasites of the different duck species can be measured by three variables: mean number of species (complexity), mean number of individuals (size) and mean similarity. Plotting these three values on a graph indicates a loosely structured cline of duck species from low complexity, small size, and low similarity to high complexity, large size and high similarity (widgeon to scoter) (Fig. 6). Gadwall and ruddy both had high similarity but low or moderate levels of complexity and size, and therefore contribute to the loose structure of the cline.

Faunal Similarity between Duck Species

The number of parasite species shared by different pairs of host species is presented in Fig. 7. Similarity between pairs of host species was also compared using the Jaccard coefficent, calculated on all parasite species occurring within each duck species. No species pairs had high similarity (>50%). Canvasback had a relatively high degree of similarity (>40%) with mallard and scaup; widgeon with gadwall and ruddy; and buffleheads with ring-necked ducks.

Figure 6. Arrangement of ten species of waterfowl along three measures of helminth community structure: Size (A) (mean number of individuals), Complexity (B) (mean number of species), and Similarity (C) (Jaccard's Coefficient).

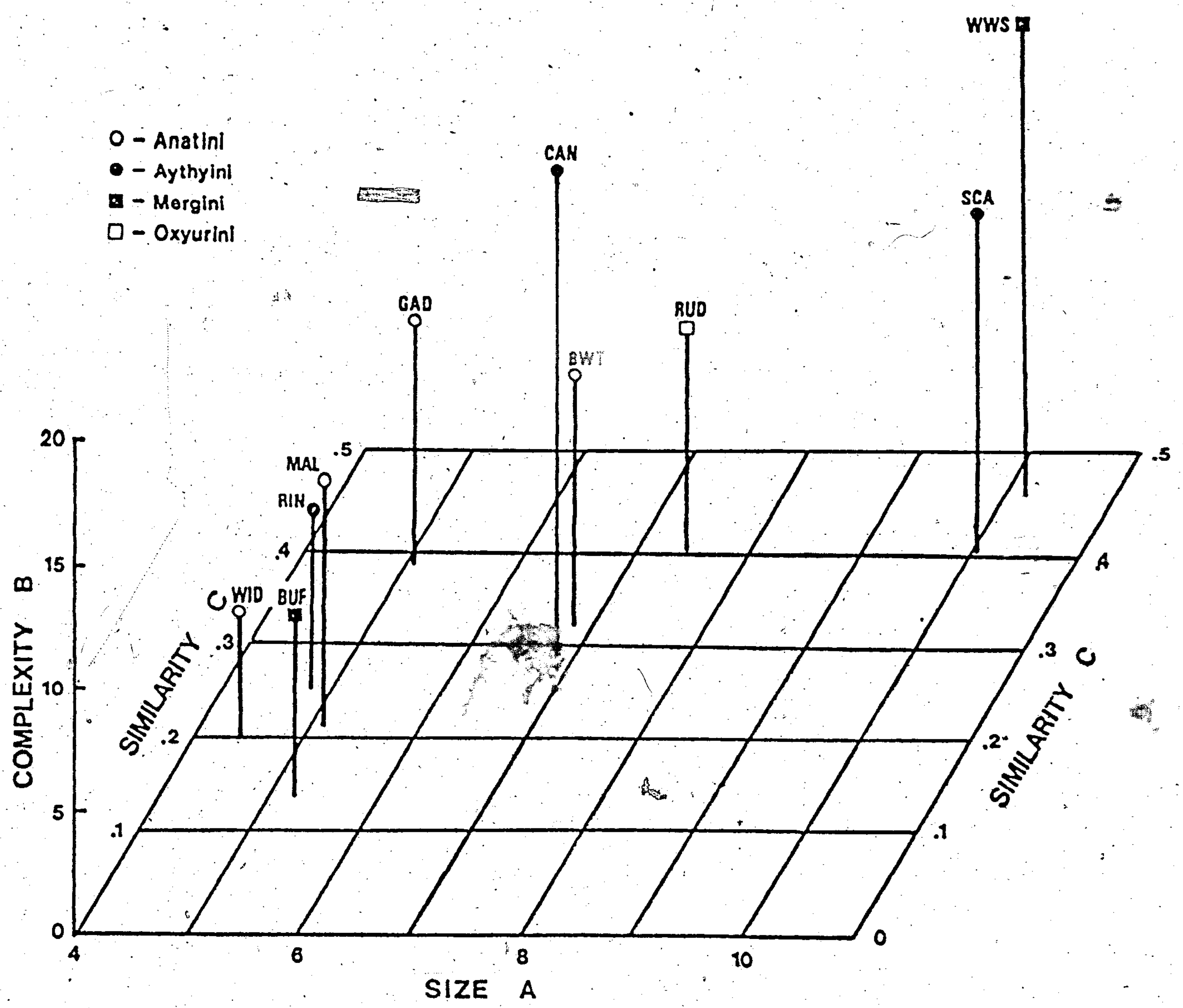

○ – Anatini
● – Aythyini
▣ – Mergini
□ – Oxyurini
WWS
CAN
SCA
GAD
RUD
BWT
MAL
RIN
WID
BUF
COMPLEXITY B
20
15
10
5
0
SIZE A
4
6
8
10
SIMILARITY C
.1
.2
.3
.4
.5
0

Figure 7. Number of helminth species shared (lower left triangle) and similarity values (upper right triangle) (Jaccard's Coefficient) between duck species. (GAD - Gadwall, WID - Widgeon, RUD - Ruddy, BWT - Blue-winged teal, BUF - Bufflehead, RIN - Ring-necked duck, MAL - Mallard, CAN - Canvasback, SCA - Scaup, WWS - White-winged scoter.)

Jaccard Similarity

		1.	2.	3.	4.	5.	6.	7.	8.	9.	10.
1.	GAD		47	27	32	32	30	23	20	16	14
2.	WID	9		44	34	34	28	21	19	19	15
3.	RUD	6	8		33	32	26	25	24	24	19
4.	BWT	11	9	10		34	22	31	23	24	28
5.	BUF	6	6	7	10		40	35	25	23	25
6.	RIN	6	7	5	6	9		32	31	19	15
7.	MAL	10	7	10	15	12	12		40	34	27
8.	CAN	10	7	12	15	12	12	24		46	23
9.	SCA	5	5	10	14	9	7	17	23		25
10.	WWS	8	6	8	12	11	6	16	[illegible]	13	

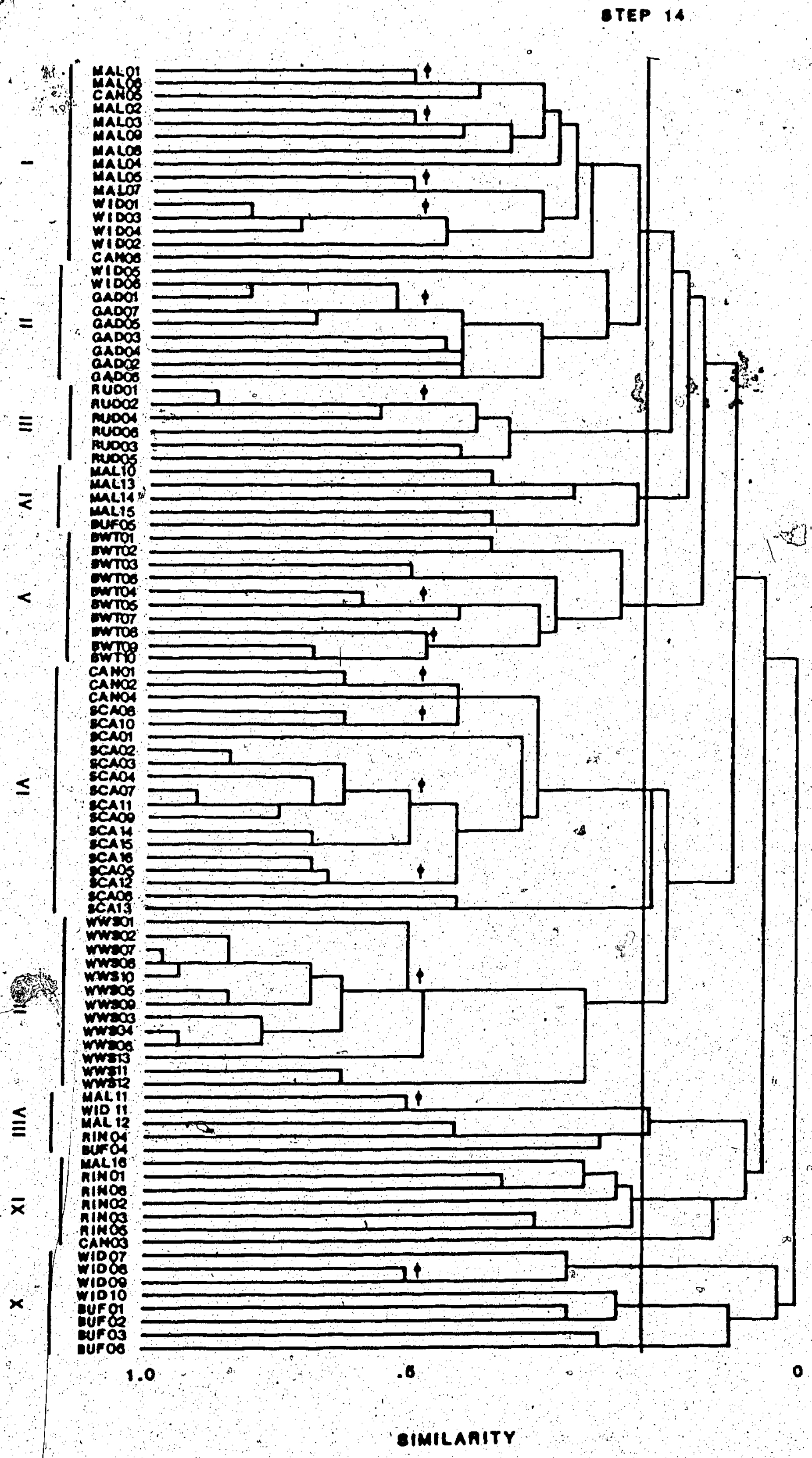
Number of Species

Cluster Analysis of Individual Birds

Initially all cluster analyses were done using all 118 taxa. Little difference was noted between the analyses on 118 and 75 taxa (43 rare species removed). Because of their infrequent occurrence and low numbers, the 43 species contributed little to the similarity between individual birds; they were not be used in the subsequent analyses.

Analysis of qualitative similarities of the 75 taxa formed 9 distinct clusters (I-IX) and 1 cluster (X) (Fig. 8) of individuals with little similarity. All individuals of the three duck species (ruddy, scoter, blue-winged teal) formed separate single species clusters (Fig. 8). In addition, all scaup (16/16) cluster with 3 (of 6) canvasbacks, all gadwall (7/7) clustered with 2 (of 11) widgeon and most of the ring-necked ducks (5/6) clustered with 1 (of 6) canvasback and 1 (of 16) mallard. In addition, smaller single species clusters may be determined within some of the larger clusters (e.g., cluster I-mallards 2, 3, 8, 9;widgeons 1 to 4). In general, individuals of one species did tend to cluster with other individuals of the same species; for six of the ten species of ducks, this cluster involved almost all of the birds. However, individual widgeon, mallards, canvasbacks and buffleheads either did not cluster together, or formed small clusters, unrelated to others of the same species.

Figure 8. Cluster analysis (normal) of similarity values of occurrence of seventy-five parasite taxa in individual birds of ten species. Vertical axis represents similarity values of Jaccards Coefficient. Vertical arrow with solid circle indicates groups with 50 percent of greater sinilarity. (WID - Widgeon, GAD - Gadwall, MAL - Mallard, BWT - Blue-winged teal, RUD - Ruddy, CAN - Canvasback, RIN - Ring-necked duck, WWS - White-winged scoter, SCA - Scaup.)

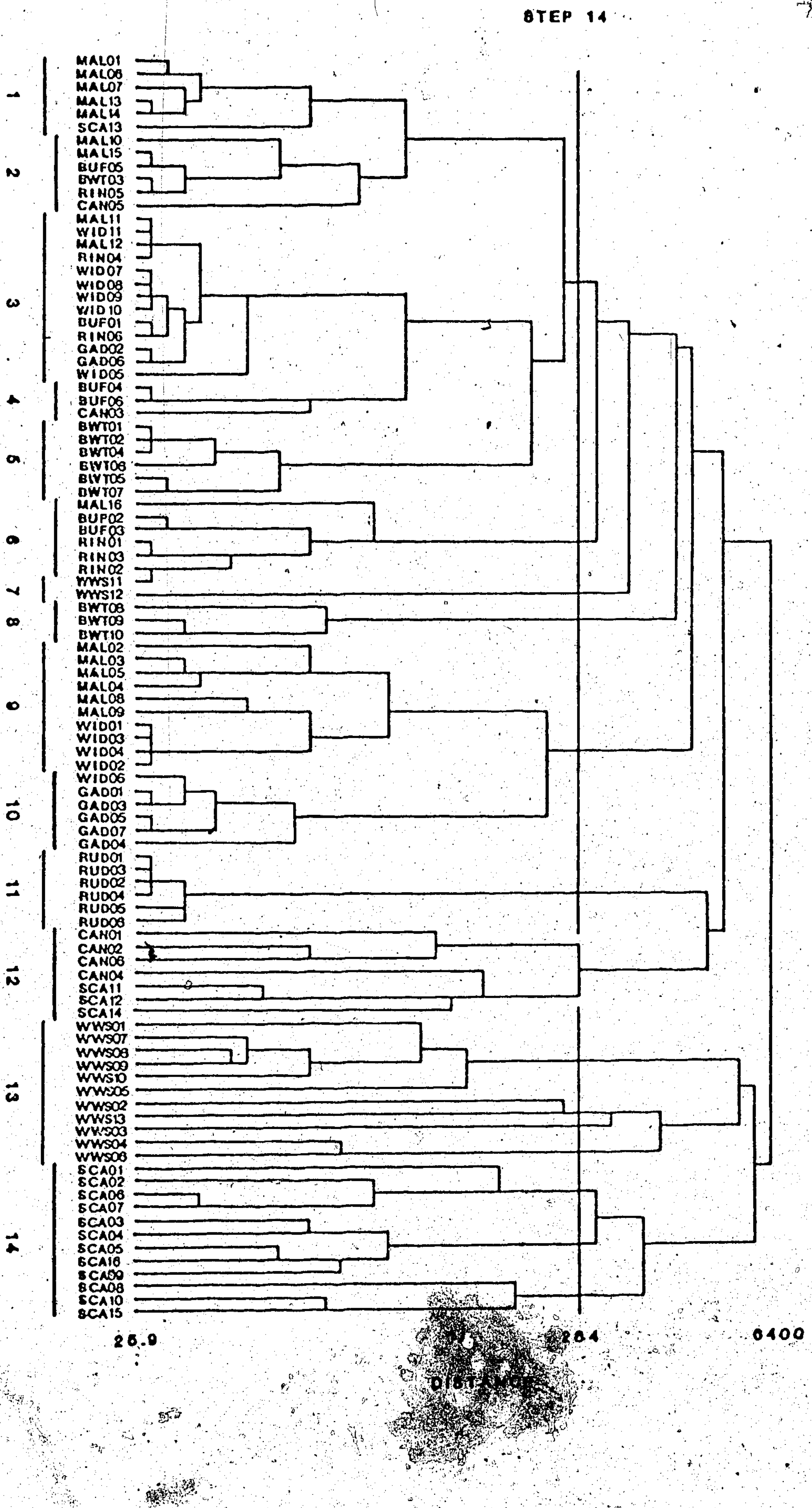

STEP 14
I
II
III
IV
V
VI
VII
VIII
IX
X
MAL01
MAL06
CAN05
MAL02
MAL03
MAL09
MAL08
MAL04
MAL05
MAL07
WID01
WID03
WID04
WID02
CAN06
WID05
WID06
GAD01
GAD07
GAD05
GAD03
GAD04
GAD02
GAD06
RUD01
RUD02
RUD04
RUD06
RUD03
RUD05
MAL10
MAL13
MAL14
MAL15
BUF05
BWT01
BWT02
BWT03
BWT06
BWT04
BWT05
BWT07
BWT08
BWT09
BWT10
CAN01
CAN02
CAN04
SCA08
SCA10
SCA01
SCA02
SCA03
SCA04
SCA07
SCA11
SCA09
SCA14
SCA15
SCA16
SCA05
SCA12
SCA06
SCA13
WWS01
WWS02
WWS07
WWS08
WWS10
WWS05
WWS09
WWS03
WWS04
WWS06
WWS13
WWS11
WWS12
MAL11
WID 11
MAL 12
RIN04
BUF04
MAL16
RIN01
RIN08
RIN02
RIN03
RIN05
CAN03
WID07
WID08
WID09
WID10
BUF01
BUF02
BUF03
BUF06
1.0
.5
0
SIMILARITY

Considering the large number of species, similarity at the 50% level is considered to be high. Seventeen clusters are apparent at this level: 10 were pairs of individuals (of which 9 were of the same duck species), 2 were triplets of single species (widgeon and ruddy), one is a group of four individuals (3 gadwall and 1 widgeon), and the other two were single species groups of nine scaup and 10 scoter.

The splitting of four species of ducks into two or more groups of individuals indicates a more complex pattern of similarity. For example, in cluster VI, three canvasbacks clustered with a group of scaup; in cluster I, 2 canvasbacks clustered with mallards and widgeon; in cluster VIII, the remaining canvasback clustered with the ring-necked ducks. The first 3 canvasbacks had high species numbers (>20), the last 3, low species numbers (<16). In part, the patterns were associated with differences between lakes. Three of the four mallards in cluster IV were collected from Rattlesnake Lake. Widgeon were split into 4 groups (clusters I, II, IX and X). Widgeon in cluster I were all from Charron Lake. Individuals in cluster II (with gadwalls) were a mated pair collected from Bellshill Lake, where gadwalls were common, and both contained a parasite, otherwise restricted to gadwalls. A second pair of widgeon collected from Bellshill Lake clustered in group X along with other birds with few parasites. The differences between these two pairs from the same lake suggests variation in parasite availability within lakes as well as between lakes.

An analysis of quantitative similarities (using the Euclidean distance analysis) distinguished a number of major clusters similar to those of the Jaccard analysis (Fig. 9). Ruddy formed a single species cluster of all individuals in group 11; scoter formed two separate single species groups, 7 (2 birds) and 13 (all the rest); blue-winged teal formed two single species groups, 5 (6 birds) and 8 (3 of remaining 4). Eleven (of 16) scaup formed a single species group while 3 scaup, all collected from Fleeinghorse Lake, clustered with 4 (of 6) canvasbacks. The three canvasback were the same individuals clustering with the scaup in the Jaccard analysis. Five (of 7) gadwall grouped with the same widgeon as in the Jaccard analysis. The most obvious difference between the analyses of the qualitative and quantitative data was the tendency to separate what were single species groups in the former into different groups in the latter. Blue-winged teal were separated into a group with high numbers of species and individuals (group 8, 3 of 10 birds, all collected from Bellshill Lake in 1979) and one (group 5) with low numbers. The two (of 13) scoter in duck group 7 had fewer species and lower numbers of individuals compared to the remaining scoter (Table 5). The group of 3 ring-necked ducks in cluster 6 were all collected in 1977. The ring-necked ducks collected in 1979 entered individually into clusters 2 and 3.

Figure 9. Cluster analysis (normal) of similarity values of numbers individuals of seventy-five parasite taxa in individual birds of ten duck species. Vertical axis represents similarity values of Euclidian distance. (WID - Widgeon, GAD - Gadwall, MAL - Mallard, BWT - Blue-winged teal, RUD - Ruddy, CAN - Canvasback, RIN - Ringneck duck, WWS - White-winged scoter, SCA - Scaup.)


STEP 14
1
MAL01
MAL06
MAL07
MAL13
MAL14
SCA13
2
MAL10
MAL15
BUF05
BWT03
RIN05
CAN05
3
MAL11
WID11
MAL12
RIN04
WID07
WID08
WID09
WID10
BUF01
RIN06
GAD02
GAD06
WID05
4
BUF04
BUF06
CAN03
5
BWT01
BWT02
BWT04
BWT06
BWT05
BWT07
6
MAL16
BUF02
BUF03
RIN01
RIN03
RIN02
7
WWS11
WWS12
8
BWT08
BWT09
BWT10
9
MAL02
MAL03
MAL05
MAL04
MAL08
MAL09
WID01
WID03
WID04
WID02
10
WID06
GAD01
GAD03
GAD05
GAD07
GAD04
11
RUD01
RUD03
RUD02
RUD04
RUD05
RUD06
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CAN01
CAN02
CAN06
CAN04
SCA11
SCA12
SCA14
13
WWS01
WWS07
WWS08
WWS09
WWS10
WWS05
WWS02
WWS13
WWS03
WWS04
WWS06
14
SCA01
SCA02
SCA06
SCA07
SCA03
SCA04
SCA05
SCA16
SCA09
SCA08
SCA10
SCA15
25.9
264
6400
DISTANCE

Table [illegible]. Mean number and range of helminth species and individuals within each duck group as derived by cluster analysis using Euclidean distance.

Duck Groups	N*	Mean Number of Species	Mean Number of Individuals
1	6	8 (5-10)	133 (18-319)
2	6	10 (4-15)	368 (23-1,453)
3	13	4 (1-9)	27 (3-123)
4	3	7 (5-9)	232 (109-399)
5	6	8 (3-16)	147 (16-274)
6	6	10 (3-19)	392 (66-1,151)
7	2	7 (6-8)	1,803 (1,082-2,525)
8	3	13 (10-16)	2,534 (840-4,586)
9	10	11 (7-20)	263 (60-660)
10	6	11 (8-18)	238 (77-461)
11	6	8 (5-10)	1,680 (304-2,627)
12	8	20 (8-31)	1,110 (81-1,784)
13	11	21 (16-27)	32,866 (5,727-128,660)
14	11	14 (10-23)	33,031 (3,130-83,548)

---

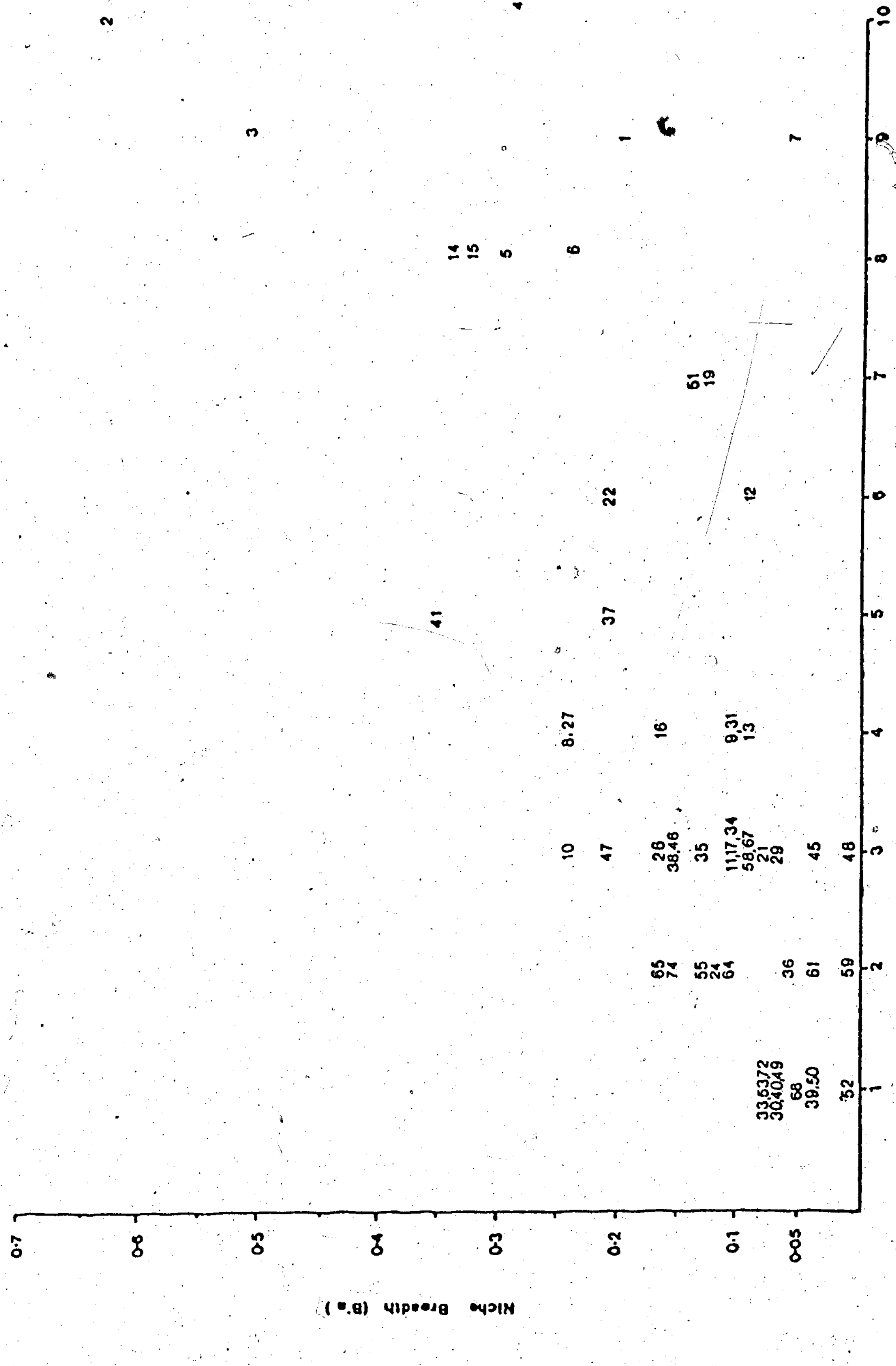
*N - number of ducks in each duck group

Host species, lake, and to a lesser extent, year or regions within a lake may all affect the similarity in the community structure of parasites of waterfowl.

Niche Breadth of Helminth Species

Niche breadth (B′a, using equation 31 of Hurlbert, 1978) was calculated for those parasite species for which mature individuals were found (Table 2). The index (B′a) requires a measure of resource abundance in its calculation. I used the sample size of each host species as a measure of resource abundance. Values of B′a can range from 0.0 for a parasite found in only one host species to 1.0 for an extreme generalist, found in equal abundances in all host species. Calculated values of B′a ranged from 0 to 0.66 (Table 2). Twenty-one parasites (of 63 which matured) could be classified as specialists (B′a<.10). Echinoparyphium recurvatum was included in this group, even though this species occurred in 9 of the 10 host species. Most individuals of this species occurred in one host species (canvasback) with one of the smaller sample sizes (6). Two of the parasites, Apatemon gracilis and Corynosoma constrictum had B′a values of greater than 0.5, indicating they are relatively broad generalists. The relation between niche breadth (B′a) and the number of hosts in which a species occurs is illustrated in Figure 10.

Figure 10. Relationship between helminth niche breadth (B'a) and the number of hosts infected with mature helminth species individuals. (Species numerical codes are peesented as listed in Appendix 2.)


Niche Breadth (B'a)
0·7
0·6
0·5
0·4
0·3
0·2
0·1
0·05
Number of Hosts
1
2
3
4
5
6
7
8
9
10
2
3
4
1
7
14
15
5
6
61
19
22
12
41
37
8,27
16
9,31
13
10
47
28
38,46
35
11,17,34
58,67
21
29
45
48
65
74
55
24
64
36
61
59
33,53,72
30,40,49
68
39,50
52

Niche breadth of mature individuals indicated a similar range from extreme host specialists (0.0) to one species (A. gracilis) with a value greater than 0.5 (Table 2). Six species, including C. constrictum, had calculated values of greater than 0.25.

Habitat specialist and generalist are relative terms which can be defined in different ways. The simplest definition of a specialist is a species which occurs in only one habitat. A generalist is a species which occurs in all habitats. This definition however, does not take into account relative abundances of the organisms or the availability of different habitats. Thus, the terms can be defined by using a measure of niche breadth that takes into account relative abundances and relative resource availabiltiy. Another definition of specialist and generalist involves the fitness of the species. A specialist has maximum fitness in one habitat, a generalist has equal fitness across all habitats (Rosenzwieg, 1981). Unfortunately, most studies do not have all information necessary to apply the last two definitons. In the above analyses (B′a and B′a (mature)) I have examined the latter two definitions. For those species which occur frequently in a host species B′a (mature) is a good measure of niche breadth as related to relative fitness.

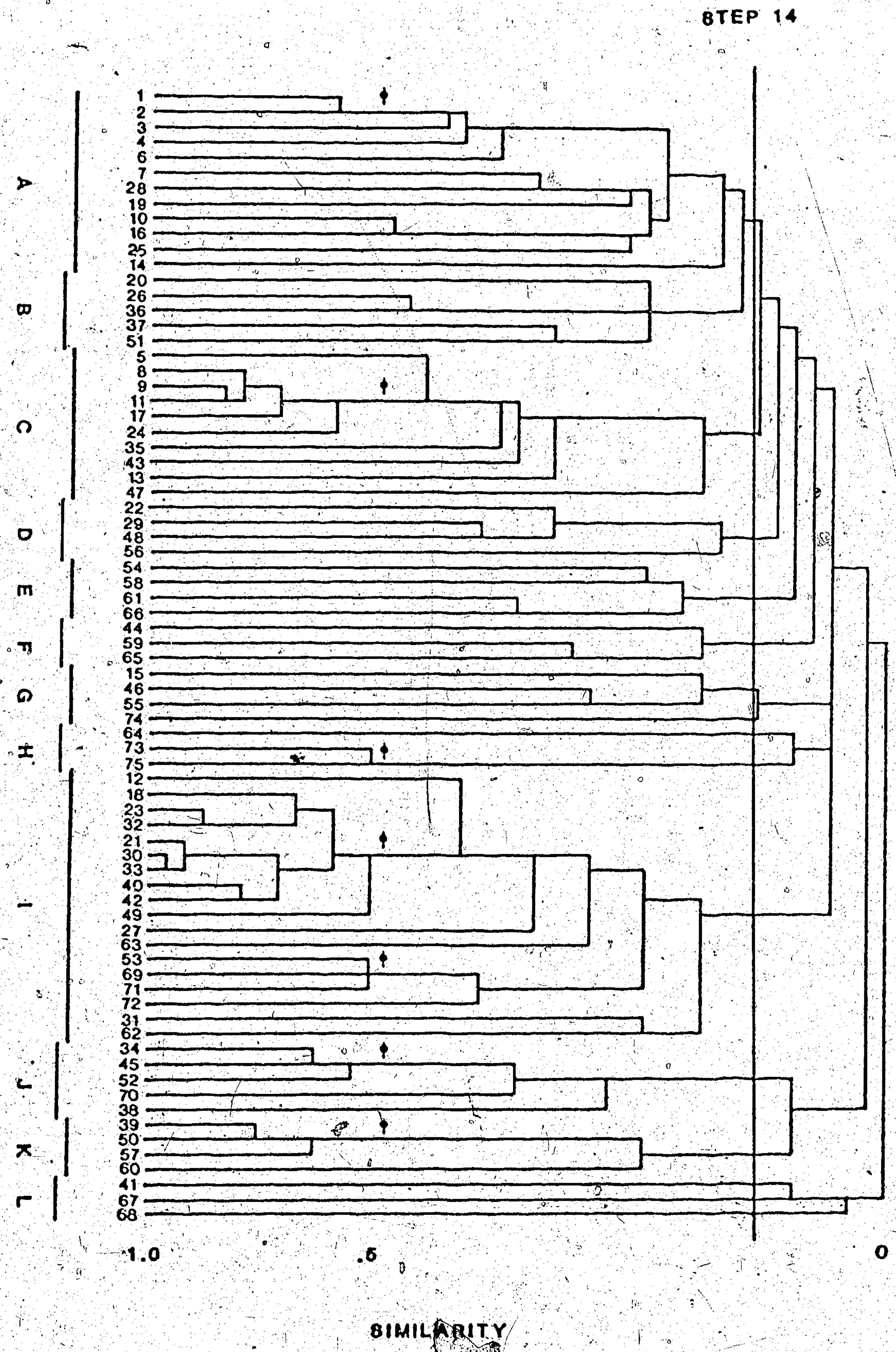
Similarity in Occurrence of Helminth Species (Inverse Analysis)

Jaccard's coefficent of similarities among parasite species indicated 12 major parasite species groups (Fig. 11; A-L; see Appendix 4 for species names). Cluster A contains eight of the fifteen most widespread species in the entire data set (Table 2). Mean niche breadth (B'a) was highest for group A (Table 6). Five groups had mean niche breadth (B'a) of less than 0.1 indicating they are composed primarily of relative host specialists.

Seven groups of interest were noted at the 50% similarity level (Fig. 11; solid arrows): one pair of widely distributed species; and one pair of parasites found in scaup, three triplets, one group of five species and another group of nine species found primarily in a single host species each.

The Euclidean distance dendrogram included seventeen major species groupings (Fig.12; AA-QQ; see Appendix 5 for species names). Cluster AA contains 4 of the most prevalent species. Mean niche breadth was highest for this group (Table 6). Five groups had mean niche breadth values of less than 0.1.

Figure 11. Cluster analysis (inverse) of seventy-five parasite taxa using similarity values of their occurrences in ninety-seven birds of ten duck species. Vertical axis represents similarity values of Jaccard's Coefficient. (Species codes for each parasite group A-L are listed in Appendix 4.)


STEP 14
1
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3
4
6
7
28
19
10
16
25
14
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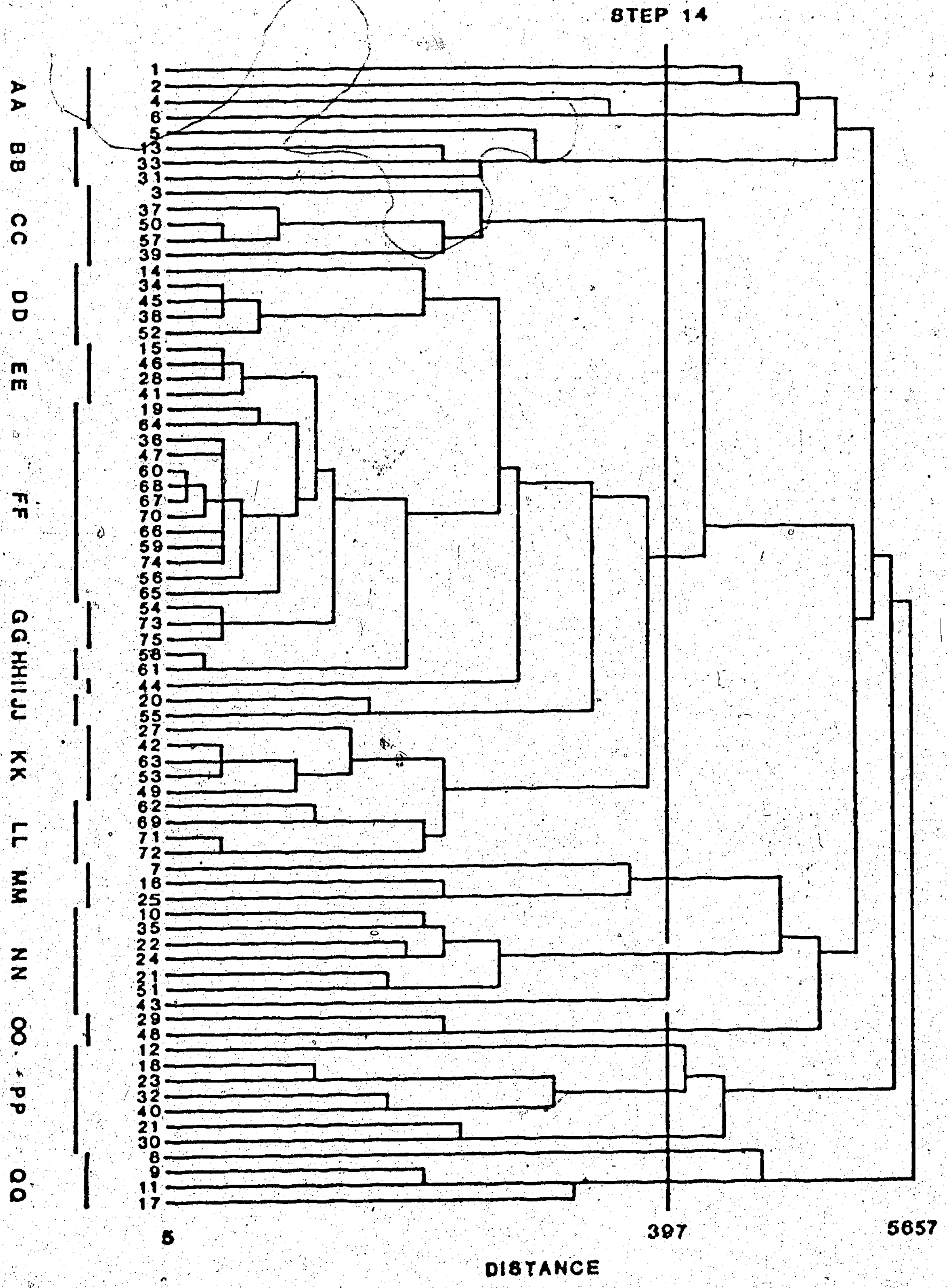
26
36
37
51
5
8
9
11
17
24
35
43
13
47
22
29
48
56
54
58
61
66
44
59
65
15
46
55
74
64
73
75
12
18
23
32
21
30
33
40
42
49
27
63
53
69
71
72
31
62
34
45
52
70
38
39
50
57
60
41
67
68
A
B
C
D
E
F
G
H
I
J
K
L
1.0
.5
0
SIMILARITY

Table 6. Mean breadth (B'a) in helminth groups derived by the Jaccard and Euclidean cluster analyses.

Jaccard Helminth Groups	B'a*	Euclidean Helminth Groups	B'a
A	.29 ± .16	AA	.35 ± .21
B	.15 ± .06	BB	.14 ± .10
C	.16 ± .07	CC	.17 ± .21
D	.09 ± .09	DD	.13 ± .14
E	.14 ± .10	EE	.26 ± .10
F	.08 ± .08	FF	.12 ± .08
G	.20 ± .11	GG	.13 ± .04
H	.11 ± .00	HH	.05 ± .06
I	.09 ± .04	II	.05
J	.06 ± .06	JJ	.14 ± .02
K	.08 ± .08	KK	.11 ± .08
L	.16 ± .16	LL	.07 ± .00
		MM	.17 ± .11
		NN	.15 ± .06
		OO	.04 ± .04
		PP	.08 ± .01
		QQ	.14 ± .07

*B'a - mean niche breadth

Figure 12. Cluster analysis (inverse) of seventy-five parasite taxa using similarity values of their occurrences of numbers of individuals in ninety-seven birds of ten duck species. Vertical axis represents similarity values of Jaccard's Coefficient. (Species codes for each parasite group AA-QQ are listed in Appendix 5.)


STEP 14
AA
BB
CC
DD
EE
FF
GG
HH
II
JJ
KK
LL
MM
NN
OO
OO
PP
QQ
1
2
4
6
5
13
33
31
3
37
50
57
39
14
34
45
38
52
15
46
28
41
19
64
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27
42
63
53
49
62
69
71
72
7
16
25
10
35
22
24
21
51
43
29
48
12
18
23
32
40
21
30
8
9
11
17
5
397
5657
DISTANCE

Common and Characteristic Species

Stephenson et al. (1972) have developed a method to compare these groupings of 'normal' and 'inverse' analyses by constructing a summary coincidence table.

Comparison of the parasite and duck groups selected from the Jaccard analysis (Fig. 13; values in Appendix 6) indicated parasite group A did not concentrate (>20% of the individuals of a parasite species) in any one duck group but was important within all groups. This group also had the highest mean niche breadth value (Table 6). Each of the other groups was concentrated in one or two duck groups. In duck group I and IV, parasite group A appeard to be the only important (>20%) group. All other duck groups had at least one other important parasite group.

Where a parasite group was concentrated in a given duck group and also was important in that duck group the parasite group can be regarded as characterizing that duck group. Six of the duck groups were characterized by one of the parasite groups (Fig. 13). All of these duck groups were dominated by a single duck species. Several of these parasite groups had mean niche breadth values of less than 1.0 (D, I, J, K). The remaining 4 duck groups were not characterized by parasite groups. All of these duck groups were a composite of host species. No parasite group characterized more than one duck group, and no duck group was characterized by more than one parasite group.

Figure 18. Concentration of helminth species groups across (+) duck groups and importance of helminth species groups within (0) duck groups derived by cluster analysis using Jaccard's Coefficient of similarity. (⊕) - helminth species groups characterizing duck groups). (See text for further explanation).

	DUCK GROUPS									
HELMINTH SPECIES GROUPS	I	II	III	IV	V	VI	VII	VIII	IX	X
A	0	0	0	0	0	0	0	0	0	0
B									⊕	
C						⊕	+			0
D			⊕							
E				+		+				
F									+	
G								0	+	
H						+				
I							⊕			
J		⊕								
K					⊕					
L	+			+						

The same procedure was repeated using duck species instead of duck groups (Fig. 14). It is not surprising that that parasite species groups which characterized duck groups dominated by single duck species, also characterized the same duck species (Table 7).

The same analyses were run on data from the Euclidean cluster analysis (Figs. 15 and 16). The group of generalists (AA) was smaller and not as important in all duck groups. Some parasite groups often characterized two duck groups. Usually (e.g., BB,CC), but not always (e.g., QQ), the two groups comprised the same duck species. Some duck groups (1[illegible], 13, 14) were also characterized by two parasite groups. These features illustrate the greater differentiating power of the Euclidean analysis.

In the analysis using duck species, six duck species were characterized by 7 of the same parasite groups which had characterized the duck groups. Five of these duck species were the same as those characterized by parasite groups in the Jaccard analysis. Ring-necked duck, characterized by a Jaccard parasite group, was replaced by the mallard, characterized by a Euclidean helminth group. Widgeon, bufflehead and canvasback could not be characterized by any species group from either the Jaccard or Euclidean distance cluster analyses.

Figure 14. Concentration of helminth species groups derived by cluster analysis using Jaccard's Coefficient of similarity across (+) duck species and the importance of helminth species within (O) duck species. The notation ⊕ indicates the helminth species group which characterizes the duck species. (See text for further details and explanation).

	DUCK SPECIES									
HELMINTH SPECIES GROUPS	WID	BUF	RIN	MAL	RUD	BWT	GAD	CAN	SCA	WWS
A	0	0	0	0	0	0	0	0	0	0
B			⊕					+		
C								+	⊕	
D					⊕					
E				+				+		
F		+						+		
G			+	+						
H								+	+	
I										⊕
J							⊕			
K						⊕				
L	+									

Table 7. Comparison of helminth species groups characterizing the duck groups and duck species as derived by cluster analysis using Jaccard's Coefficient of similarity.

Helminth Species Group	B	[illegible]	D	I
Duck Group	9-1/16 Mallard* 1/6 Canvasback 5/6 Ring-necked duck	6-3/6 Canvasback 16/16 Scaup	3-6/6 Ruddy	7-13/13 Scoter
Duck Species	Ring-necked duck	Scaup	Ruddy	Scoter
Helminth Species	D. laevis**	P. marilis** H. spinocirrosa** H. abortiva** H. pusilla** H. tuvensis** R. pittalugi** H. recurvata L. skrjabini**	C. hebraicus R. cyrtoides** D. excentricus**	H. albertensis** H. spiraliburssata** L. mathevossianae** H. melanittae** H. AB** H. formosoides**

Table 7 (continued).

Helminth Species Group	J	K	
Duck Group	2-7/7 Gadwall 2/11 Widgeon	5-10/10 Blue-winged teal	Not characterized by cluster analysis using Jaccard coefficient (see text)
Duck Species	Gadwall	Blue-winged teal	Canvasback
Helminth Species	*H.* WWW** *E.* QQQ** *D. spinata***	*E. rosseteri*** *E.* NNN**	*D. n.sp.* TT** *A. spinulosa***

* Duck group number - number of individual birds / total number of birds for each duck species (see Figure 8).

** Denotes characteristic species of helminths.

Figure 15. Concentration of helminth species groups across (+) duck groups and the importance of helminth species groups within (O) duck groups derived by cluster analysis using Euclidean distance. (⊕ - helminth species groups characterizing duck groups). (See text for further explanation).

HELMINTH SPECIES GROUPS	DUCK GROUPS													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
AA	0		0						0	0	0			
BB							⊕						⊕	
CC					⊕			⊕						
DD			0							⊕				
EE		+				+								
FF														
GG												+		
HH		+										+		
II				⊕										
JJ						⊕								
KK							+						+	
LL													+	
MM	0	⊕												
NN												⊕		⊕
OO											⊕			
PP							0	0					⊕	
QQ												⊕		⊕

Figure 16. Concentration of helminth species groups derived by cluster analysis using Euclidean distance across (+) duck species and importance of helminth species groups within (O) duck species. (⊕ - helminth species groups characterizing duck species). (See text for further explanation).

HELMINTH SPECIES GROUPS	DUCK SPECIES									
	WID	BUF	RIN	MAL	RUD	BWT	GAD	CAN	SCA	WWS
AA	0		0	0	0		0			
BB									+	+
CC						⊕				
DD							⊕			
EE		+		+						
FF								+		
GG										
HH				+				+		
II		+						+		
JJ		+	+							
KK										+
LL										+
MM				⊕				+		
NN								+	⊕	
OO					⊕					
PP						0				⊕
QQ									⊕	

The above analyses were done to determine if duck species (or groups) have distinct parasite groups. Because the analyses included species which occurred infrequently (<3 birds) some of the parasite species groups include species which were found in less than 50% of a duck species sample. In addition, some of the helminth species did not mature in any of the duck species. Only those parasite species, within parasite groups which characterized duck species, which occurred in more than 50% of any duck species sample and matured will be considered a characteristic species. Species of parasites which characterized the above host species in the Jaccard and Euclidean analysis overlapped extensively (Tables 7 and 8). Only one species, Polymorphus marilis, characterized two different duck species, scaup in the Jaccard analysis and white-winged scoter in the Euclidean analysis. However, P. marilis rarely matured in scoter; I consider it to be a characteristic parasite of scaup.

Table 8. Comparison of helminth species groups characterizing the duck groups and duck species as derived by cluster analysis using Euclidean distance.

Helminth Species Group	BB	CC	DD	II	JJ
Duck Group	7-2/13 White-winged scoter* 13-11/13 White-winged scoter	5-6/10 Blue-winged teal 8-3/10 Blue-winged teal	10-5/7 Gadwall 1/11 Widgeon	4-2/6 Bufflehead 1/6 Canvasback	6-3/6 Ring-necked duck 2/6 Bufflehead 1/6 Mallard
Duck Species		Blue-winged teal	Gadwall		
Helminth Species	<u>P</u>. <u>marilis</u> <u>L</u>. <u>mathevossianae</u>**	<u>E</u>. <u>rosseteri</u>** <u>E</u>. NNN**	<u>H</u>. WWW** <u>E</u>. QQQ** <u>D</u>. <u>spinata</u>**		<u>H</u>. <u>parvula</u>

Table 8 (continued).

Helminth Species Group	MM	NN	OO	PP	QQ
Duck Group	1-2/16 Mallard 1/10 Blue-winged teal 1/6 Bufflehead 1/6 Ring-necked duck	12-4/6 Canvasback 3/16 Scaup 14-11/16 Scaup	11-6/6 Ruddy	13-11/13 White-winged scoter	12-4/6 Canvasback 4/16 Scaup 14-11/16 Scaup
Duck Species	Mallard	Scaup	Ruddy	White-winged scoter	Scaup
Helminth Species	*H. fausti*	*H. recurvatum*** *R. pittalugi*** *H. tuvensis*** *D. coronula*	*R. cyrtoides*** *D. excentricus***	*H.* AD** *H. melanittae*** *H. spiraliborsata*** *H. albertensis***	*H. spinocirrosa*** *H. abortiva*** *H. pusilla*** *H. tuvensis***

* Duck-group number - number of individual birds / total number of birds for each duck species (see Figure 9).

** Denotes characteristic species of helminths.

Species Exchange

The majority of parasite species which matured in the waterfowl occurred in 2 or more duck species. Only seven species occurred exclusively in one duck species. In contrast, 15 of the parasites which matured occurred in 5 or more duck species and nine of these matured in 5 or more host species. Thus, ducks are not isolated habitat units, at the host species level but allow considerable parasite exchange (the spreading of a parasite species from a primary host to another, via an infective pool of intermediate hosts). A primary host is defined by Holmes et al. (1979) as the species which maintains the greatest proportion of mature individuals in the system, and depends in part on host population sizes, data which I do not have. For purposes of this study the potential primary host will be that duck species with the highest abundance (prevalence x mean number of individuals in infected hosts) of mature individuals of a parasite species. That parasite must also occur in >50% of the individuals of that duck species (because of small sample sizes).

Because populations sizes of host species are an important factor in determining primary hosts, the greater the number of host species in which a parasite species matures the more important the relative host population sizes become in assessing in which host that parasite species has the greatest reproductive potential, and contribution to the infective pool. Therefore, regional population sizes of waterfowl (Turner and Weaver, 1977) were also considered when assigning a host species as the potential primary host. For this reason I considered eight parasite species which occurred in eight or more host species separately. (A ninth species, Polymorphus marilis, has already been identified as a characteristic species of scaup despite its wide host range). Two of these species, Echinoparyphium recurvatum and Hymenolepis hopkinsi had mature individuals concentrated in one host species (Table 9). Large numbers of mature H. hopkinsi were found in gadwall, with lesser numbers in mallard. However, since mallard are the dominant waterfowl in this region it cannot be determined which is the primary host. The mature individuals of H. hopkinsi in mallard could be contributing more to the infective pool than those in gadwall. It is clear however, that the dabblers are the primary hosts. Both the prevalence (dabblers-36% vs divers-15%; G-test) and intensity (number of worms in each individual) (dabblers-54 ± 58.9 vs divers-9 ± 127.3; Mann Whitney U-test) were significantly different between the groups. Mature E. recurvatum were concentrated in canvasback. Canvasback populations are relatively sparse (10th in abundance; Turner and Weaver, 1977) in this region and cannot be considered as the primary host. Mature Polymorphus contortus and Corynosoma constrictum had the greater majority of their mature individuals in dabblers. For P. contortus both prevalence and intensity were

Table 9. Number of birds infected and abundance of mature individuals of 9 parasite species occurring in 8 or more host species.

	Widgeon		Bufflehead		Ring-necked duck		Mallard		Ruddy		Blue-winged teal		Gadwall		Canvasback		Scaup		White-winged scoter	
	N*	A**	N	A	N	A	N	A	N	A	N	A	N	A	N	A	N	A	N	A
1. _F._ _fasciolaris_	5/11	--	1/6	--	2/6	0.2	7/16	1.0	6/6	--	3/10	--	[illegible]	0.4	6/6	--	15/16	0.8	13/13	--
2. _A._ _gracilis_	5/11	2.0	1/6	0.2	4/6	3.5	12/16	24.0	5/6	26.0	6/10	3.0	4/7	--	4/6	43.0	11/16	18.0	7/13	19.0
3. _C._ _constrictum_	5/11	8.0	2/6	--	--	--	10/16	3.0	3/6	0.3	10/10	4.00	1/7	0.7	4/6	0.6	4/16	0.4	9/13	0.2
4. _H._ _hopkinsi_	5/11	2.0	1/6	--	2/6	0.2	12/16	22.0	1/6	--	2/10	--	5/7	69.0	3/6	11.0	2/16	--	11/13	5.2
5. _P._ _marilis_	1/11	0.2	4/6	2.0	--	--	2/16	0.1	2/6	0.8	1/10	--	--	--	4/6	3.2	15/16	21.0	11/13	0.6
6. _P._ _contortus_	8/11	24.0	2/6	--	1/6	--	8/16	11.0	2/6	0.2	--	--	7/7	14.0	3/6	9.0	--	--	5/13	0.1
7. _E._ _recurvatum_	2/11	0.4	2/6	2.0	2/6	5.0	8/16	17.0	1/6	4.5	7/10	1.0	1/7	2.0	5/6	101.0	2/16	0.7	--	--
14. _N._ _attenuatus_	1/11	0.2	3/6	2.0	--	--	5/16	0.9	2/6	0.1	3/10	--	3/7	--	--	--	1/16	--	3/13	0.7
15. _C._ _anatis_	4/11	0.5	3/6	2.0	2/6	1.0	5/16	0.3	1/6	--	1/10	0.2	1/7	--	--	--	3/16	0.4	--	--

*N - number of hosts infected / number of birds examined.

**A - abundance of mature individuals (with shelled eggs).

significantly higher than in divers (prevalence: dabblers-48% vs divers 9%; intensity: dabblers-25 ± 32.8 vs divers-11 ± 11.2). For C. constrictum prevalence was significantly different but not intensity (prevalence: dabblers-52% vs divers-11%; intensity: dabblers-8 ± 18.5 vs divers-2 ± 1.1). Greater numbers of mature individuals of Apatemon gracilis were found in divers (prevalence: dabblers-39% vs divers-57%; intensity: dabblers-26 ± 83.8 vs divers-32 ± 59.5). The intensity was significantly different but prevalence was not. Notocotylus attenuatus, Capillaria anatis and Fimbriaria fasciolaris could not be associated with any host species or group. These eight parasite species are considered to be host generalists.

Of the other 55 parasite species which matured in one or more hosts, 28 did not occur in more than 50% of any one host species sample. It is unlikely that such hosts would be the primary hosts in the system. Instead, it is possible the potential primary hosts of these species are other waterbirds not examined in this study. All but two of the remaining parasite species (Table 10) were identified as characteristic parasite species by either the Jaccard analysis or the Euclidean analysis. Two exceptions, Diorchis n.sp. TT and Anatinella spinulosa, were present in 6/6 and 4/6 individuals respectively, and matured only in canvasbacks. On that basis I consider them to be characteristic species of canvasbacks.

Table 10. Number of birds infected and abundances of mature individuals of 20 helminth species for which primary hosts can be determined.

HELMINTH SPECIES	WIDGEON		BUFFLEHEAD		RING-NECKED DUCK		MALLARD		RUDDY		BLUE-WINGED TEAL		GADWALL		CANVASBACK		SCAUP		SCOTER	
	N*	A**	N	A	N	A	N	A	N	A	N*	A**	N	A	N	A	N	A	N	A
8. H. spinocirrosa	--	--	--	--	--	--	2/16	--	--	--	--	--	--	--	4/6	50.5	15/16	4183.9	6/13	350.8
9. H. abortiva	--	--	--	--	--	--	1/16	--	--	--	--	--	--	--	2/6	3.7	15/16	4084.4	7/13	--
10. D. coronula	--	--	--	--	--	--	10/16	1.7	--	--	--	--	--	--	4/6	--	10/16	1.6	--	--
11. M. pusilla	--	--	--	--	--	--	--	--	--	--	--	--	--	--	3/6	13.2	15/16	2068.4	4/13	--
12. H. AB	--	--	--	--	--	--	3/16	0.1	1/6	--	6/10	221.5	1/7	--	1/6	--	--	--	11/13	2181.6
13. L. skrjabini	--	--	2/6	--	--	--	--	--	--	--	2/10	--	--	--	--	--	9/16	0.4	--	--
16. M. fausti	--	--	--	--	--	--	11/16	2.5	--	--	1/10	--	--	--	4/6	5.7	3/16	0.7	--	--
17. M. tuvensis	--	--	--	--	--	--	--	--	--	--	--	--	--	--	2/6	0.3	15/16	49.8	2/13	--
21. M. spiralibursata	--	--	--	--	--	--	1/16	--	--	--	--	--	--	--	--	--	1/16	0.2	13/13	202.9
22. C. hebraicus	--	--	--	--	--	--	--	--	4/6	6.2	1/10	0.2	--	--	2/6	0.2	7/16	3.9	1/13	0.9
24. R. pittalugi	--	--	--	--	--	--	--	--	--	--	--	--	--	--	3/6	--	12/16	5.4	--	--
28. D. n.sp. TT	--	--	--	--	3/6	--	--	--	--	--	--	--	--	--	6/6	3.7	3/16	--	--	--
29. B. cyrtoides	--	--	--	--	--	--	--	--	6/6	551.6	--	--	--	--	2/6	8.2	4/16	--	--	--
34. E. OOQ	2/11	0.5	--	--	--	--	--	--	--	--	4/10	0.1	6/7	2.6	--	--	--	--	--	--
35. M. recurvatum	--	--	1/6	--	--	--	--	--	--	--	--	--	--	--	1/6	0.2	9/16	48.1	--	--
36. D. laevis	--	--	--	--	6/6	1.8	--	--	--	--	--	--	--	--	5/6	0.2	--	--	--	--
45. D. spinata	2/11	0.1	--	--	--	--	--	--	--	--	2/10	--	6/7	4.3	--	--	--	--	--	--
48. D. excentricus	--	--	--	--	--	--	--	--	6/6	0.2	--	--	--	--	1/6	--	2/16	--	--	--
55. M. parvula	--	--	--	--	4/6	18.7	2/16	0.7	--	--	--	--	--	--	--	--	--	--	--	--
59. A. spinulosa	--	--	--	--	--	--	--	--	2/6	--	--	--	--	--	4/6	1.2	--	--	--	--

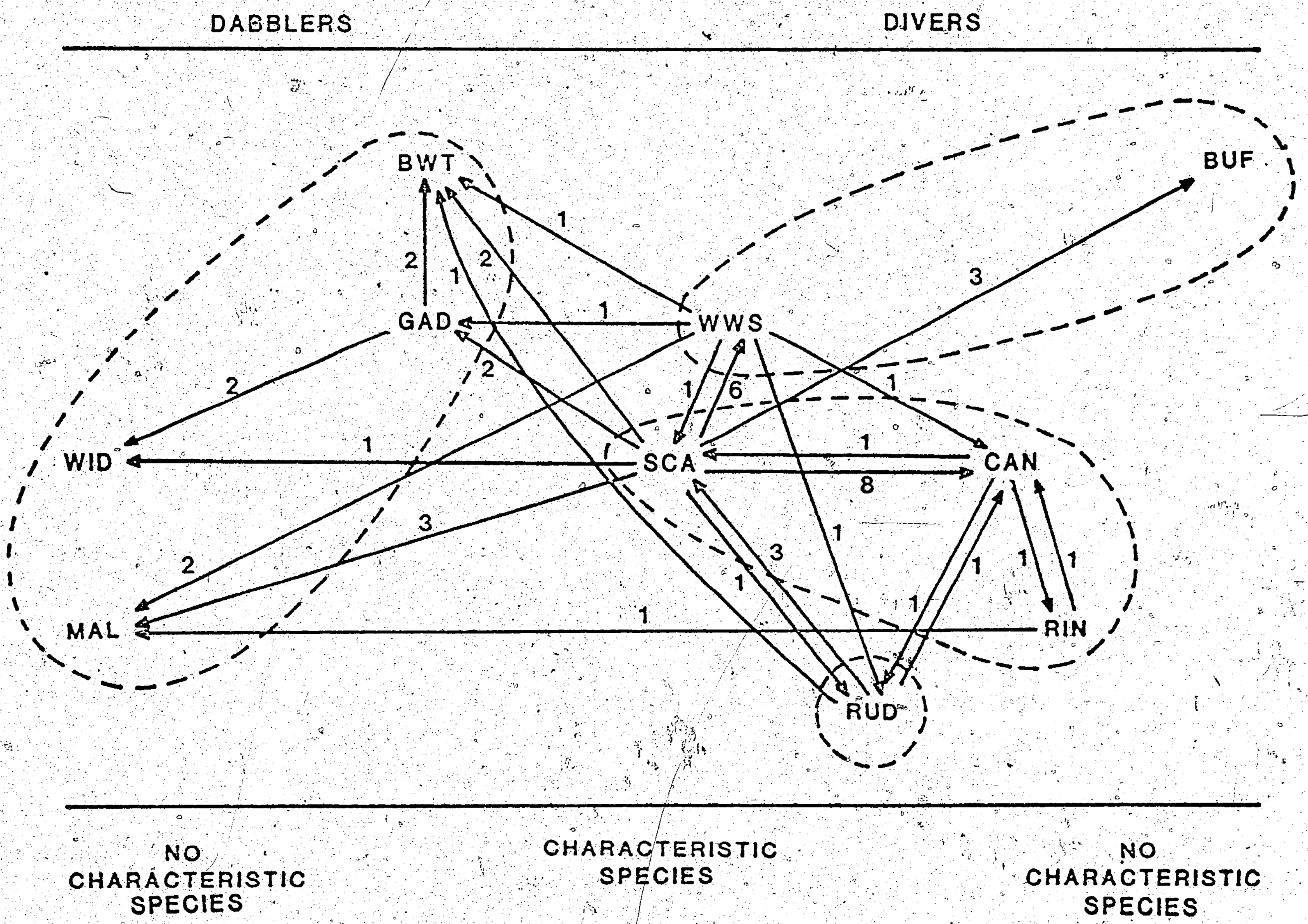
* Number of infected hosts / number of birds examined.

** Abundance of mature helminth individuals.

Hymenolepis fausti, was selected as a characteristic species of mallards by the Euclidean distance analysis but mature individuals were abundant in canvasback. Mallards are abundant in this region, while canvasback are sparse, thus a primary host for H. fausti cannot be determined (nor can it be considered a characteristic species of mallard). The same arguments hold for two other species, Cotylurus hebraicus, a characteristic species of ruddy according to the Jaccard analysis but with mature individuals common in scaup, and Dicranotaenia coronula a characteristic species of scaup by the Euclidean analysis, but with mature individuals common in mallards. Primary hosts of these three species cannot be determined; they will be omitted from some of the subsequent analyses. In general, comparison of the characteristic parasite species with the primary hosts and their parasite species agrees with the Jaccard analysis. The Euclidean analysis may be more useful in partitioning parasite species within host groups (i.e., parasite species which may characterize host individuals collected from one lake and not another). Therefore, I regard those species selected by the Jaccard analysis (with the exceptions noted above), and those species for which single primary host species can be determined, as characteristic species (specialists) of that host. These species are indicated in Tables 7 and 8. All of these species had low B′a (mature) values indicating specialization in resource use (Table 2).

The characteristic species which occurred in more than one duck species were examined for exchange to other host species (Fig. 17). Most of the exchange occurred between divers, or from divers to dabblers, which had well established characteristic species. Very little exchange occurred between the dabblers. The greatest amount of exchange involved the spread of characteristic species of scaup to other ducks.

Figure 17. Number of helminth species exchanged from primary hosts to other duck species. (MAL - Mallard, WID - Widgeon, GAD - Gadwall, BWT - Blue-winged teal, SCA - Scaup, WWS - White-winged scoter, RUD - Ruddy, CAN - Canvasback, RIN - Ring-necked duck, BUF - Bufflehead). Numbers refer to parasite species from primary host to other duck species.


DABBLERS
DIVERS
BWT
BUF
GAD
WWS
WID
SCA
CAN
MAL
RIN
RUD
1
2
2
1
1
2
2
3
1
6
1
1
8
3
1
1
1
1
1
1
3
2
1
1
NO CHARACTERISTIC SPECIES
CHARACTERISTIC SPECIES
NO CHARACTERISTIC SPECIES

DISCUSSION

Price (1980) supported his conclusion that parasites are specialists primarily by comparing the number of host taxa used by parasites to the number of prey items used by predators. Holmes and Price (1980) conducted a similar analysis of the range of host taxa used on a list of parasites of fishes of Canada (Margolis and Arthur, 1979); they concluded that generalists are not uncommon. Using the same analysis on my data, nine of the 75 parasite species found in three or more birds were found in eight or more species of hosts, and only 18 were found in only one species of host.

However, it is clear that the presence or absence of a species in a host is not a good measure of specialization. Quantitative methods (cluster analyses, B′a measures) revealed a wide range of degrees of specialization, again spanning the complete range from total generalists to those concentrating their individuals in only a single host species. The best measure of whether a parasite species is a specialist or generalist involves an assessment of its reproductive fitness across host species (i.e., B′a(mature) or primary host analysis). Within this study, only seven parasite species were host specific, occurring and maturing in only one duck species. Seventeen others occurred in several hosts but maintained most of their reproductive populations in one host (primary host). These specialist parasites characterized the parasite communities in their host species.

Another large group of parasites occurred in only one host but occurred so infrequently (or did not mature) that referring to these parasites as specialists may be misleading. They may be specialists in other hosts not examined in this study. Three parasite species could be identified as broad generalists, and four others as relative generalists which maintain most of their reproductive potential in either dabblers or divers. Another parasite species had significant worm populations of mature individuals in one host species, with sparse bird populations, and occurred in eight others and is considered a broad generalist. In addition, three species had large populations of mature individuals in two or more unrelated host species. Clearly, the data indicate considerable exchange of parasites, which does not support Price's conclusion that parasites are specialists at the host species level.

Two critical features of the waterfowl-intestinal helminth system are: 1) parasites are ingested with the food items of the final host and 2) once ingested by a host they cannot actively transfer to another host. As a consequence those parasites ingested by a host other than the primary host (common, since most diets of the duck species overlap), would be selected for their ability to mature (if possible) in these "secondary hosts" (Holmes, 1976), particularly when these hosts are more abundant than the primary host.

These patterns of host specificity give rise to the pattern of community structure described by Bush (1980) for the helminth community of scaup. He recognized two components: a deterministic component (specialists in scaup and generalists in waterfowl) and a stochastic component of rare species (specialists in other hosts). The parasite communities in all of the duck species examined in this study had such a structure, with a deterministic component ranging from 1 to 23 parasite species. However, my analyses suggest that it is more useful to recognize three components: characteristic parasites (relative specialists in that host), common parasites (relative generalists in waterfowl plus some commonly occurring characteristic species of other hosts), and the stochastic, uncommon specialists of other hosts. The relative numbers of the three components indicate what habitat (above the individual bird) is recognized by the parasites. Where the proportion of characteristic species is high, there was relatively high similarity between host individuals, and those individuals formed relatively tight single species clusters in both the cluster analyses. Such a pattern was seen in five of these host species: ruddy, gadwall, blue-winged teal, scaup and scoter. In these host species the parasites appear to recognize the host species as a distinct habitat level. In the remaining five duck species, the proportion of generalists, or of specialists for other hosts, was high. There was low similarity between individuals within each duck species, and cluster analyses formed mixed (related species) clusters of individuals, in some cases, related to lake, or year of collection. In these cases, parasites may recognize multispecies populations as distinct habitats.

Three hypotheses have been proposed for helminth community structure at the host multispecies population level. The phylogenetic hypothesis predicted that helminth communities in duck species should be most similar between phylogentically related hosts. The diet hypothesis predicted that species with similar food habits should have similar parasites. The numerical dominance hypothesis predicted that the most numerous host should determine the fauna of the other duck species which I have examined from the standpoint of species exchange.

The specific predictions of the phylogenetic hypothesis were: 1) the parasite fauna is specific at the tribe level, 2) the parasite fauna should show greater similarity within tribes rather than between tribes, 3) the similarity within tribes should be related to phylogenetic affinity between species, and 4) the Mergini should be more similar to the Aythyini than the Anatini and that the Oxyurini should be least similar to any other tribe. The first prediction was not supported, the relative generalists (within a host group) were rare. The second prediction was supported in part within the Anatini, with high similarity between parasite communities in widgeon and gadwall and within the Aythyini with high similarity between parasite communities in canvasback and scaup. However, comparison of other duck species did not support this prediction and therefore I do not regard it as the principal determinant of the overall pattern of helminth community structure in waterfowl. The third prediction was not supported by any of the patterns of similarity between communities. Parasite communities of duck species within tribes did not show similarity patterns comparable to their phylogenetic relationships. The last prediction of similarity between tribes was supported in part by the parasite communities in the Oxyurini (ruddy) which formed a distinct group of individuals of one species. In summary, the parasite communities were most similar at the host species level, but in most cases, the patterns of similarity were not determined by the phylogenetic relationships between host species.

The specific predictions of the diet hypothesis are: 1) duck species consuming a high proportion of animal matter should have larger amd more complex parasite faunas and 2) species consuming high proportions of similar taxonomic groups of animal matter should have similar parasite faunas. The first prediction was supported in part by the relationship of the size (mean number of individuals) of the parasite communities and the percent animal matter consumed (rho= 0.73, n=9, P<0.05) in the nine duck species. Those duck species consuming a low proportion of animal matter had few parasite individuals (small size component) those species consuming a high proportion of animal matter had larger sized parasite communites. Complexity was not correlated with percent of animal matter consumed. The second prediction was supported only by the similarity between widgeon and gadwall. However, the lack of support for this prediction may indicate a need to examine the data at a more detailed level relating to the taxonomic differences of the major parasite groups and the type of intermediate hosts involved in their life cycles.

The numerical dominance hypothesis is somewhat more difficult to analyze. If based on regional population sizes (Turner and Weaver, 1977), the expected pattern of species exchange should be from mallards, blue-winged teal and scaup to other birds. The analysis of exchange showed, however, that mallards and blue-winged teal contributed little, whereas scaup contributed most of the parasites. However, the primary breeding habitats for dabblers are ponds and sloughs, not lakes. The pattern of exchange may be entirely different on sloughs. For the divers, lakes constitute the primary breeding habitat. Census counts indicated scaup ranked higher in abundance than either mallard or blue-winged teal on 8 of 14 lakes in 1977 and 1978, intermediate between the others on 3 lakes and below both on only 3 lakes (Bush 1980). On this local population basis, the pattern of exchange, with most of the exchange occurring among the divers, particularly from scaup to others or from the divers (especially scaup) to the dabblers, agrees with the prediction of the numerical dominance hypothesis. In a specific instance, Hymenolepis AB was found only in blue-winged teal collected where scoter were common. Blue-winged teal collected from lakes where scoter were rare or absent did not have this parasite. The exchange of species from high complexity helminth communities to low complexity communities is not surprising as in most cases the high complexity communities also had large size (large abundances of worms). The failure of the specialists (characteristic species) of the dabblers (gadwall and blue-winged teal) to colonize the high complexity helminth communities suggests that these latter communities are saturated.

In conclusion, the helminth communities of waterfowl are organized on a nested or heirarchical basis with the host individual being the only unequivocal level of habitat; the host species and multispecies populations are also recognized as distinct levels of habitat. The relative influence each level has in influencing the parasite communities varies between host species. In scaup and scoter, the parasite community is composed primarily of a group of specialists (characteristic species), which recognize the host species as their unit of habitat. At the other end of the scale in widgeon and mallard the parasite community is composed of relative generalists and specialists from other hosts which recognize a multispecies population as their unit of habitat. How these features affect the organization of infracommunities will be examined in the next section.

III.

STRUCTURE AND ORGANIZATION OF INTESTINAL HELMINTH COMMUNITIES WITHIN INDIVIDUAL BIRDS

INTRODUCTION

Price's (1980) proposal that parasite species are specialists was partially supported by the microhabitat specificity reported for many parasite species (Crompton, 1973; Holmes, 1973). Four studies, three examining the intestinal helminth communities in scaup (Hair and Holmes, 1975; Hair, 1975; Bush, 1980) and one examining intestinal communities in mallard (Avery, 1969), have demonstrated that helminth species occupy predictable, restricted locations within the intestine of waterfowl. In contrast to the restricted microhabitat specificity exhibited by parasites in the above studies, <u>H. diminuta</u> and <u>Trichinella spiralis</u> have both been shown to be capable of occupying most of the intestine in rodents (rats and mice respectively) (Cannon and Mettrick, 1970; Sukhdeo and Croll, 1981). Two species of cestodes (<u>Tetrabothrius minor</u> and <u>T. procerus</u>) are reported to have the potential to occupy most of the small intestine in fulmar (<u>Fulmar glacialis</u>) (Riley and Owen, 1975). However, Riley and Owen (1975) have demonstrated that the distribution of the two species in individual birds very rarely involved the entire intestine and was related to population size of the species which occupied the anterior end. Thus, the spatial distribution of each parasite must be examined specifically in each host individual to determine the degree of microhabitat specificity.

Holmes (1973) has proposed that microhabitat specificity in parasite communities reflects the importance of past interactions between parasite species. Community structure is interpretated as evidence for organization between species. Organization is regarded as the maintenance of structure by some mechanism(s) within the community. In contrast Price (1980) has suggested that parasite communities are unsaturated, exist under nonequilibrium conditions and that the microhabitat specificity demonstrated in parasite communities is not a result of organization between helminth species. In general, the interpretation of community structure as evidence for organization between species has been challenged by the view that communities are chance aggregations of individual species (Caswell, 1976; Conner and Simberloff, 1979).

Bush (1980) demonstrated that the distributions of the helminth species in the 'recurrent group' were predictable in their sequence of occurrence and that these exhibited low niche overlap with adjacent helminth species along the intestine of lesser scaup. The ordered sequence suggests either interactions between parasite species or independent differential adaptation to locations within the intestine. In addition to showing low niche overlap, Bush demonstrated that there was a significant difference between the realized niche overlap (average overlap across individual birds) and the fundamental niche overlap (overlap calculated on the basis of summed distribution across all birds) of adjacent 'recurrent' helminth species. He considered these significant differences to indicate that interactions were important in organizing the spatial distributions of the common helminth species. Bush (1980) also compared the overlap between the infrequent helminth species and adjacent helminth species within the intestine and found the realized and fundamental overlaps showed no significant difference. He concluded that the two opposing views of community organization (noninteractive and interactive) could be applied to the two components he recognized in the intestinal helminth communities, infrequent (stochastic) and common or recurrent (deterministic) parasite species. Interactions appear important in organizing the basic community structure provided by the recurrent helminth species but not important for the infrequent helminth species in scaup.

Interactions can only occur within the host individual. However, the importance of interactions in parasite community structure is a function of how frequent such interactions may be (Holmes and Price, 1980), and can only be assessed by examining parasite communities in several host individuals. The intestinal helminth community in waterfowl is an excellent system in which to study the importance of interactions in determining community structure.

The intestinal tract in waterfowl consists of the small intestine, the large intestine and two caeca. In the small intestine changes in chemical constituents, such as amino acids, carbohydrates and proteins, and changes in the physical substrate, such as changes in the mucosal morphology and density of villi, are correlated with position along the intestine (Crompton and Nesheim, 1968). The large intestine is similar in structure to the distal small intestine but tends to be more homogenous in morphology and function (water absorption) (Ziswiler and Farner, 1972). The combined small and large intestines therefore represent a single complex resource gradient or axis along which helminth species can locate (Hair, 1975; Bush, 1980). The caeca also vary in physical and chemical characteristics along their length, but represent a second and largely independent gradient or resource axis (Calhoun, 1954).

The first section of this study demonstrated three components within the intestinal helminth communities in the 10 species of waterfowl: host generalists, characteristic helminth species and helminth species which are specialists within other hosts. The first two make up Bush's deterministic component. In this section I will compare the distribution of the helminth species along the length of the intestine within individual birds of each of the duck species. I intend to examine the importance of the interactive and noninteractive views of community structure to the first two components of the different parasite communities.

METHODS

For field and laboratory methods see Chapter II.

Analytical Methods

Four parameters were used to measure helminth species distribution along the intestines: location (section number) of the median individual in each helminth species population (median location), anterior location, posterior location and range of each helminth species. The minimum range a helminth species occupied was one section, or 5% of the small intestine. Some helminths extended their distribution into the large intestine and I have equated the large intestine to a 5% section of the small intestine, making the total length of the intestinal axis 105%. All locations are expressed as percent of small intestine length.

Because the caeca represent a distinctly different microhabitat, helminth species occupying this region were not included in the analyses of linear distributions. Helminth species occurring in this region were simply recorded as occupying the caeca.

The distributional measures were averaged across all birds infected for each parasite species in each duck species. Within each duck species only those parasite species which occurred in three or more host individuals will be compared. Because sample sizes were small for some parasite species, comparison of variances around mean values, such as those for the median points (see below) are not comparable between duck species. Therefore, variation in these measures was compared using the range of values or the average difference (in % of gut) between the individual values and their mean. Relationships between population sizes and distributional measures were analyzed with Spearman's rank correlation. All analyses were done using programs in APL.

Agreement in the sequential distribution of median positions along the intestine was tested, using Spearman's rank correlation. For each pair of individual birds, ranks were assigned only to those parasite species occurring in both birds. The number of pairs showing significant correlations, and the mean rho values, were calculated. (The test of concordance (Pielou, 1977), usually applied to such data, was inappropriate because of differences in helminth species composition between individual birds.)

Determination of the pattern of distribution of median locations of helminth species within the intestines of individual birds was examined using a model derived by Pielou and Routledge (1976). The model calculates the probability of finding a specified number of median positions within a fixed number of sections. This value is compared to the number of sections occupied by the median points at a 50% probability level. The model was applied to individual birds with five or more helminth species. A sign test was used to compare the number of birds in which the median locations were found in fewer versus more sections than the calculated value (Pielou and Routledge, 1976). If a significantly large excess of values fall below the calculated value the overall distributions were considered to be clustered; if a significant excess of values were above the calculated value, the overall distributions were considered to be regular. For small numbers of species the model is biased in favour of a clustered pattern.

Percent similarity (equation 1 of Hurlbert, 1978) was used to calculate overlap between the ranges of pairs of parasite species. This measure calculates the proportion of the individuals of two species which have identical distributions. Overlap was calculated for each species pair in individual birds. Average overlap was calculated for each pair of parasite species. Summed overlap values were calculated by adding the distributions of parasite species across all individuals of one host species. Percent similarity was then calculated for all pairs of parasite species within this matrix of of summed distributions. A t-test was used to compare differences between summed and average overlap values.

RESULTS

Linear Distributions

Data on the linear distributions of helminth species which occurred in 3 or more birds are given in Tables 11 to 20. The variability around the mean of the median points, as measured by the average difference from that mean, was generally less than 10%. There was no difference in this measure between the frequent species (those occurring in over half of the individual birds of one duck species) and those encountered less frequently (Table 21). In addition, for most helminth species, the median location for an infrapopulation was independent of the number of worms in that infrapopulation (significant rho values are indicated in Tables 11-20). There were only three exceptions: the median position of Hymenolepis spinocirrosa in scaup and H. WWW in gadwall were negatively correlated with total number of worms (i.e., median points were further anterior in larger infrapopulations), and the median position of Corynosoma constrictum in blue-winged teal was positively correlated with total numbers of worms (i.e., median points were further posterior in larger infrapopulations). These basic patterns of relatively constant median points, independent of infrapopulation size, indicate that the median position is a good measure of the site occupied.

Table 11. Linear distribution of helminth species within the intestines of Widgeon (expressed as a percentage) and correlation of these measures with numbers of individuals of helminths of each parasite species.

Helminth species	n*	N**	Median	Rho***	End points of distribution				Range	Rho	Maximum range
					Anterior	Rho	Posterior	Rho			
1 -F. fasciolaris	5/11	2± 1.7[a]	25±18.4[b] 5- 50(14)	0	21±20.4[a]	0	28±17.5[a]	0	12±13.0[a]	+	35
2 -A. gracilis	5/11	11±14.4	21± 2.2 20- 25(1)	0	16± 6.5	0	29± 5.5	0	18± 9.7	0	30
3 -C. constrictum	5/11	4± 1.6	71± 7.4 60- 80(5)	0	67± 4.5	0	80±15.4	0	18±12.0	0	35
6 -P. contortus	8/11	55±89.2	104± 2.3 100-105(1)	0	96±15.3	0	104± 1.8	0	13±15.6	0	45
38-D. danutae	5/11	4± 4.7	68± 2.7 65- 70(2)	0	61± 9.6	0	72± 6.7	0	16±14.8	0	40
15-C. anatis	4/11	1± 0.5	Caeca								
19-Z. lunata	3/11	2± 1.0	Caeca								
4 -H. hopkinsi	5/11	11± 5.0	Caeca								

* - Number of hosts infected / number of birds examined.

** - Mean number of individual helminths per infected bird ± 1 S.D.

*** - Spearman rank correlation of number of individuals and distributional measure (i.e. range) (+ - significant (P< .05) positive correlation; 0 - no significant correlation; — - negative significant correlation; blank - sample size too small to test).

a - All values expressed as the mean position ± 1 S.D.

b - Mean of median location ± 1 S.D. / range of median location (average difference from median location).

All values expressed as a percentage of the intestine.

Table 12. Linear distribution of helminth species within the intestines of Gadwall (expressed as a percentage) and correlation of these measures with numbers of individuals of helminths of each parasite species.

Helminth species	n*	N**	Median	Rho***	End points of distribution				Range	Rho	Maximum Range
					Anterior	Rho	Posterior	Rho			
1 -*F.* *fasciolaris*	3/7	11±10.8[a]	22±17.6[b] 5- 40(12)		8± 2.9[a]		50±18.0[a]		47±16.1[a]		65
2 -*A.* *gracilis*	4/7	4± 2.1	16± 4.8 10- 40(5)		16± 4.8		18± 2.9		6± 2.5		10
3 -*C.* *constrictum*	3/7	2± 1.5	63± 2.9 60- 65(2)		63± 2.9		70± 8.7		12± 5.8		15
4 -*H.* *hopkinsi*	3/7	4± 2.9	102± 2.9 100-105(2)		102± 2.9		103± 2.9		7± 2.9		10
6 -*P.* *contortus*	7/7	16±31.8	104± 1.9 100-105(1)	0	104± 2.4	0	104± 1.9	0	6± 1.9	0	10
34-*E.* QQQ	6/7	4± 4.1	17± 4.1 10- 20(3)	0	13± 4.1	0	21± 5.8	0	13± 6.1	0	20
38-*D.* *danutae*	3/7	4± 2.6	65± 5.0 60- 70(3)		62± 7.6		70± 5.0		13± 7.6		20

Table 12. (Continued)

Helminth species	n*	N**	Median	Rho***	End points in distribution				Range	Rho	Maximum Range
					Anterior	Rho	Posterior	Rho			
45-*D. spinata*	6/7	19±24.2^a	84±22.4^b 45-100(18)	0	76±24.4^a	0	92±16.9^a	0	21±15.3^a	0	40
52-*H.* WWW	7/7	32±33.3	6± 2.4 5- 10(1)	-	5± 0.0	0	11± 1.9	0	11± 1.9	0	15
70-*H.* XXX	3/7	3± 2.0	5± 0.0 5 (0)		5± 0.0		5± 0.0		5± 0.0		5
4 -*H. hopkinsi*	3/7	4± 2.9	Caeca								
14-*N. attenuatus*	3/7	17±13.0	Caeca								
19-*Z. lunata*	3/7	2± 2.3	Caeca								

* - Number of hosts infected / number of birds examined.

** - Mean number of individual helminths per infected bird ± 1 S.D.

*** - Spearman rank correlation of number of individuals and distributional measure (i.e. range) (+ - significant ($P < .05$) positive correlation; 0 - no significant correlation; — - negative significant correlation; blank - sample size too small to test).

a - All values expressed as the mean position ± 1 S.D.

b - Mean of median location ± 1 S.D. / range of median location (average difference from median location).

All values expressed as a percentage of the intestine.

Table 13. Linear distribution of helminth species within the intestines of Blue-winged teal (expressed as a percentage and correlation of these measures with numbers of individuals of helminths of each parasite species.

Helminth species	n*	N**	Median	Rho***	End points of distribution				Range	Rho	Maximum Range
					Anterior	Rho	Posterior	Rho			
1 -_F_. _fasciolaris_	3/10	3± 2.1^{a}	17± 7.6^{b} 10- 25(5)		13±10.4^{a}		23±12.6^{a}		15±17.3^{a}		35
2 -_A_. _gracilis_	6/10	18± 23.8	21± 5.8 15- 30(5)	0	16± 5.8	0	33± 9.4	0	22± 8.2	0	30
3 -_C_. _constrictum_	10/10	8± 6.5	87± 11.6 70-105(10)	+	75± 8.3	0	98±12.3	+	28±14.6	0	50
7 -_E_. _recurvatum_	7/10	20± 2.9	11± 8.9 5- 30(5)	0	6± 1.9	0	21±21.0	0	21±21.5	+	60
12-_H_. AB	6/10	684±849.7	23± 9.3 15- 40(7)	0	9± 6.7	0	56±26.3	+	52±31.8	+	85
23-Abort?	4/10	7± 5.7	51±39.7 5-100(29)		49±37.3		56±42.3		13±11.9		30
32-AB?	3/10	33± 51.1	45±35.0 10- 80(23)		43±35.1		68±50.6		30±27.9		60

Table 13. (Continued)

Helminth species	n*	N**	Median	Rho***	End points of distribution				Range	Rho	Maximum Range
					Anterior	Rho	Posterior	Rho			
34-E. QQQ	4/10	1± 0.5^a	16±16.5^b		16±16.5^a		16±16.5^a		5± 0.0^a		5
			5- 40(11)								
37-D. elisae	3/10	17± 14.0	90± 5.0		78± 2.9		98± 7.6		25± 8.7		30
			85- 95(3)								
39-E. rosseteri	10/10	359±940.1	12± 5.3	0	7± 4.8	-	29±15.2	+	27±17.5	+	55
			5- 20(4)								
50-E. NNN	7/10	8± 8.2	5± 0.0	0	5± 0.0	0	10± 9.1	0	10± 9.1	0	30
			5 (0)								
51-Unciunia n. sp.	3/10	8± 3.5	15± 5.0		10± 5.8		25± 0.0		20± 0.0		20
			10- 20(3)								
57-S. octacantha	6/10	37± 36.9	59± 8.0	0	48± 8.3	0	70±13.8	+	27±17.5	+	45
			45- 65(6)								
14-N. attenuatus	3/10	2± 1.5	Caeca								

* - Number of hosts infected / number of birds examined.
** - Mean number of individual helminths per infected bird ± 1 S.D.
*** - Spearman rank correlation of number of individuals and distributional measure (i.e. range) (+ - significant ($P < .05$) positive correlation; 0 - no significant correlation; — - negative significant correlation; blank - sample size too small to test).
a - All values expressed as the mean position ± 1 S.D.
b - Mean of median location ± 1 S.D. / range of median location (average difference from median location). All values expressed as a percentage of the intestine.

Table 14. Linear distribution of helminth species within the intestines of Mallard (expressed as a percentage) and correlation of these measures with numbers of individuals of helminths of each parasite species.

Helminth species	n*	N**	Median	Rho***	End points of distribution				Range	Rho	Maximum Range
					Anterior	Rho	Posterior	Rho			
1 -*F.* *fasciolaris*	8/16	23± 21.2[a]	14± 7.4[b] 5- 30(5)	0	6± 1.8[a]	0	33±15.6[a]	0	32±15.3[a]	0	55
2 -*A.* *gracilis*	11/16	59±127.6	24± 6.6 15- 35(6)	0	19± 8.9	-	36±14.0	+	22±15.2	+	45
3 -*C.* *constrictum*	10/16	8± 11.3	79±12.2 50- 90(8)	0	70±12.9	0	87±16.5	+	22±15.3	+	45
6 -*P.* *contortus*	8/16	26± 25.1	105± 0.0 105 (0)	0	101± 8.2	0	105± 0.0	0	9± 8.2	0	25
7 -*E.* *recurvatum*	8/16	59±113.1	18± 8.5 10- 35(5)	0	11± 5.8	-	34±13.6	0	28±17.3	+	60
10-*D.* *coronula*	10/16	5± 5.6	95± 9.0 8-105(7)	0	91± 9.3	0	96± 9.0	+	10± 9.4	0	35
12-*H.* AB	3/16	5± 2.5	37±10.4 25- 45(7)		30±15.0		50± 0.0		25±15.0		40

Table 14. (Continued)

Helminth species	n*	N**	Median	Rho***	End points of distribution				Range	Rho	Maximum Range
					Anterior	Rho	Posterior	Rho			
16-H. fausei	11/16	34± 30.9[a]	23± 4.0[b] 15- 30(3)	0	11± 5.5[a]	0	34± 6.0[a]	+	27± 9.0[a]	+	40
25-R. macroacanthus	7/16	17± 14.7	46± 8.0 30- 55(6)	0	38± 9.1	0	53± 9.5	0	20± 8.1	+	30
27-P. paradoxus	4/16	28± 31.4	78± 6.5 70- 85(6)		66± 6.3		95± 7.1		34± 8.5		45
28-Echino?	3/16	28± 44.5	75±22.9 50- 95(17)		68±16.1		85±13.2		22±14.4		30
41-E. revolutum	3/16	5± 5.2	97±14.1 80-105(12)		97±14.4		98±11.5		7± 2.9		10
46-C. flabelliformis	6/16	6± 3.3	72±24.4 30- 95(20)	0	66±25.6	0	77±25.8	0	16±10.2	0	30
54-S. gracilis	3/16	3± 0.6	65± 5.0 60- 75(3)		60± 5.0		67± 2.9		12± 2.9		15

Table 14. (Continued)

Helminth species	n*	N**	Median	Rho***	End points of distribution				Range	Rho	Maximum Range
					Anterior	Rho	Posterior	Rho			
61-*H*. compressa	3/16	5± 6.1[a]	52±10.4[b]		50± 8.7[a]		57±15.3[a]		12± 7.6[a]		20
			40- 60(6)								
66-RR	3/16	2± 1.0	58±12.6		58±12.6		60±15.0		7± 2.9		10
			45- 70(8)								
4 -*H*. hopkinsi	12/16	63± 72.5	Caeca								
14-*N*. attenuatus	3/16	5± 7.5	Caeca								
15-*C*. anatis	5/16	1± 0.5	Caeca								
19-*Z*. lunata	3/16	2± 2.3	Caeca								

* - Number of hosts infected / number of birds examined.
** - Mean number of individual helminths per infected bird ± 1 S.D.
*** - Spearman rank correlation of number of individuals and distributional measure (i.e. range) (+ - significant ($P < .05$) positive correlation; 0 - no significant correlation; - - negative significant correlation; blank - sample size too small to test).
a - All values expressed as the mean position ± 1 S.D.
b - Mean of median location ± 1 S.D. / range of median location (average difference from median location).
All values expressed as a percentage of the intestine.

Table 15. Linear distribution of helminth species within the intestines of Ruddy (expressed as a percentage) and correlation of these measures with numbers of individuals of helminths of each parasite species.

Helminth species	n*	N**	Median	Rho***	End points of distribution				Range	Rho	Maximum Range
					Anterior	Rho	Posterior	Rho			
1 -_F_. _fasciolaris_	6/6	16+ 13.0^{a}	10+ 8.4^{b} 5- 25(6)	0	8+ 8.2^{a}	0	23+14.4^{a}	0	20+14.8^{a}	0	45
2 -_A_. _gracilis_	5/6	39+ 22.1	25+ 7.1 20- 35(1)	0	11+ 8.9	0	48+10.4	0	42+11.5	0	55
3 -_C_. _constrictum_	3/6	2+ 1.5	105+ 0.0 105 (0)		105+ 0.0		105+ 0.0		5+ 0.0		5
20-PP	3/6	2+ 0.6	60+27.8 35- 90(23)		60+27.8		83+16.1		28+20.8		45
22-_C_. _hebraicus_	4/6	10+13.0	73+ 2.9 70- 75(5)		68+ 6.5		83+11.9		20+17.3		35
29-_R_. _cyrtoides_	6/6	1460+867.3	32+ 6.1 25- 40(5)	0	5+ 0.0	0	74+ 8.0	0	74+ 8.0	0	85
48-_D_. _excentricus_	6/6	150+217.6	79+ 7.4 70- 90(6)	0	62+ 2.6	0	96+ 5.8	0	39+ 3.8	0	45

* - Number of hosts infected / number of birds examined.
** - Mean number of individual helminths per infected bird ± 1 S.D.
*** - Spearman rank correlation of number of individuals and distributional measure (i.e. range) (+ - significant ($P < .05$) positive correlation; 0 - no significant correlation; — - negative significant correlation; blank - sample size too small to test).
a - All values expressed as the mean position ± 1 S.D.
b - Mean of median location ± 1 S.D. / range of median location (average difference from median location).
All values expressed as a percentage of the intestine.

Table 16. Linear distribution of helminth species within the intestines of Canvasback (expressed as a percentage) and correlation of these measures with numbers of individuals of helminths of each parasite species.

Helminth species	n*	N**	Median	Rho***	End points of distribution				Range	Rho	Maximum Range
					Anterior	Rho	Posterior	Rho			
1 -_F._ _fasciolaris_	6/6	26± 26.1[a]	19±13.6[b] 5- 40(13)	0	11±12.0[a]	0	33± 6.8[a]	0	28±10.4[a]	0	40
2 -_A._ _gracilis_	4/6	27± 29.4	20±12.9 5- 35(10)		14± 8.5		34±18.0		25±18.7		50
3 -_C._ _constrictum_	4/6	4± 3.2	63± 16.6 40- 80(10)		60±16.3		65±17.3		10± 5.3		15
5 -_P._ _carilis_	4/6	16± 16.7	53±11.9 40- 65(10)		45±15.8		65±17.8		25±16.3		45
6 -_P._ _contortus_	3/6	27± 15.0	105± 0.0 105 (0)		97±10.4		105± 0.0		13±10.4		25
7 -_E._ _recurvatum_	5/6	376±507.4	15±11.8 5- 35(8)	0	6± 2.2	0	25±16.6	0	24±17.8	+	40
8 -_H._ _spinocirrosa_	4/6	253±129.5	40± 8.2 30- 50(5)		25±20.4		51±10.3		31±14.9		50

Table 16. (Continued)

Helminth species	n[*]	N[**]	Median	Rho[***]	End points of distribution				Range	Rho	Maximum Range
					Anterior	Rho	Posterior	Rho			
10-*D. coronula*	4/6	3± 1.0[a]	61±11.1[b] 50-75(8)		60±10.8[a]		69± 9.5[a]		14± 7.5[a]		20
11-*H. pusilla*	3/6	56± 90.4	85±15.0 70-100(10)		82±20.2		93± 5.7		17±16.1		35
16-*H. fausti*	4/6	96±104.3	20± 8.2 10- 30(5)		9± 2.5		31±11.8		28±13.2		40
20-PP	3/6	5± 3.6	27±15.3 10- 40(12)		25±18.0		28±12.6		8± 5.7		15
24-*R. pittalugi*	3/6	8± 6.0	52± 7.6 45- 60(5)		48±12.6		58± 7.6		15± 8.7		20
25-*R. macroacanthus*	5/6	25± 10.0	40±11.7 20- 50(8)	0	19±15.2	0	47± 8.4	0	33±16.0	0	55
26-*Diorchis* n. sp. TT	6/6	24± 22.0	73±15.7 55- 95(12)	0	63±12.9	0	87± 9.8	0	29± 8.6	0	40

Table 16. (Continued)

Helminth species	n*	N**	Median	Rho***	End points of distribution				Range	Rho	Maximum Range
					Anterior	Rho	Posterior	Rho			
36-D. laevis	5/6	3± 5.4[a]	49± 5.5[b] 45- 55(5)	0	48± 6.7[a]	0	51± 5.5[a]	0	8± 6.7[a]	0	20
51-Unciunia n. sp.	3/6	181±302.8	18± 5.8 15- 25(5)		12± 7.6[a]		28± 2.9		22±10.4		30
59-A. spinulosa	4/6	6± 5.7	19± 4.8 15- 25(4)		16± 6.3		21± 4.8		10± 7.1		20
4 -H. hopkinsi	3/6	5± 5.9	Caeca								
19-Z. lunata	4/6	10± 15.5	Caeca								

* - Number of hosts infected / number of birds examined.
** - Mean number of individual helminths per infected bird ± 1 S.D.
*** - Spearman rank correlation of number of individuals and distributional measure (i.e. range) (+ - significant (P< .05) positive correlation; 0 - no significant correlation; — - negative significant correlation; blank - sample size too small to test).
a - All values expressed as the mean position ± 1 S.D.
b - Mean of median location ± 1 S.D. / range of median location (average difference from median location).
All values expressed as a percentage of the intestine.

Table 17. Linear distribution of helminth species within the intestines of Ring-necked duck (expressed as a percentage) and correlation of these measures with numbers of individuals of helminths of each parasite species.

Helminth species	n*	N**	Median	Rho***	End points of distribution				Range	Rho	Maximum Range
					Anterior	Rho	Posterior	Rho			
1 -*F. fasciolaris*	3/6	1± 0.6[a]	20±18.0[b] 5- 40(13)		20±18.0[a]		22±16.1[a]		7± 2.9[a]		10
2 -*A. gracilis*	[illegible]/6	69±108.3	15±13.5 5- 35(10)		5± 0.0		23±21.8		23±21.8		55
7 -*E. recurvatum*	4/6	15± 18.0	8± 2.9 5- 10(3)		6± 2.5		18±18.5		16±19.3		45
20-PP	3/6	77± 50.8	50±17.3 40- 70(13)		32±20.8		70±32.8		43±12.6		55
26-*Diorchis* n. sp. TT	3/6	2± 1.2	83± 5.8 80- 90(3)		83± 5.8		83± 5.8		5± 0.0		5
36-*D. laevis*	6/6	2± 0.4	43±14.4 15- 55(11)	0	43±14.4	0	45±12.7	0	8± 2.7	0	10
55-*H. parvula*	4/6	43± 78.3	13± 5.0 5- 15(3)		8± 5.0		24± 6.3		21± 7.5		30

* - Number of hosts infected / number of birds examined.

** - Mean number of individual helminths per infected bird ± 1 S.D.

*** - Spearman rank correlation of number of individuals and distributional measure (i.e. range) (+ - significant ($P < .05$) positive correlation; 0 - no significant correlation; — - negative significant correlation; blank - sample size too small to test).

a - All values expressed as the mean position ± 1 S.D.

b - Mean of median location ± 1 S.D. / range of median location (average difference from median location).
All values expressed as a percentage of the intestine.

Table 18. Linear distribution of helminth species within the intestines of Lesser Scaup (expressed as a percentage) and correlation of these measures with numbers of individuals of helminths of each parasite species.

Helminth species	n*	N**	Median	Rho***	End points of distribution				Range	Rho	Maximum Range
					Anterior	Rho	Posterior	Rho			
1 -*F. fasciolaris*	15/16	45± 47.3[a]	11± 3.9[b] 5- 20(2)	0	5± 1.3[a]	0	23± 8.6[a]	0	23± 9.0[a]	0	40
2 -*A. gracilis*	11/16	29± 25.0	26±13.9 10- 50(11)	0	10± 7.4	-	46±16.7	+	41±20.8	+	75
3 -*C. constrictum*	4/16	2± 1.0	69± 6.3 60- 75(4)		66± 7.5		69± 6.3		8± 5.0		15
5 -*P. marilis*	15/16	26± 56.0	68± 5.9 60- 80(6)	0	61± 5.1	0	78± 8.6	+	78± 8.6	+	35
8 -*H. spinocirrosa*	15/16	8228±10553.0	48± 5.2 35- 55(3)	-	22±15.7	-	57± 4.1	0	40±15.4	+	60
9 -*H. abortiva*	15/16	9712±13332.5	65± 9.3 50- 90(6)	0	55± 6.9	-	80±10.1	+	31±11.6	+	50
10-*D. coronula*	10/16	16± 9.5	78±20.2 40-100(15)	0	67±31.6	0	93± 8.6	0	31±27.8	0	90

Table 18. (Continued)

Helminth species	n*	N**	Median	Rho***	End points of distribution				Range	Rho	Maximum Range
					Anterior	Rho	Posterior	Rho			
11-*H. pusilla*	15/16	5044± 6742.9^a	90± 4.6^b 80-100(3)	0	77± 7.8^a	0	101± 3.4^a	+	29± 9.3^a	+	45
13-*L. skrjabini*	9/16	16± 25.5	29± 7.7 20- 45(6)	0	24± 7.8	0	34± 8.6	+	15±11.7	+	35
16-*H. fausti*	3/16	33± 16.9	12± 5.8 5- 15(%0		7± 2.9		25±15.0		23±12.6		35
17-*H. tuvensis*	15/16	1010± 1286.1	57± 9.6 40- 75(8)	0	42±11.6	0	72±14.6	+	35±20.1	+	80
22-*C. hebraicus*	7/16	11± 9.5	68±10.4 50- 80(7)	0	64± 8.0	0	77±16.8	+	19±14.6	+	40
24-*R. pittalugi*	12/16	50± 63.2	43±11.8 25- 60(8)	0	32±10.3	-	50±10.8	0	23±15.3	+	60
26-*Diorchis* n. sp. TT	3/16	105±122.3	75±10.0 65- 85(7)		67±16.1		87±12.6		25±20.0		45

Table 18. (Continued)

Helminth species	n*	N**	Median	Rho***	End points of distribution				Range	Rho	Maximum range
					Anterior	Rho	Posterior	Rho			
29-R. cyrtoides	4/16	86± 119.0[a]	41± 4.8[b] 35- 45(4)		29± 9.5[a]		49±11.1[a]		25±16.8[a]		45
31-H. microskrjabini	4/16	111± 170.9	34±10.3 20- 45(6)		23±13.2		39±16.5		21±11.1		35
35-H. recurvata	9/16	172± 332.5	27± 7.9 20- 45(5)	0	16±10.4	-	48±21.4	0	37±24.9	+	95
43-H. tuv?	7/16	687± 737.2	74± 7.3 60- 80(5)	0	65±11.2	0	87± 7.0	0	27± 8.1	+	35
47-C. obsignata	4/16	3± 2.4	48±18.9 20- 60(13)		40±21.6		59± 6.3		24±26.0		60
51-Unciunia n. sp.	4/16	136± 191.3	19± 2.5 15- 20(1)		8± 2.9		36± 4.8		34± 6.3		40
64-H. arcuata	3/16	61± 98.4	65±10.0 55- 75(4)		58± 2.9		75± 8.7		22± 7.6		30

Table 18. (Continued)

Helminth species	n*	N**	Median	Rho***	End points of distribution				Range	Rho	Maximum range
					Anterior	Rho	Posterior	Rho			
66-RR	4/16	14 ± 12.2^{a}	64 ± 19.3^{b} 35- 75(8)		60 ± 16.8^{a}		79 ± 16.5^{a}		24 ± 6.3^{a}		30
15-*C. anatis*	3/16	2 ± 2.3	Caeca								

* - Number of hosts infected / number of birds examined.

** - Mean number of individual helminths per infected bird ± 1 S.D.

*** - Spearman rank correlation of number of individuals and distributional measure (i.e. range) (+ - significant ($P < .05$) positive correlation; 0 - no significant correlation; — - negative significant correlation; blank - sample size too small to test).

a - All values expressed as the mean position ± 1 S.D.

b - Mean of median location ± 1 S.D. / range of median location (average difference from median location).

All values expressed as a percentage of the intestine.

Table 19. Linear distribution of helminth species within the intestines of Bufflehead (expressed as a percentage) and correlation of these measures with numbers of individuals of helminths of each parasite species.

Helminth species	n*	N**	Median	Rho***	End points of distribution				Range	Rho	Maximum Range
					Anterior	Rho	Posterior	Rho			
5 -*P. marilis*	4/6	10± 11.1^{a}	71± 6.3^{b} 65- 80(4)		68± 8.7^{a}		91±18.9^{a}		29±18.4^{a}		50
44-X	5/6	106±162.6	48± 9.1 35- 60(6)	0	48± 9.1	-	67±10.4	0	57±14.4	+	75
51-*Unciunia* n. sp.	3/6	1± 0.6	12± 2.9 10- 15(2)		12± 2.9		12± 2.9		5± 0.0		5
14-*N. attenuatus*	3/6	4± 4.4	Caeca								
15-*C. anatis*	3/6	5± 6.9	Caeca								

* - Number of hosts infected / number of birds examined.
** - Mean number of individual helminths per infected bird ± 1 S.D.
*** - Spearman rank correlation of number of individuals and distributional measure (i.e. range) (+ - significant ($P < .05$) positive correlation; 0 - no significant correlation; — - negative significant correlation; blank - sample size too small to test).
a - All values expressed as the mean position ± 1 S.D.
b - Mean of median location ± 1 S.D. / range of median location (average difference from median location).
All values expressed as a percentage of the intestine.

Table 20. Linear distribution of helminth species within the intestines of White-winged Scoter (expressed as a percentage) and correlation of these measures with numbers of individuals of helminths of each parasite species.

Helminth species	n*	N**	Median	Rho***	End points of distribution				Range	Rho	Maximum range
					Anterior	Rho	Posterior	Rho			
1 -*F. fasciolaris*	13/13	214± 354.2[a]	17± 9.7[b] 5- 35(3)	0	9± 7.7[a]	0	37±17.0[a]	+	33±19.2[a]	+	65
2 -*A. gracilis*	7/13	37± 87.4	51± 7.4 40- 60(6)	0	37±15.2	0	61±13.0	0	29±23.8	+	65
3 -*C. constrictum*	9/13	6± 10.2	76±17.8 45-105(12)	0	72±17.7	0	85±19.5	0	18±14.8	+	50
5 -*P. marilis*	11/13	50± 54.8	89± 8.1 80-105(6)	0	69±13.9	0	101± 5.0	0	37±14.4	0	55
6 -*P. contortus*	5/13	3± 3.6	101± 8.9 85-105(4)	0	93±16.8	-	104± 2.2	0	16±16.0	+	40
8 -*H. spinocirrosa*	6/13	18585±31357.2	52±12.1 35- 65(10)	0	21±25.0	0	82±14.0	0	66±34.1	0	95
9 -*H. abortiva*	7/13	109± 165.7	75±15.3 55- 95(13)	0	69±13.1	0	86±14.8	0	22±17.5	+	50

Table 20. (Continued)

Helminth species	n*	N**	Median	Rho***	End points of distribution				Range	Rho	Maximum range
					Anterior	Rho	Posterior	Rho			
11-*H.* *pusilla*	4/13	38± 66.3[a]	99± 2.5[b] 95-100(1)		98± 2.9[a]		100± 4.0[a]		8± 5.0[a]		15
12-*H.* AB	11/13	7498± 9551.4	63±20.5 10- 85(14)	0	29±24.4	0	88±18.7	+	65±32.8	+	105
13-*L.* *skrjabini*	9/13	307± 757.6	38±12.5 15- 55(10)	0	25±15.4	0	67±27.5	+	47±34.5	+	105
18-Spino?	11/13	4162± 7869.8	46±15.3 25- 80(11)	0	13±13.8	0	76±15.9	0	68±19.5	0	105
21-*H.* *spiralibursata*	13/13	562± 943.3	98± 2.4 95-100(2)	0	89± 8.9	-	102± 2.4	0	17± 8.1	+	35
23-Abort?	10/13	1526± 1968.1	69±10.8 50- 85(8)	0	55±15.5	0	97± 7.8	+	47±17.7	+	70
27-*P.* *paradoxus*	8/13	8± 8.5	86±11.5 65- 95(9)	0	82±12.2	0	93±11.3	0	16± 7.3	+	30

Table 20. (Continued)

Helminth species	n*	N**	Median	Rho***	End points of distribution				Range	Rho	Maximum rang
					Anterior	Rho	Posterior	Rho			
11-*H*. *pusilla*	4/13	38± 66.3[a]	99± 2.5[b] 95-100(1)		98± 2.9[a]		100± 4.0[a]		8± 5.0[a]		15
12-*H*. AB	11/13	7498± 9551.4	63±20.5 10- 85(14)	0	29±24.4	0	88±18.7	+	65±32.8	+	105
13-*L*. *skrjabini*	9/13	307± 757.6	38±12.5 15- 55(10)	0	25±15.4	0	67±27.5	+	47±34.5	+	105
18-Spino?	11/13	4162± 7869.8	46±15.3 25- 80(11)	0	13±13.8	0	76±15.9	0	68±19.5	0	105
21-*H*. *spiralibursata*	13/13	562± 943.3	98± 2.4 95-100(2)	0	89± 8.9	-	102± 2.4	0	17± 8.1	+	35
23-Abort?	10/13	1526± 1968.1	69±10.8 50- 85(8)	0	55±15.5	0	97± 7.8	+	47±17.7	+	70
27-*P*. *paradoxus*	8/13	8± 8.5	86±11.5 65- 95(9)	0	82±12.2	0	93±11.3	0	16± 7.3	+	30

2

Table 20. (Continued)

Helminth species	n[*]	N[**]	Median	Rho[***]	End points of distribution Anterior	Rho	Posterior	Rho	Range	Rho	Maximum range
53-*C. nyrocinarium*	6/13	6± 7.9[a]	78±25.6[b] 40-105(20)	0	73±23.4[a]	0	103± 2.6[a]	0	36±22.5[a]	0	70
63-*L. clerci*	4/13	7± 10.8	50± 4.1 45- 55(3)		46± 8.5		53± 6.4		11±12.5		30
69-Pusilla?	3/13	123± 130.4	93± 2.9 90- 95(2)		92± 2.9		100± 0.0		13± 2.9		15
71-*H.* tuvAB?	4/13	157± 128.9	79±15.5 65-100(11)		73±18.5		96± 7.5		29±18.0		45
4 -*H. hopkinsi*	11/13	31± 21.6	Caeca								
14-*N. attenuatus*	3/13	6± 4.6	Caeca								

* - Number of hosts infected / number of birds examined.
** - Mean number of individual helminths per infected bird ± 1 S.D.
*** - Spearman rank correlation of number of individuals and distributional measure (i.e. range) (+ - significant ($P < .05$) positive correlation; 0 - no significant correlation; — - negative significant correlation; blank - sample size too small to test).
a - All values expressed as the mean position ± 1 S.D.
b - Mean of median location ± 1 S.D. / range of median location (average difference from median location).
All values expressed as a percentage of the intestine.

Table 21. Variation around the mean median location of frequent and infrequent helminth species.

Average Difference*	Frequent Species**	Infrequent Species***
0-4	17	22
5-9	31	19
10-14	16	11
15 or more	3	6

Chi square = 4.82; 3 d.f.; N.S.

* Average difference from mean median location (percent of intestine)

** Frequent species - represented in greater than 50% of the individual birds infected.

*** Infrequent species - represented in less than or equal to 50% of the individual bireds infected. (From Tables 11-20)

In 47 of 48 comparisons between pairs of birds which had five or more similar helminth species there was a significant positive rank correlation in order of occurrence. Mean correlation coefficents were all greater than 0.75 (Table 22). Sample sizes were large enough to allow similar analyses of the sequential distribution of the characteristic helminth species in scaup and scoter. The order of these species also showed significant positive correlations (scoter mean Rho=0.89, scaup mean rho=0.88). Thus, the sequence of occurrence along the intestine is predictable for the frequent and characteristic helminth species.

Another important feature of the linear distributions was whether the median locations of the parasite species were positioned along the gut in a clustered, regular or random pattern. Pielou and Routledge (1976) developed a model which they used to test the randomness of the locations of upslope and downslope boundaries of salt marsh grasses on a transect along an intertidal gradient. This model was applied to the median position of the parasite species within an individual bird, using sections as analogues of quadrats along a transect. The data (Table 23) indicated that overall distributions, and those in five of six duck species with large enough sample sizes to test independently, were distinctly non-random,

Table 22. Rank correlation of order of the median locations of helminth species in ten species of duck.

Species	N*	Rho**	n***	NS****
Bufflehead	0			
Widgeon	2	0.89±0.03	5,6	2
Ring-necked duck	2	0.88±0.13	5,6	2
Gadwall	3	0.97±0.03	6-9	3
Ruddy	4	0.93±0.09	5	4
Blue-winged teal	5	0.81±0.15	5-9	5
Canvasback	5	0.88±0.08	6-19	5
Mallard	8	0.89±0.11	5-8	7
Lesser scaup	10	0.92±0.04	5-12	10
White-winged scoter	10	0.77±0.16	6-14	10

* - Number of pairwise comparisons. A maximum of 10 were analysed.
** - Mean of Rho values ± one standard deviation.
*** - Range of helminth species in comparisons.
**** - Number of significant pairwise comparisons.

Table 23. Comparison of the distribution of median positions of helminths in ten duck species.

Species	N*	Clustered	Regular	Sign Test**
Bufflehead	1		1	n.a.
Widgeon	1		1	n.a.
Gadwall	2	1	1	n.a.
Ring-necked duck	2		2	n.a.
Ruddy	5		5	sig.
Canvasback	6	1	5	n.s.
Blue-winged teal	6		6	sig.
Mallard	10		10	sig.
Lesser scaup	15		15	sig.
White-winged scoter	13		13	sig
Total		2	59	sig.

* Number of birds with distributions detectable from random.

** n.a. = sample size too small to use sign test; n.s. = not significant; sig. = significant ($P < 0.05$).

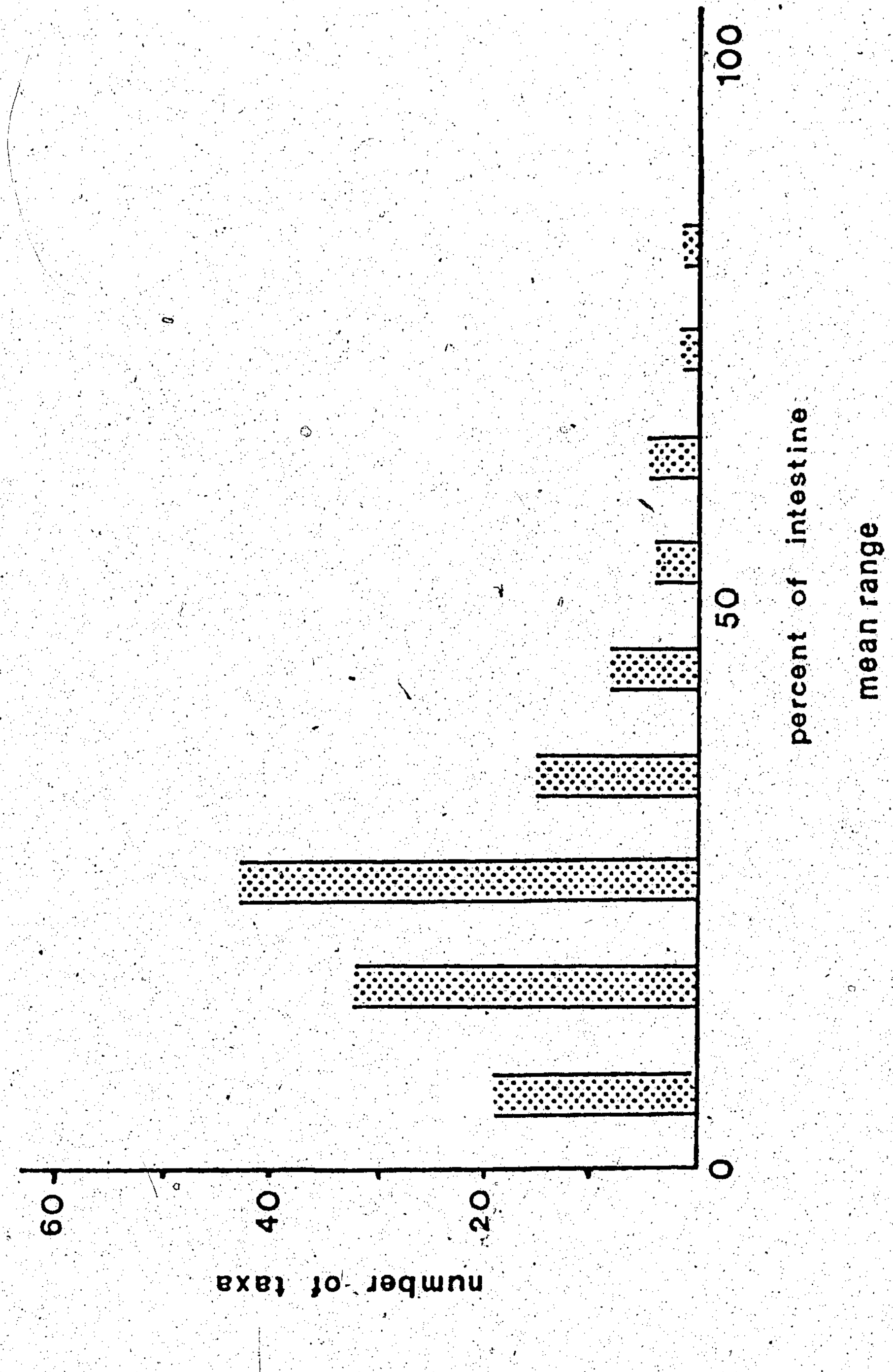
with a marked preponderance of distributions more regular than expected by chance.

The anterior and posterior ends of the distribution of most parasite species were more variable than the median position (Tables 11 to 20). The anterior and posterior ends were compared to the population sizes (Spearman's rank correlation) of each parasite species which infected five or more individual birds of one duck species. Most parasite species showed no correlation with population size. In those that did three patterns were distinguished: 1) equilateral spreading of the end points (i.e., *Apatemon gracilis* in mallard and scaup, *Hymenolepis abortiva* in scaup, *Echinocotyle rosseteri* in blue-winged teal), 2) anterior position extended anteriorly (8 cases), and 3) posterior position extended posteriorly (16 cases).

The average range of the majority of helminth species was less than 1/3 of the small intestine (Fig. 18). Eight parasite species had ranges greater than 50% of the small intestine (e.g., *Hymenolepis* AB in scoter and blue-winged teal). In all cases they were among the most abundant parasites in their respective hosts. Comparison of the mean ranges of the ten most abundant species to ten of the least abundant species (mean no. of individuals <30; chosen at random) indicated a significant difference (Mann-Whitney U-test). In addition, there was a significant positive rank correlation of the mean numbers of individuals and mean range for three of the host generalists (*Apatemon gracilis*,


(rho=.67),

Figure 18. The distribution of the mean ranges of seventy-five (75) helminth taxa across ten duck species.


60
40
20
0
number of taxa
50
100
percent of intestine
mean range

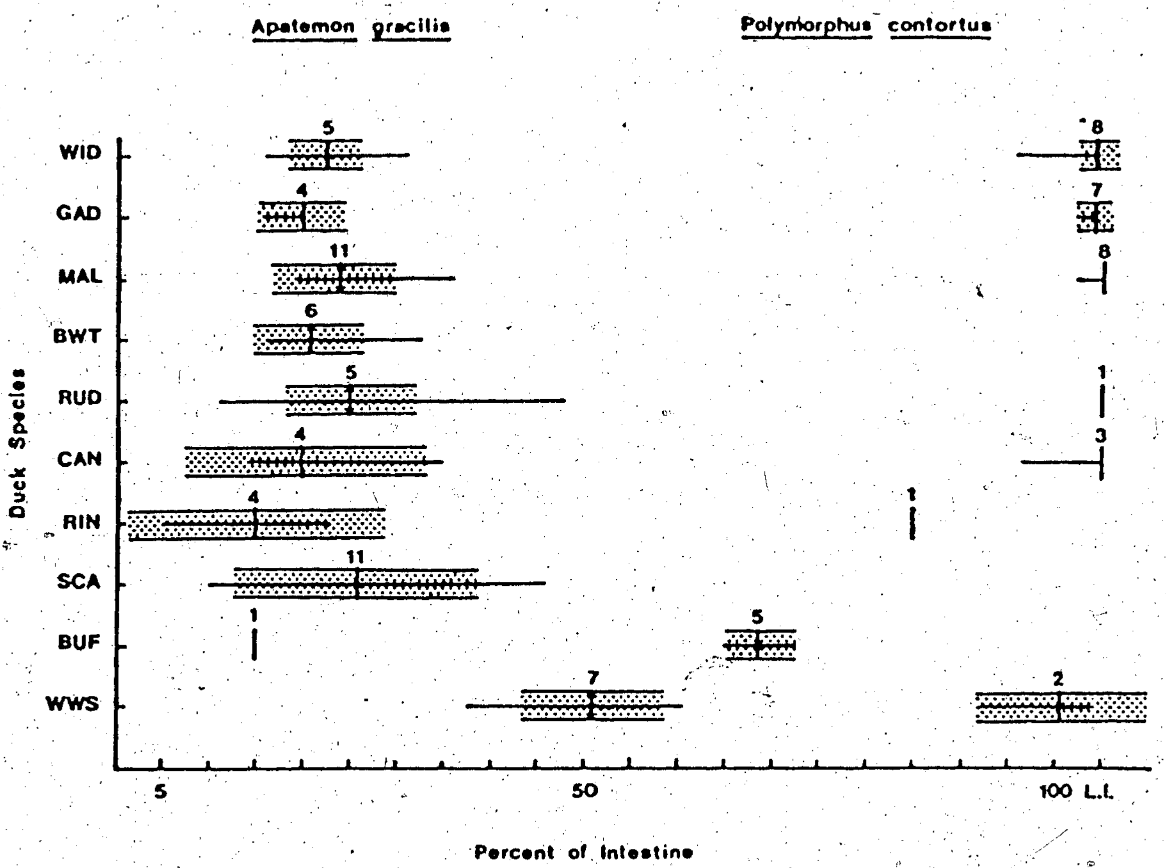
Fimbriaria fasciolaris (rho=.68), Corynosoma constrictum (rho=.89)).

Within individual birds, ranges of several helminth species were positively correlated with their respective population sizes (Tables 11-20). Most of the positive correlations of range with population size occurred in mallard, blue-winged teal, scaup and scoter, the species with the larger sample sizes. This suggests the phenomenon may be more prevalent than demonstrated by this study.

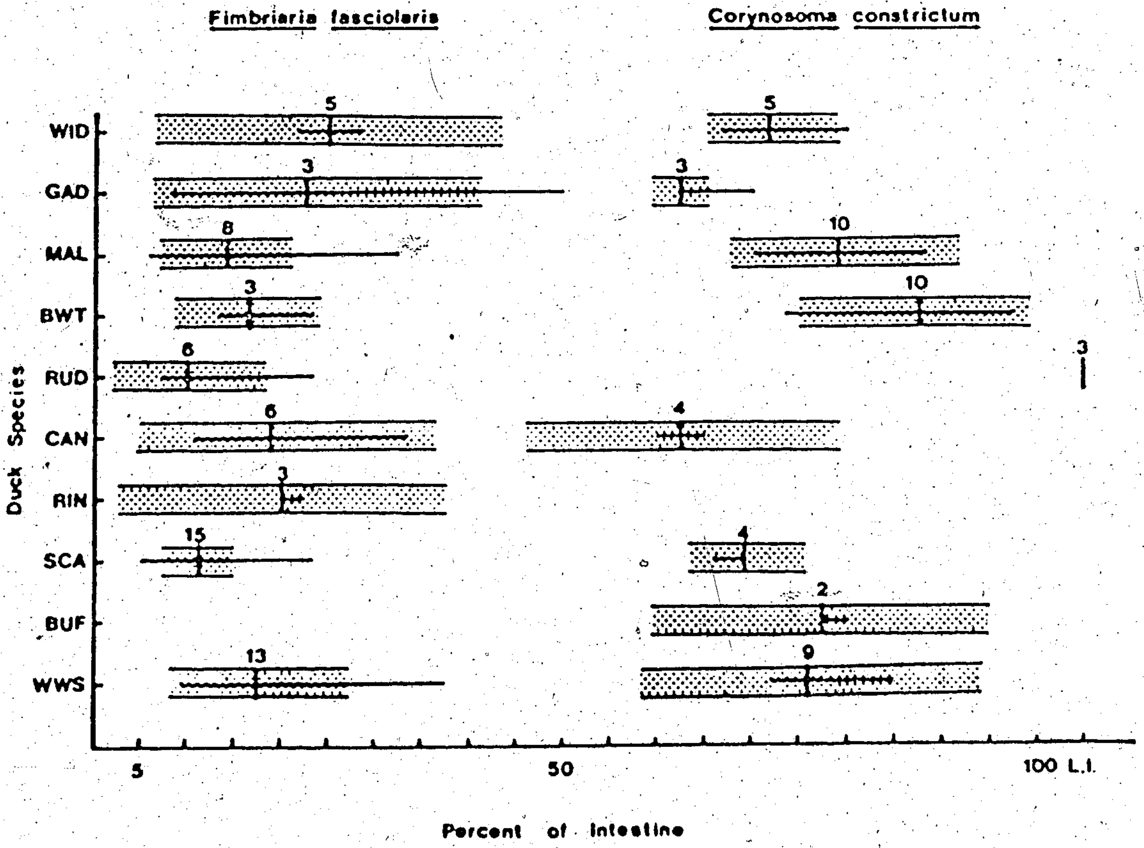
Comparison of the distributional measures of the helminth species considered to be host generalists indicated that most of these species occupied similar positions in the different duck species (Figs. 19 and 20). The only exception was A. gracilis; in scoter its median location was posterior to its location in the other duck species.

In the previous chapter examination of the exchange of helminth species indicated that several of the characteristic helminth species occurred in more than one host. Most of these species occupied similar portions of the intestine in different hosts (Figs. 21 to 25). However exceptions did occur; Hymenolepis AB was a characteristic species of scoter in which it occupied most of the intestine, with its median position in the posterior portion. However, in mallards, blue-winged teal, gadwall and ruddy its median position was in the anterior portion of the intestine. In one scoter its position was in the anterior end (median location-10%), similar to that in blue-winged teal.

Figure 19. Linear distributions of four host generalists across ten duck species. (vertical bar - mean median position, stipled bar - + 1 S.D., horizontal bar - mean of end points of distribution, number - no. of birds infected). (Duck codes are as in Figure 17).


Apatemon gracilis

Polymorphus contortus


Fimbriaria fasciolaris

Corynosoma constrictum

Figure 20. Linear distributions of <u>Echinoparyphium recurvatum</u> across nine duck species. (See Figure 18 for explanation of distributions).

Echinoparyphium recurvatum

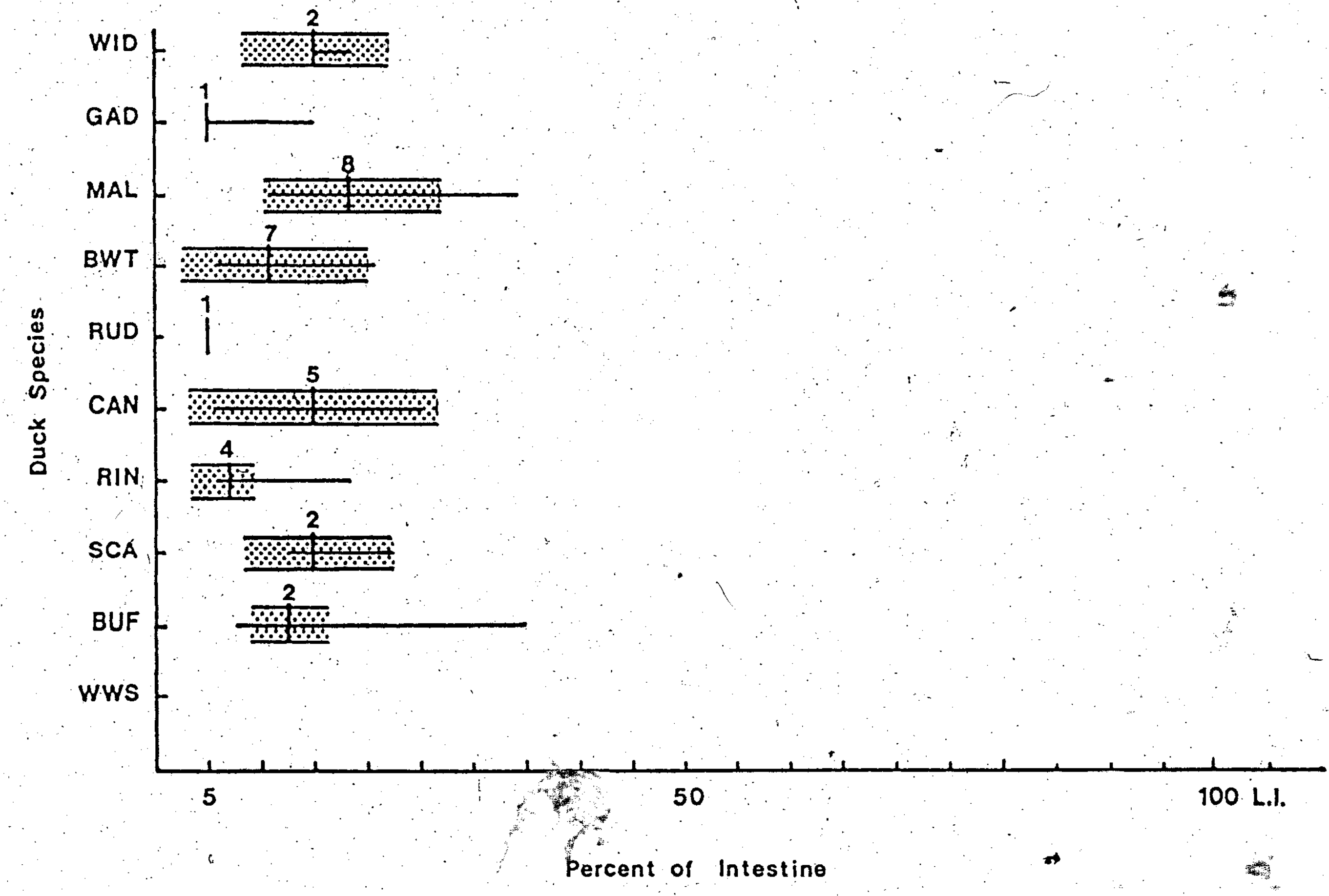


Figure 21. Linear distributions of the characteristic species of Ring-necked duck across duck species. (See Figure 18 for explanation of distributions) (duck codes as in Figure 17).

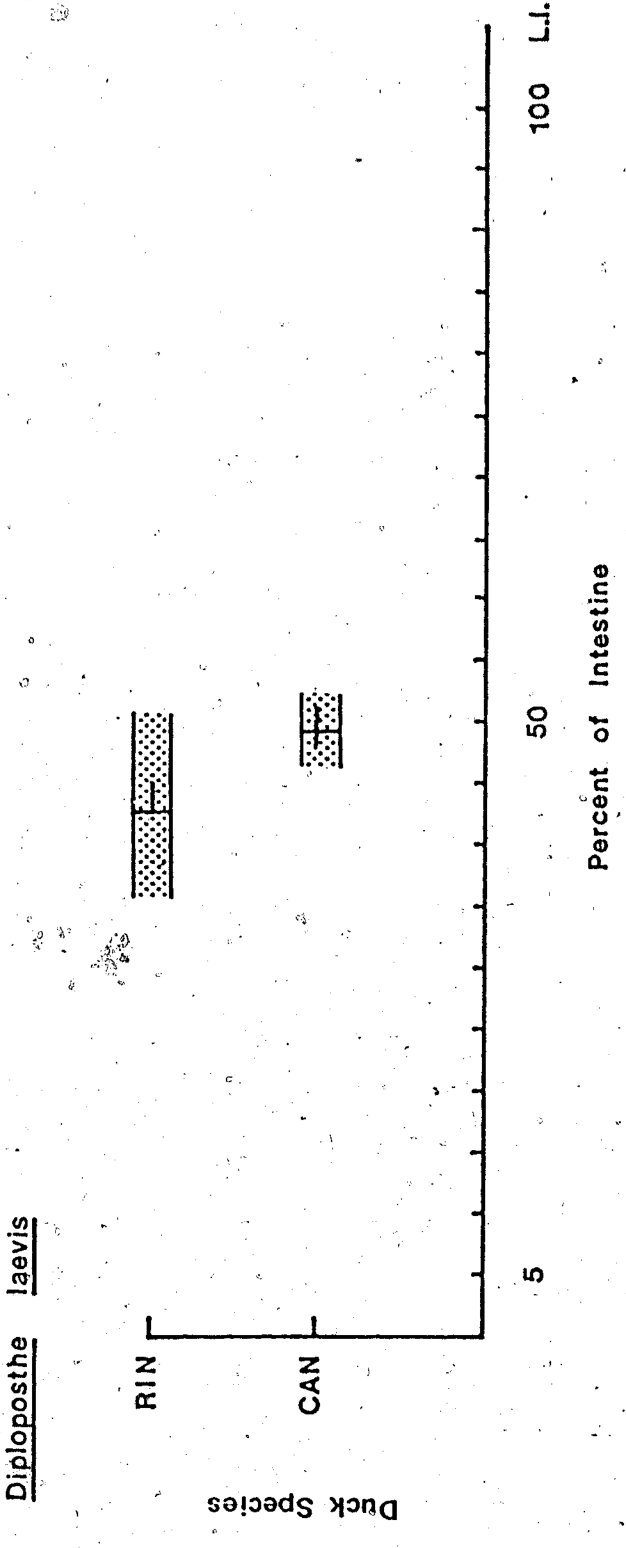
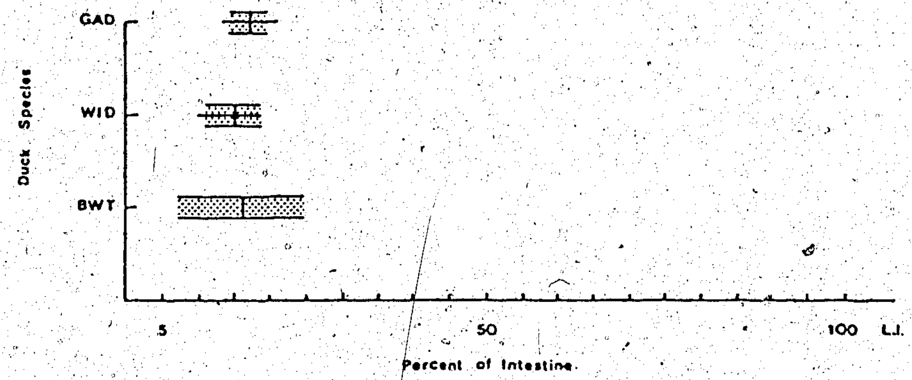

Diploposthe laevis
RIN
CAN
Duck Species
5
50
100
L.I.
Percent of Intestine

Figure 22. Linear distributions of the characteristic species of Gadwall across duck species. (See Figure 18 for explanation of distributions) (duck codes as in Figure 17).

Echinocotyle ooo



Diorchis spinata

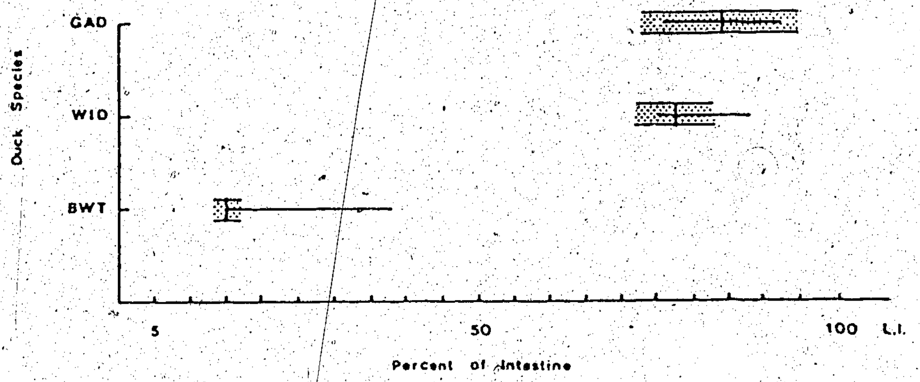
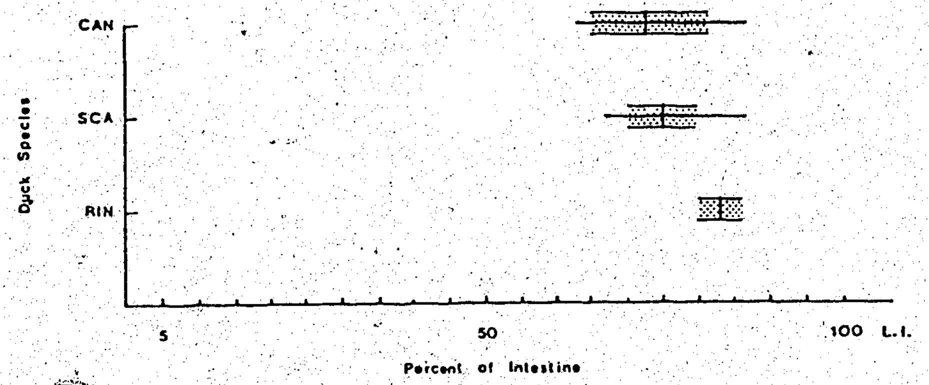


Figure 23. Linear distributions of characteristic species of Canvasback across duck species. (See Figure 18 for explanation of distributions) (duck codes as in Figure 17).

Diorchis n.sp. TT



Anatinella spinulosa

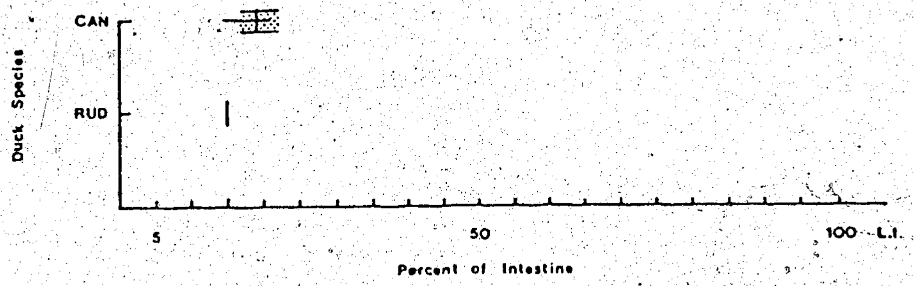
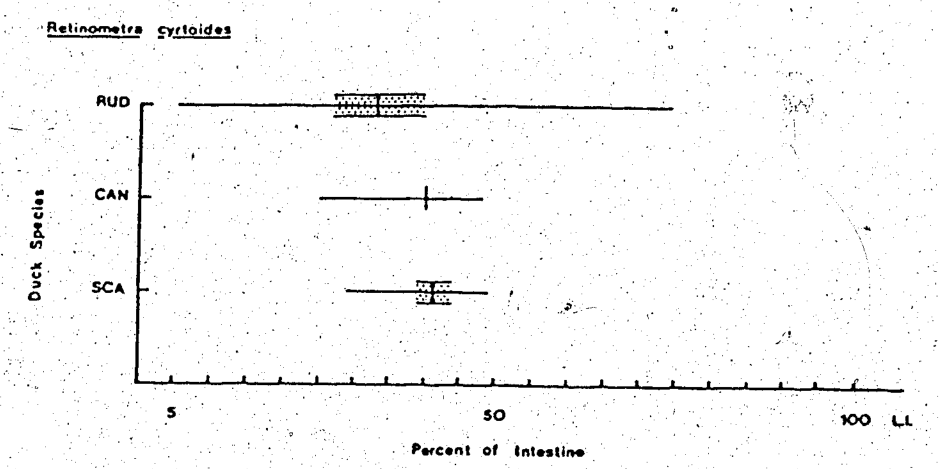


Figure 24. Linear distributions of characteristic species of Ruddy. (See Figure 18 for explanation of distributions) (duck species codes as in Figure 17).


Retinometra cyrtoides
RUD
CAN
SCA
Duck Species
5
50
100
L.I.
Percent of Intestine

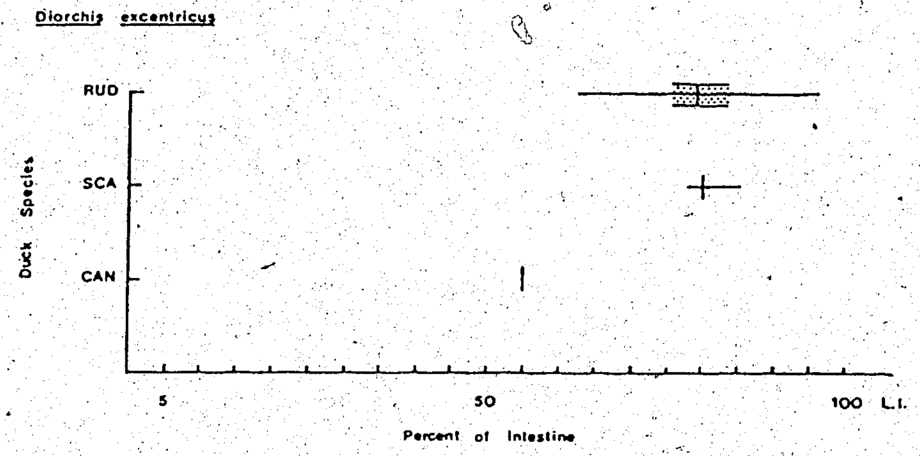
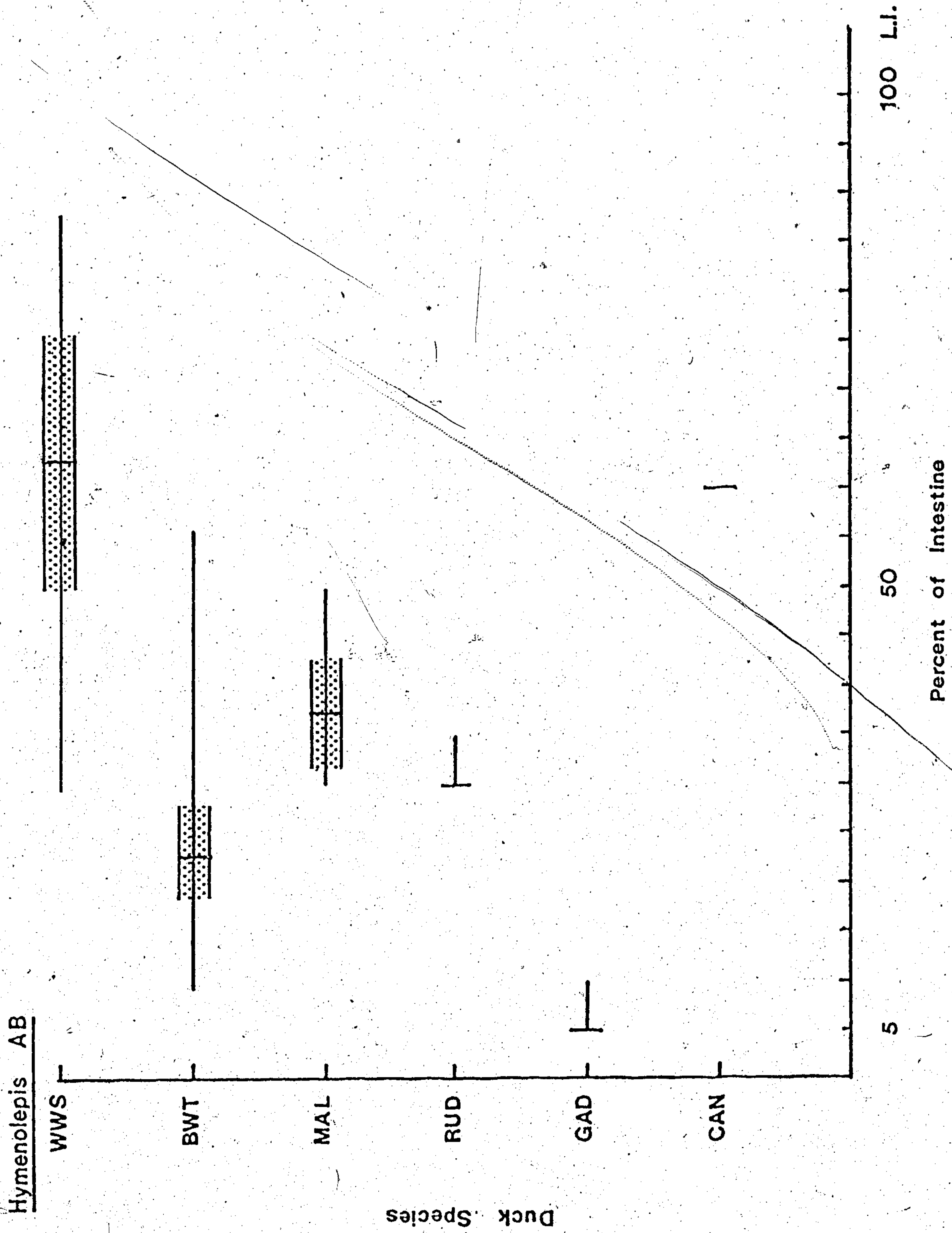

Diorchis excentricus
RUD
SCA
CAN
Duck Species
5
50
100
L.I.
Percent of Intestine

Figure 25. Linear distribution of a characteristic helminth species of White-winged scoter across host species. (See Figure 18 for further details and explanation of the distribution).


Hymenolepis AB
WWS
BWT
MAL
RUD
GAD
CAN
Duck Species
5
50
100
L.I.
Percent of Intestine

Organization and Maintenance of Infracommunity Structure

In the preceding paragraphs, I have equated resource use to, and measured it by, spatial distribution along the intestine. Unused resources therefore, are represented by unoccupied sections within the intestine. Comparison of the number of unoccupied sections indicated widgeon had the largest mean number of empty sections (13) and scoter the least (0) (Table 24). These are the two duck species with the lowest and highest mean number of species and individuals. The number of unoccupied sections was significantly correlated with the mean number of individuals (rho=.603) but not correlated with mean number of species.

Bush (1980) examined the potential for interactions between helminth species in the infracommunities of lesser scaup on the basis of their spatial utilization patterns. Average distributions were calculated across infracommunities for each helminth species as "the best measure of realized niche"; distributions summed across infracommunities were equated to the best available measure of fundamental niche (in the absence of experimental evidence). Percent similarity was used as a measure of overlap between helminth species. Significant reductions in average overlap from summed overlap was interpreted as evidence of interaction.

Because fifteen of the sixteen scaup were part of the analyses done by Bush (1980) and the analyses of niche overlap are the same, I will only do the analyses on the

Table 24. Mean number of unoccupied sections in each species of duck.

Species	NS*
Widgeon	14±7.3
Gadwall	9±5.1
Ring-necked duck	7±4.7
Mallard	5±6.3
Bufflehead	5±3.3
Blue-winged teal	4±5.0
Canvasback	2±1.7
Ruddy	1±1.3
Lesser scaup	1±1.0
White-winged scoter	0±0.0

* NS - Number of unoccupied section(s)

nine other host species were compared to the patterns found by Bush (1980).

In the previous chapter three components were identified in the helminth communities of the ten species of waterfowl: 1) characteristic species, 2) common species (generalist species plus commonly-occurring specialists from other hosts) and 3) the stochastic element of infrequently occurring specialists from other hosts. These data were also examined for evidence of interactions (average overlap significantly less than summed overlap) both within and between the first two components. Widgeon had only one species which occurred frequently (P. contortus), so no overlap values could be determined. Two duck species, mallard and bufflehead, did not have any characteristic species, therefore interactions between this component and others could not be examined. In scoter, three immature cestodes were frequent and two of these co-occurred with adult parasites which may have been the same species. These were considered separately. Three species, Cotylurus hebraicus, Hymenolepis fausti and Dicranotaenia coronula, for which primary hosts could not be determined were not included.

Six of 21 comparisons between pairs of characteristic species had average overlap values of less than one percent (Figs. 26 to 32). I consider average overlap of less than one percent to be too small for detection of potential interactions between pairs of species.

Figure 26. Average overlap values (Percent Similarity) between the common helminth species of Mallard. (** indicates $P < 0.01$).

	7	16	2	3	10
1. *Fimbriaria fasciolaris*	.481	.303**	.295**	.000	.000
7. *Echinoparyphium recurvatum*		.301	.411	.000	.000
16. *Hymenolepis fausti*			.344**	.000	.000
2. *Apatemon gracilis*				.000	.000
3. *Corynosoma constrictum*					.061
10. *Dicranotaenia coronula*					

Figure 27. Average overlap values (Percent Similarity) between common helminth species and characteristic helminth species of Ring-necked duck. (Code numbers of characteristic species are underlined).

	55	2	36
7. *Echinoparyphium recurvatum*	.750	.511	.000
55. *Hymenolepis parvula*		.268	.750
2. *Apatemon gracilis*			.052
36. *Diploposthe laevis*			

Figure 28. Average overlap values (Percent Similarity) between the common helminth species and characteristic helminth species of Ruddy. (Characteristic species are underlined; ** $P < 0.01$).

	2	29	22	48
1. *Fimbriaria fasciolaris*	.271**	.269**	.000	.000
2. *Apatemon gracilis*		.515**	.000	.000
29. *Retinometra cyrtoides*			.058	.043
22. *Cotylurus hebraicus*				.409**
48. *Diorchis exentricus*				

Figure 2[illegible] Average overlap values (Percent Similarity) between the common helminth species and the characteristic helminth species of Gadwall. (Characteristic species are underlined; ** $P < 0.01$).

	2	34	45	6
52. *Hymenolepis* WWW	.273	.230**	.000	.000
2. *Apatemon gracilis*		.667**	.000	.000
34. *Echinocotyle* QQQ			.000	.000
45. *Diorchis spinata*				.329
6. *Polymorphus contortus*				

Figure 30. Average overlap values (Percent Similarity) between the common helminth species and characteristic helminth species of Blue-winged teal. (Characteristic species are underlined; ** $p < 0.01$).

	7	39	2	12	57	3
50. *Echinocotyle* NNN	0.654	0.419	0.087	0.429**	0.028	0.000
7. *Echinoparyphium recurvatum*		0.548**	0.419	0.361**	0.024	0.000
39. *Echinocotyle rosseteri*			0.243**	0.434**	0.018	0.000
2. *Apatemon gracilis*				0.429**	0.028	0.000
12. *Hymenolepis* AB					0.058	0.006
57. *Sobolevicanthus octacantha*						0.099
3. *Corynosoma constrictum*						-----

Figure 31. Average overlap values (Percent Similarity) between the common helminth species and the characteristic helminth species of Canvasback. (Characteristic species are underlined; * $P < 0.05$, ** $P < 0.01$).

	1	59	16	2	8	25	36	5	10	3	26
7. *Echinoparyphium recurvatum*	.531**	.115**	.459	.245**	.316**	.185	.000	.000	.000	.000	.000
1. *Fimbriaria fasciolaris*		.107**	.504	.269**	.121**	.270	.000	.026	.000	.000	.000
59. *Anatinella spinulosa*			.231**	.800	.129	.168**	.000	.000	.000	.000	.000
16. *Hymenolepis fausti*				.208**	.057	.275	.000	.000	.000	.000	.000
2. *Apatemon gracilis*					.240	.167**	.063	.128	.063	.000	.063
8. *Hymenolepis spinocirrosa*						.479**	.000	.218*	.000	.589	.275
25. *Retinometra macracanthos*							.786	.075	.111	.075	.146
36. *Diploposthe laevis*								.239**	.404	.000	.309
5. *Polymorphis marilis*									.218*	.621	.337
10. *Dicranotaenia coronula*										.750	.422**
3. *Corynosoma constrictum*											.406
26. *Diorchis* n. sp. TT											

Figure 32. Average overlap values (Percent Similarity) between the common helminth species and the characteristic helminth species of White-winged scoter. (Characteristic species are underlined; * $P < 0.05$, ** $P < 0.01$).

	30	40	13	18	32	2	33	12	23	49	9	3	42	27	5	21
1. F. fasciolaris	.315**	.259**	.208	.255**	.275	.188	.092	.108	.036	.007	.000	.023	.026	.000	.007	.000
30. H. albertensis		.507	.293**	.438**	.192**	.155**	.206	.109	.098*	.044	.022**	.055	.012	.002	.009	.002
40. H. melanittae			.256**	.424**	.200	.113**	.249	.053	.044*	.001	.000	.016	.120	.000	.013	.000
13. L. skrjabini				.397**	.136**	.231**	.268	.194	.318	.112	.196	.143	.025	.026*	.102	.030
18. Spino?					.140**	.245**	.244	.230	.228	.355	.148*	.095*	.098	.026	.087	.015
32. AB?						.217**	.298**	.357	.402*	.390	.302*	.085*	.036	.083*	.146	.007
2. A. gracilis							.356	.194*	.239*	.295	.237**	.171	.000	.000	.047	.005
33. L. mathevossianae								.160**	.186**	.131**	.181**	.197**	.097	.034	.096**	.042**
12. H. AB									.537	.497	.390**	.155**	.115**	.111**	.316**	.048**
23. Abort?										.364	.316**	.177**	.140**	.101**	.247	.149
49. H. formosoides											.444	.266*	.176**	.241	.236*	.073
9. H. abortiva												.283**	.172**	.174**	.147**	.167*
3. C. constrictum													.416	.625	.302**	.419
42. P														.650	.245**	.094*
27. P. paradoxus															.305**	.480**
5. P. marilis																.230**
21. H. spiralibursata																

Only five of the remaining 15 comparisons between characteristic species had significantly reduced average overlaps. Four of these occurred in scoter with the highest number of characteristic species (6). The remaining pair of characteristic species with significantly reduced average overlap occurred in gadwall. In a comparison of the potential interactions between characteristic species and the second component (common species), 21 of 90 pairs had average overlap values of less than one percent. Thirty-five of the remaining average overlap values were significantly reduced from the summed overlap values. Fewer interactions occurred betweeen the characteristic species than between these parasite species and those of the second component. However, this difference was not significant (Chi-square= 1.27 , d.f.=1). The lack of difference may be due to sample size. The number of significantly reduced average overlap values greater than one percent and overlap values not significantly reduced between the other common species were similar (46 and 51, respectively). Analysis combining these values and the values between characteristic species and other species and comparing them to values between the characteristic species also showed no significant difference in the proportion of interactions between groups (Chi-square= 1.5, d.f.=2).

The average overlap between characteristic species was significantly less than the overlap in all other comparisons (Chi-square= 28.3, d.f.=2). In contrast, the mean ranges of the characteristic species were significantly greater than the mean ranges of the other species (Chi-square= 4.26, d.f.=2). Thus, despite having larger ranges the characteristic species had smaller average overlap values. In the previous section the median location of *Hymenolepis* AB occurred in a more posterior location in scoter compared to its position in mallard, gadwall and blue-winged teal (Fig. 26). This species had significantly reduced average overlap values with two of the six characteristic species in scoter, one with its median location anterior to *Hymenolepis* AB and one posterior. The host generalist *Apatemon gracilis* also occurred more posteriorly in scoter compared to its location in other host species (Fig. 19). This species had significantly reduced overlap values with three characteristic species of scoter, two of which had median locations anterior to *A. gracilis* (Fig. 32). Thus, the evidence suggests that the characteristic species in scoter influenced the distribution of some of the other species and interacted among themselves. Within scoter an immature taxon, Abort?, occurred with *Hymenolepis abortiva* (characteristic species of scaup), with which it had morphological similarities, the average overlap value between these two taxa was significantly reduced. This suggests that the immature individuals are being forced to the extremes of their microhabitat.

Comparison of the number of interactions between parasite species in the different host species indicated that the proportion of interactions in duck species with low size and complexity (mallard, gadwall, ring-necked duck, bufflehead, blue-winged teal, ruddy) and duck species with higher size and complexity (canvasback, scoter) were similar (Chi-square= 0.13, 0.42, d.f.=1). Comparison of the amount of average overlap (<10%, 10-20%, >20%), however, indicated there was significantly more overlap between parasite species in scoter and canvasback than the other duck species (Chi-square=6.6, d.f.=2)

DISCUSSION

Price's (1980) conclusion that parasite species are specialists in resource exploitation was in part based upon evidence in the literature of microhabitat specificity shown by several parasite species. Within this study, most parasite species in the intestine showed little variability in their median locations, either within or between different host species. In addition, the median location did not change with increasing population size, although range occupied often did. Most taxa had mean ranges of less than 30% of the small intestine, but eight had mean ranges of greater than 50%, and even more had maximum ranges spanning almost the entire intestine. These features indicate that within individual birds, most of these parasites were microhabitat specialists, but that some, for which microhabitat specificity appeared to be a function of population size, were at least potentially microhabitat generalists.

The predictable and restricted locations occupied by most helminth species within the intestine, the predictable sequence of those locations, and their regular distribution along the intestine all imply that the infracommunities are structured. The fact that median points are more regularly distributed than expected by chance strongly suggests that an interactive mechanism is involved, and argues against the independent adaptation to different locations within the intestine suggested by Price (1980).

Bush (1980) suggested that within the intestinal helminth communities of scaup, the deterministic component was structured through interactive mechanisms, but that the stochastic component was noninteractive. Sample sizes within this study precluded examination of the stochastic component. However, the number of ducks examined allowed me to separate the deterministic component of Bush (1980) into two parts, the characteristic species and other frequently occurring species. The characteristic species were the host specialists, which presumably have co-occurred with each other regularly, and which would be expected to show the greatest evolutionary co-adaptation (Holmes and Price, 1981). The other frequently occurring species are generalists and species which were specialists in other hosts. Although these species may co-occurred frequently, their major populations were more widely distributed (and subject to more varied selection pressures) or were in other hosts, where they were subject to evolutionary pressures from other groups of parasites. It is not suprising therefore that, there was significantly less overlap between the characteristic species (despite their large average ranges within the intestine). Although these species had proportionally fewer interactions, the difference was not significant and needs to be examined with larger sample sizes. However, the smaller amount of overlap despite larger ranges is a feature expected from a group of coevolved specialists.

In scoter, in which the parasite communities had high complexity and large numbers of individuals, the number of interactions between the characteristic species (4) was higher than in the other duck species (1). In scaup, Bush (1980) noted that most of the frequent species, including the eight characteristic species identified in this study, showed significantly reduced average overlap values. The increased number of interactions with increasing number of characteristic species may indicate that these infracommunities are saturated. However, scoter have a much larger intestine, both in length and radius (personal observation), than the other duck species. At least two of the overlapping characteristic species in scoter were observed to form irregular aggregations, within individual 5% sections of the intestine, with empty space separating groups of individuals and co-occurring helminth species. This pattern was not observed in scaup, in which parasites tended to be uniformly distributed around and along the intestine.

The duck species with few parasite species and individuals had many unoccupied sections, in these situations the aggregations of individual parasite may have been a result of selection pressures to mate in sparse populations (Rohde, 1979).

In conclusion, both interactive and noninteractive explanations can be applied to the helminth communities in waterfowl. However, Price's (1980) statement that most cases of parasite coexistence involve predominantly noninteractive niche occupation is not supported by this study. Interactions between species were not uncommon and for at least two species in white-winged scoter (Apatemon gracilis, Hymenolepis AB), the different position they occupied (as compared to their position in other hosts) appeared to be a direct response to interactions with characteristic species within the same region of the intestine.

IV.

ORGANIZATION OF INTESTINAL HELMINTH COMMUNITIES IN WATERFOWL ALONG TWO RESOURCE AXES

Generalist and Specialist Species on Two Resource Axes

In the previous two chapters I examined the resource use of helminth parasites along two nested resource axes: host species and the microhabitats within the intestine. Resource use across host species was measured by the niche breadth of mature individuals (B′a(mature)). Resource use within the intestine was determined by mean range occupied within infracommunities. The analysis demonstrated that, on each axis, parasite species may fall anywhere along a continuum from extreme specialist to extreme generalist. Obviously, generalist and specialist are relative terms. However, describing a species as a specialist or generalist, only applies to one resource axis.

Because specialist and generalist are relative terms along a continuum it is difficult to assign a critical value to separate one group from another. The simplest method is to compare the extremes of the continuum. For this purpose I will use the seven species which are at each extreme of the continuum in comparing niche breadth (B′a(mature)) along the host resource axis. The seven host generalists include *Hymenolepis hopkinsi*, *Capillaria anatis*, *Notocotylus attenuatus*, *Polymorphus contortus*, *Corynosoma constrictum*, *Fimbriaria fasciolaris*, and *Apatemon gracilis* (Table 25).

The seven host specialists include *H.* WWW, *Echinocotyle NNN*, *E. rosseteri*, *Lateriporus mathevossianae* *H. albertensis*, *H. melanittae*, and *H. formosoides*.

Three of the host generalist species inhabited the caeca in all hosts and were obviously microhabitat specialists relative to those which occupy the intestine (Table 25). Within the intestine two of the generalist species had mean ranges of less than 15% of the intestine and two species had mean ranges greater than 20% of the intestine.

The host specialists showed similar variation between parasite species. Two species had mean ranges of less than 15% and two species had mean ranges of greater than 50% of the intestine. Comparison of the maximum range occupied by a parasite species in one host individual demonstrated similar relationships between the two parasite groups. The caeca were equated to a 5% section of the intestine. Some of the host specialists occupied a maximum range of the entire intestine.

An alternative, and perhaps better analysis is to examine the distribution of all common species as defined by their positions along both resource axes (using mean range as the measure of microhabitat resource use and B′a(mature) as the measure of resource use along the host axis) (Fig. 33). Since parasites which mature in several host species may have very different microhabitat ranges in the different host species, each parasite entered the figure separately

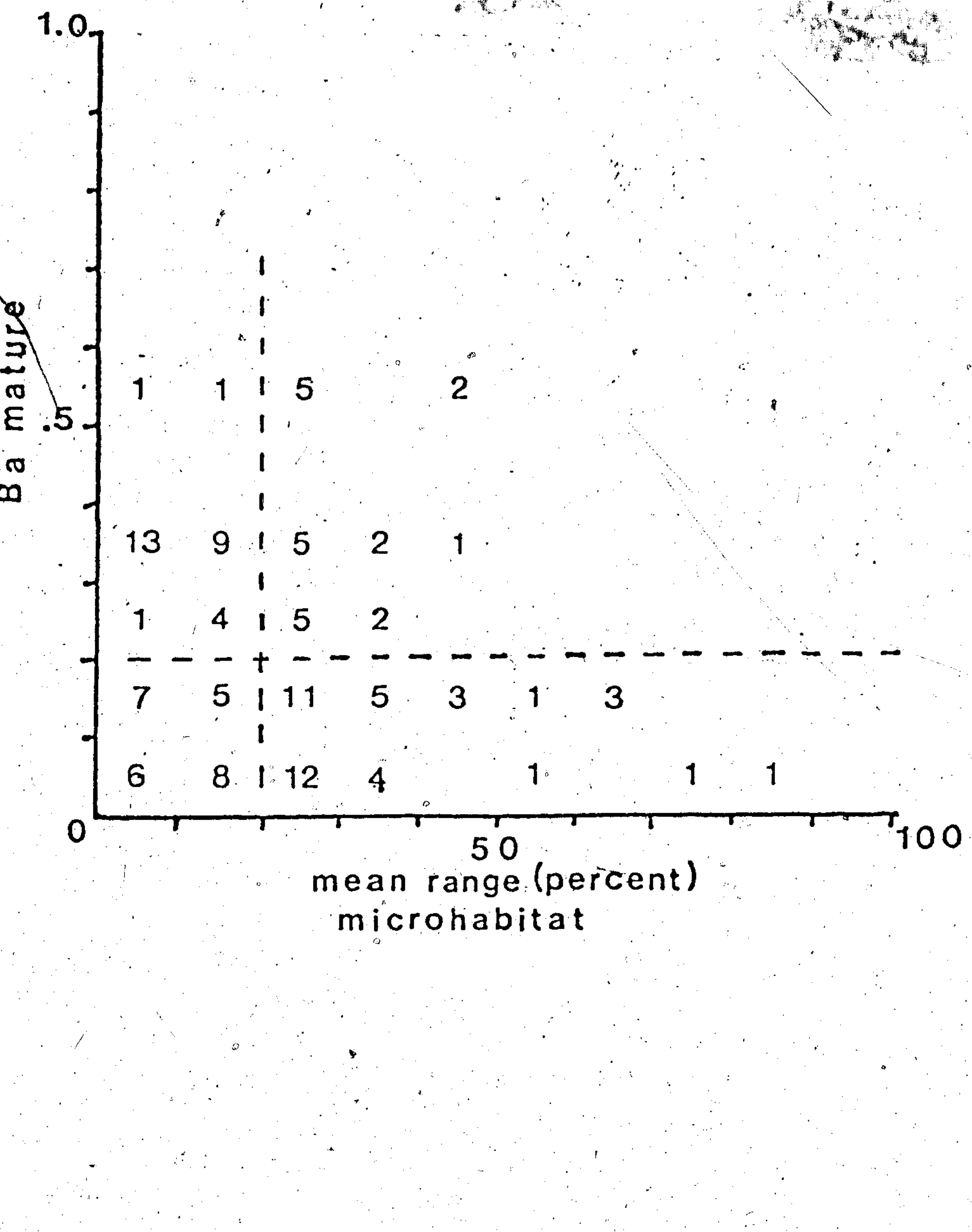
Table 25. Niche breadth measures along two resource axes (host and microhabitat) of generalist and specialist helminth species from ten species of ducks.

	N_h^*	B'a(mature)	Mean range**	Maximum range
GENERALISTS				
H. hopkinsi	10	0.16	Caeca	5
C. anatis	8	0.34	Caeca	5
N. attenuatus	8	0.34	Caeca	5
P. contortus	8	0.35	11± 4.1	45
C. constrictum	9	0.35	12± 8.6	50
A. gracilis	10	0.57	23±12.3	75
F. fasciolaris	9	0.36	24±12.4	65
SPECIALISTS				
H. WWW	1	0.01	11± 1.9	15
E. rosseteri	1	0.04	27±17.5	55
E. NNN	1	0.04	10± 9.1	30
L. mathevossianae	1	0.11	41±22.9	70
H. melanittae	1	0.08	52±28.0	100
H. formosoides	1	0.07	21±10.6	40
H. albertensis	1	0.08	85±17.0	105

$*N_h$ - number of hosts infected

** Mean range for generalists is the mean of the mean range in all hosts infected.

Figure 33. Comparison of the number of helminth species along two resource axes (host and microhabitat). Host axis is measured by the niche breadth of mature species (B'a (mature)) and the microhabitat axis is measured by the mean range of helminth species location in the intestine. Dotted line indicates separation between relative specialists and generalists along each axis (e.g. lower left quadrat are specialists on both axes).


1.0
.5
0
50
100
B'a mature
mean range (percent)
microhabitat
1 1 5 2
13 9 5 2 1
1 4 5 2
7 5 11 5 3 1 3
6 8 12 4 1 1 1

for each host in which it matured. Many species were specialists on both axes, others were specialists on one and generalists on another, and some were generalists on both. A chi-square test indicated the distribution along the two axes were not independent (Chi-square= 4.07, p<.05), but complementary. Thus, there is no reason to assume the use of resources by sympatric species will be the same on all resource axes, nor is there reason to conclude that all parasite species are specialists. Parasites show the same variation in specialization on resource axes, and the same pattern of complementarity of specialization (Pianka, 1978) on different resource axes as other organisms.

Interactive and Noninteractive Community Structure

Two basically different explanations have been proposed for the microhabitat specificity observed in parasites and the consequent nature of parasite communities. Holmes (1973) proposed that parasite communities were mature and that selective site segregation was a response to interactions with other parasite species. Price (1980) proposed that parasite communities are assemblages of specialists adapted to specific microhabitats because of unspecified selection pressures other than competition.

Holmes and Price (1980) have compared the two hypotheses of parasite community structure to the theory of community development proposed by Wilson (1969). Price's view was equated with Wilson's initial noninteractive phase during which helminth species colonize a new and underutilized habitat. Holmes's view was equated with Wilson's final evolutionary phase in which helminth species no longer interact because they have adapted to coexist with the pattern of exploitation of resources by other species.

Holmes and Price (1980) have also provided predictions as to five features one would expect to observe in parasite communities if they conformed with either the initial noninteractive phase of community development or the final evolutionary phase of development. Predictions concerning three of these features are applicable to this study.

The first prediction states that parasite communities in the initial noninteractive phase should have many vacant niches available for colonization, whereas in the final evolutionary phase there will be few or no vacant niches. Within this study, the ten duck species were arranged on a loose cline of complexity, size and similarity between helminth communities. The species with low complexity and small sized helminth communities had unused resources (unoccupied sections) available for colonization and thus correspond to the view of a young parasite community. The helminth communities with high complexity and large size had no unoccupied sections, and thus correspond to the view of a mature parasite community.

The second prediction states that the parasite communities in the initial phase will have few helminth species not abutting in distribution, and some helminth species showing considerable overlap (>70%) on relevant resource gradients. Parasite communities in the final phase of development will have many adjacent helminth species abutting, or if overlapping, the overlap will be less than 70%. This prediction can be examined along the loose cline of helminth communities from low to high complexity. I will measure "abutting" distributions as those which have a mean overlap of 1-10%. Using this criterion, the complex parasite communities in scoter and canvasback had a high proportion (33% of pairs) of abutting distributions, and a small proportion (12%) of distributions with 50% overlap or more. Parasite communities in scaup showed a similar pattern (46% abutting, 1% with 50% overlap or more- Bush, 1980). The parasite communities in the other six ducks had a very small proportion of abutting distributions (8%) but about the same proportion showing high overlap (9%). In addition, there was significantly less overlap between the characteristic species than between the other species within the intestine even though the ranges of the characteristic species were significantly larger than the ranges of the other species. Clearly, the extremes of the parasite communities (low complexity, low similarity and high complexity, high similarity) correspond with the young and mature views of community structure, respectively.

The third prediction states that hosts with similar sets of resources (i.e., adult ducks of one species) should support an unpredictable number of helminth species in the initial noninteractive phase of development, but a predictable number in the final phase. Restated, there will be few common or characteristic helmith species in parasite communities in the initial phase of community development. In the evolutionary phase, a predictable number of helminth species should be present. This prediction of a consistent number of species is again reflected along the cline of helminth communities. Widgeon and bufflehead with low similarity between individuals had no characteristic species and had an unpredictable suite of parasites. Helminth communities with high similarity obviously have a predictable component.

Thus, it is clear the two ends of the continuum of parasite communities, from low complexity, small size and low similarity to high complexity, large size and high similarity agree with the predictions of the two views of parasite community structure, the former with predictons for a young community the latter for a mature community. The fact that parasite communites in waterfowl agree with the initial and final phases of community development and show evidence for both interactive and noninteractive mechanisms of community structure, is not surprising if parasites are viewed as being capable of spanning all options of resource use in a similar manner to freeliving organisms and not restricted to being extreme specialists in resource exploitation.

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Appendix 1. Species, lake, month, year, sex and weight of birds used in this study.

Bird No.	Lake*	Month	Year	Sex**	Weight***	Examined****
Mallard						
MAL01	CH	06	1979	F	1050	
MAL02	CH	06	1979	F	950	
MAL03	CH	07	1977	F	960	
MAL04	BL	06	1979	M	1400	
MAL05	BL	08	1979	U	1100	
MAL06	WD	07	1978	F	1100	1
MAL07	CP	06	1980	M	1150	1
MAL08	CP	06	1977	F	900	1
MAL09	CK	05	1977	M	1030	1
MAL10	BO	06	1978	M	1300	1
MAL11	LA	06	1977	M	1250	1
MAL12	LA	06	1977	M	1250	1
MAL13	RS	05	1977	M	1150	1
MAL14	RS	05	1977	F	900	1
MAL15	RS	05	1977	M	1050	1
MAL16	CW	06	1980	F	950	2
Widgeon						
WID01	CH	06	1979	F	560	
WID02	CH	06	1979	F	620	
WID03	CH	06	1979	F	570	
WID04	CH	06	1979	F	510	
WID05	BL	06	1979	M	690	
WID06	BL	06	1979	F	800	
WID07	BL	06	1979	F	795	
WID08	BL	06	1979	M	775	
WID09	BL	07	1979	U	690	
WID10	RS	05	1977	M	690	1
WID11	RS	05	1977	M	670	1
Gadwall						
GAD01	BL	06	1979	M	790	
GAD02	BL	06	1979	M	795	
GAD03	BL	06	1979	M	760	
GAD04	BL	06	1979	F	780	
GAD05	BL	06	1979	M	715	
GAD06	DU	06	1977	M	990	
GAD07	DU	06	1977	M	1000	
Blue-winged teal						
BWT01	CW	06	1978	M	405	
BWT02	CW	06	1979	U	350	
BWT03	CW	06	1979	U	370	
BWT04	CP	06	1977	M	365	
BWT05	CP	06	1977	M	355	
BWT06	BL	07	1977	U	340	
BWT07	BL	06	1979	M	370	
BWT08	BL	06	1979	M	360	
BWT09	BL	06	1979	M	400	
BWT10	BL	06	1979	F	425	
Ruddy						
RUD01	BL	06	1979	M	600	
RUD02	BL	[illegible]	1979	M	600	
RUD03	LA	[illegible]	1977	F	500	
RUD04	LA	07	1977	M	645	
RUD05	LA	07	1977	F	540	
RUD06	BL	06	1979	M	660	
Bufflehead						
BUF01	CH	06	1979	F	270	
BUF02	CP	06	1977	M	425	
BUF03	CP	08	1977	U	470	
BUF04	CH	08	1979	U	320	
BUF05	CH	08	1979	U	400	
BUF06	CP	06	1977	F	265	
Canvasback						
CAN01	CH	07	1977	F	1000	
CAN02	CH	07	1977	M	1000	
CAN03	CH	07	1977	M	1100	
CAN04	BL	07	1980	M	805	
CAN05	BL	07	1980	F	1060	
CAN06	BL	07	1980	U	1278	
Ring-necked duck						
RIN01	CW	06	1977	M	670	
RIN02	CW	06	1977	M	700	
RIN03	CW	06	1977	F	590	
RIN04	CW	06	1979	M	590	
RIN05	CW	06	1979	F	800	
RIN06	CW	06	1979	F	615	
White-winged scoter						
WWS01	WF	06	1978	M	1450	
WWS02	WF	06	1978	M	1650	
WWS03	WF	06	1978	M	1800	
WWS04	CP	06	1977	F	1200	
WWS05	CP	06	1977	M	1650	
WWS06	CP	06	1977	M	1600	
WWS07	BL	06	1979	M	1600	
WWS08	BL	06	1979	M	1600	
WWS09	BL	06	1979	M	1800	
WWS10	BL	08	1979	M	1350	
WWS11	FH	06	1978	M	1550	
WWS12	FH	06	1978	M	1500	
WWS13	FH	06	1978	M	1600	
Lesser scaup						
SCA01	BL	06	1979	M	660	
SCA02	CP	06	1977	F	-0	3
SCA03	CP	06	1977	M	-0	3
SCA04	CP	06	1977	F	-0	3
SCA05	WF	06	1978	F	-0	3
SCA06	WF	06	1978	M	-0	3
SCA07	WF	06	1978	M	-0	3
SCA08	BL	06	1977	F	-0	3
SCA09	BL	06	1977	M	-0	3
SCA10	BL	06	1977	M	-0	3
SCA11	FH	06	1978	M	-0	3
SCA12	FH	06	1978	F	-0	3
SCA13	FH	06	1978	F	-0	3
SCA14	FH	06	1978	M	-0	3
SCA15	FH	06	1978	F	-0	3
SCA16	FH	06	1978	M	-0	3

* Lake codes: BL-Bellshill; BO-Bistcho; CH-Charron; CP-Chip; CK-Cowoki; CW-Cow; DU-Dusty; FH-Fleeinghorse; LA-Lanes; RS-Rattlesnake; WD-Wadlin; WF-Wolf.

**Sex M-males; F-females; U-unknown.

***Weight: grams

****Examined by: 1-K.M.Nielsen; 2-J.M.Aho; 3-A.O.Bush ; all others examined by E.W. Butterworth.

Appendix 2. Helminth species codes (numerical) for 118 taxa recovered from ten species of ducks.

1. *Fimbriaria fasciolaris*
2. *Apatemon gracilis*
3. *Corynosoma constrictum*
4. *Hymenolepis hopkinsi*
5. *Polymorphis marilis*
6. *Polymorphus contortus*
7. *Echinoparyphium recurvatum*
8. *Hymenolepis spinocirrosa*
9. *Hymenolepis abortiva*
10. *Dicranotaenia coronula*
11. *Hymenolepis pusilla*
12. *Hymenolepis* AB
13. *Lateriporus skrjabini*
14. *Notocotylus attenuatus*
15. *Capillaria anatis*
16. *Hymenolepis fausti*
17. *Hymenolepis tuvensis*
18. Spino ?*
19. *Zygocotyle lunata*
20. PP*
21. *Hymenolepis spiralibursata*
22. *Cotylurus hebraicus*
23. Abort?*
24. *Retinometra pittalugi*
25. *Retinometra macracanthos**
26. *Diorchis* n.sp. TT
27. *Polymorphus paradoxus*
28. Echino?*
29. *Retinometra cyrtoides*
30. *Hymenolepis albertensis*
31. *Hymenolepis microskrjabini*
32. AB?*
33. *Lateriporus mathevossianae*
34. *Echinocotyle* QQQ
35. *Hymenolepis recurvata*
36. *Diploposthe laevis*
37. *Diorchis elisae*
38. *Diorchis danutae*
39. *Echinocotyle rosseteri*
40. *Hymenolepis melanittae*
41. *Echinostoma revolutum*
42. P*
43. *Hymenolepis* tuv?*
44. X*
45. *Diorchis spinata*
46. *Cotylurus flabelliformis*
47. *Capillaria obsignata*
48. *Diorchis excentricus*
49. *Hymenolepis formosoides*
50. *Echinocotyle* NNN
51. *Unciunia* n.sp.
52. *Hymenolepis* WWW
53. *Capillaria nyrocinarum*
54. *Sobolevicathus gracilis**
55. *Hymenolepis parvula*
56. *Diorchis* AD*
57. *Sobolevicanthus octacantha**
58. *Hymenolepis paracompressa*
59. *Anatinella spinulosa*
60. TTT*
61. *Hymenolepis compressa*
62. Micro?*
63. *Lateriporus clerci**
64. *Hymenolepis arcuata*
65. *Sobolevicanthus kenaiensis*
66. RR*
67. *Hypoderaeum conoideum*
68. *Aploparaksis fucigera*
69. Pusilla?*
70. *Hymenolepis* XXX*
71. *Hymenolepis* tuv AB?*
72. *Microphallus* sp 1
73. *Oligorchis* n.sp.*
74. *Hymenolepis* GGG
75. D*
76. NN*
77. *Sobolevicanthus bissacata*
78. *Hymenolepis* PHI
79. *Diorchis* n.sp.B
80. Parvula?*
81. AE*
82. AL*
83. III*
84. EE*

85. T*
86. QQ
87. Plagiorchis Sp
88. JX*
89. ABN*
90. US*
91. Hymenolepis spiralibursata**
92. Diorchis inflata*
93. NJ*
94. ABZ*
95. JJJ*
96. Microphallus sp. 2
97. DDD*
98. ZZZ*
99. Sobolevicanthus krabbela
100. Delta*
101. CCC*
102. Diorchis PHLY*
103. FFF*
104. ENNNA*
105. KKK*
106. AN*
107. C*
108. L*
109. BD*
110. H?
111. Hymenolepis hop?
112. AZ*
113. ABK*
114. ABHH*
115. AXXX*
116. AJA*
117. Schistocephalus sp.
118. Lambda*

* No mature individuals found (presence of shelled eggs) ; all immature individuals.

** Hymenolepis spiralibursata (nec Denny, 1969)

Appendix 3. Taxonomic characters of helminth species that could not be identified. Hook lengths are in micrometers.

Numerical Code	Designation	Hooks			Remarks
		Number	Length	Shape	
Trematoda					
20	PP	--	--	--	Strigeidae? (immature)
28	Echino?	38 - 44	--	--	*Echinoparyphium*? (immature)
72	Microphallid sp 1	--	--	--	*Spleotrema*?
96	Microphallid sp 2	--	--	--	*Maritrema*?
Cestoda					
12	*Hymenolepis* AB	10	46 - 48	diorchoid	*Hym*. *paramicrosoma*?
18	Spino?	10	42 - 46	dio.	*Hym*. *spinocirrosa*? (immature)*
23	Abort?	10	32 - 38	dio.	*Hym*. *abortiva*? (immature)*
26	*Diorchis* TT	10	40 - 42	dio.	eggs with one polar filament at each pole
32	AB?	10	46 - 48	dio.	*Hym*. AB? (immature)*
34	*Echinocotyle* QQQ	10	52 - 62	dio.	spiny accessory sec
42	P ——	10	18	aploporaksis	--
43	*Hym*. tuv.?	10	34 - 38	dio.	*Hym*. *tuvensis*?
44	X	8	70 - 74	skrjabini	*Retinometra*?

Numerical Code	Designation	Number	Length	Shape	Remarks
50	*Echinocotyle* NNN	10	48 - 52	dio.	sclerotized accessory sac
52	*Hym*. WWW	10	48 - 52	dio.	*Hym*. collaris?
56	TTT	8	32 - 34	skrjabini	--
62	Micro?	10	32 - 38	dio.	*Hym*. *microskrjabini* (immature)*
66	RR	10	50 - 60	dio.	*Hym*. *compressa*/*paracompressa*?
69	Pusilla?	10	18 - 22	arcuctoid	*Hym*. *pusilla* (immature)*
70	*Hym*. XXX	8	23	skrjabini	large scolex
71	*Hym*. tuv AB?	10	34 - 38	dio.	--
74	*Hym*. GGG	10	42 - 46	dio.	long spiny cirrus (abortiva type)
75	D	10	26 - 28	dio.	see Bush (1980) (*Hym*. sp. 2)
76	NN	10	48	dio.	--
78	*Hym*. PHI	10	88	dio.	spiny cirrus
79	*Diorchis* B	10	28 - 30	recurvatoid	spiny cirrus
80	Parvule?	10	42 - 44	recurvatoid	spiny cirrus
81	AE	10	50	dio.	--
82	AL	10	68	dio.	--
83	III	10	50	dio.	--

Numerical Code	Designation	Number	Length	Shape	Remarks
84	EE	10	18	aploporaksis	--
85	T	10	26 - 27	dio.	see Bush (1980)
86	QQ	8	76	skrjabini	*Sobolevicanthus?*
88	JX	10	40 - 43	--	*Dubinolepis?*
89	ABN	10	30 - 31	dio.	see Bush (1980)
90	US	10	20	dio.	--
93	NJ	10	24 - 28	dio.	--
94	AB2	10	88	dio.	see Bush (1980)
95	JJJ	10	26	arcuatoid	long handle
97	DDD	10	100	dio.	--
98	ZZZ	10	43	dio.	--
100	Delta	8	52	skrjabini	--
101	CCC	10	12 - 14	apoloraksis	--
102	*Diorchis* PHLY	10	72 - 74	dio.	flask-like vagina
103	FFF	22	18	aploporaksis	*Dicrano coronula*
104	*Echinocotyle* NNNA	10	60 - 64	dio.	--
105	KKK	8	60 - 62	skrjabini	--
106	AN	10	60	dio.	--

Numerical Code	Designation	Number	Length	Shape	Remarks
107	C	10	32	dio.	Abort?
108	L	10	38	dio.	--
109	BD	10	30	arcuatoid	spiny cirrus
110	H?	10	30 - 31	arcuatoid	--
111	*Hym*. hop?	--	--	--	no hooks *Hym*. *hopkinsi*?
112	AZ	10	88	dio.	--
113	ABK	10	113 - 115	dio.	--
114	ABHH	8	56 - 58	skrjabini	--
115	AXXX	10	52	recurvatoid	--
116	AJA	8	87	skrjabini	--
118	LAMBDA	10	50	arcuatoid	--

* Immature - everted larval stage with no proglottid development.

Appendix 4. Composition of parasite species groups derived by cluster analysis using Jaccard's coefficient of similarity for 75 helminth taxa.

A

1. *Fimbraria fasciolaris*
2. *Apatemon gracilis*
3. *Corynosoma constrictum*
4. *Hymenolepis hopkinsi*
6. *Polymorphus contortus*
7. *Echinoparyphium recurvatum*
10. *Dicranotaenia coronula*
14. *Notocotylus attenuatus*
16. *Hymenolepis fausti*
19. *Zygocotyle lunata*
25. *Retinometra macroacanthus*
28. Echino?*

B

20. PP*
26. *Diorchis* n. sp. TT
36. *Diploposthe laevis*
37. *Diorchis elisae*
50. *Unciunia* n. sp.

C

5. *Polymorphus marilis*
8. *Hymenolepis spinocirrosa*
9. *Hymenolepis abortiva*
11. *Hymenolepis pusilla*
17. *Hymenolepis tuvensis*
24. *Retinometra pittalugi*
13. *Lateriporus skrjabini*
35. *Hymenolepis recurvata*
43. *Hymenolepis* tuv?*
47. *Capillaria obsignata*

D

22. *Cotylurus hebraicus*
29. *Retinometra cyrtoides*
48. *Diorchis excentricus*
56. *Diorchis* AD*

E

54. *Sobolevicanthus gracilis**
58. *Hymenolepis paracompressa*
61. *Hymenolepis compressa*
66. RR*

F

44. X*
59. *Anatinella spinulosa*
65. *Sobolevicanthus kenaiensis*

G

15. *Capillaria anatis*
46. *Cotylurus flabelliformes*
55. *Hymenolepis parvula*
74. *Hymenolepis* GGG

H

64. *Hymenolepis arcuata*
73. *Oligorchis* n. sp.
75. D*

Appendix 4. (Continued).

I

12. *Hymenolepis* AB
18. Spino?*
23. Abort?*
32. AB?*
21. *Hymenolepis spiraliburstata*
30. *Hymenolepis albertensis*
27. *Polymorphus paradoxus*
33. *Lateriporus mathevossinae*
40. *Hymenolepis melanittae*
42. P*
49. *Hymenolepis formosoides*
53. *Capillaria nyrocinarum*
62. Micro?
63. *Lateriporus clerci*
69. Pusilla?*
71. *Hymenolepis* tuvAB?*
72. *Microphallus* sp. 1

J

34. *Echinocotyle* QQQ
45. *Diorchis spinata*
52. *Hymenolepis* WWW
70. *Hymenolepis* XXX*
38. *Diorchis donutae*

K

39. *Echinocotyle rosseteri*
50. *Echinocotyle* NNN
57. *Sobolevicanthus octacantha**
60. TTT*

L

41. *Echinostoma revolutum*
67. *Hypoderaeum conoideum*
68. *Aploparaxis fucigera*

* Denotes no mature individual specimens (no presence of shelled eggs) were found.

Appendix 5. Composition of parasite species groups derived by cluster analysis using Euclidean distance for 75 taxa of helminths.

AA

1. Fimbriara fasciolaris
2. Apatemon gracilis
4. Hymenolepis hopkinsi
6. Polymorphus contortus

BB

5. Polymorphus marilis
13. Lateriporus skrjabini
33. Lateriporus mathevossinae
31. Hymenolepis microskrjabini

CC

3. Corynosoma constrictum
37. Diorchis elisae
50. Echinocotyle NNN
57. Sobolevicanthus octacantha*
59. Echinocotyle rosseteri

DD

14. Notocotylus attenuatus
34. Echinocotyle QQQ
43. Diorchis spinata
38. Diorchis danutae
52. Hymenolepis WWW

EE

15. Capillaria anatis
46. Cotylurus flabelliformes
28. Echino?
41. Echinostoma revolutum

FF

19. Zygocotyle lunata
64. Hymenolepis arcuata
36. Diploposthe laevis
47. Capillaria obsignata
60. TTT*
68. Aploparaxis fucigera
67. Hypoderaeum conoideum
70. Hymenolepis XXX*
66. RR*
59. Anatinella spinulosa
56. Diorchis AD*
65. Sobolevicanthus kenaiensis
74. Hymenolepis GGG*

GG

54. Sobolevicanthus gracilis*
73. Oligorchis N. sp.
75. D*

HH

61. Hymenolepis compressa
58. Hymenolepis paracompressa

II

44. X*

JJ

20. PP*
55. Hymenolepis parvula

KK

27. Polymorphus paradoxus
42. P*
63. Lateriporus cleri
53. Capillaria nyrocinarum
49. Hymenolepis formosoides

LL

62. Micro?*
69. Pusilla?*
71. Hymenolepis tuvAB?*
72. Microphallus sp. 1

Appendix 5. (Continued).

MM

7. *Echinoparyphium recurvatum*
16. *Hymenolepis fausti*
25. *Retinometra macroacanthus*

NN

10. *Dicranotaenia coronula*
22. *Cotylurus hebraicus*
35. *Hymenolepis recurvata*
43. *Hymenolepis* tuv?*

OO

48. *Diorchis excentricus*
27. *Retinometra cyrtoides*

PP

12. *Hymenolepis* AB
18. Spino?*
21. *Hymenolepis spiraliburaata*
23. Abort?*
30. *Hymenolepis albertensis*
32. AB?*
40. *Hymenolepis melanittae*.

QQ

8. *Hymenolepis spinocirrosa*
9. *Hymenolepis abortiva*
11. *Hymenolepis pusilla*
17. *Hymenolepis tuvensis*

* Denotes no mature individual specimens (no presence of shelled eggs) were found.

Appendix 6. Proportional values of helminth species groups derived by cluster analyses using Jaccard's Coefficient and Euclidean distance in each duck group and duck species.

The proportion of each helminth species group in each duck group derived by cluster analysis using Jaccard's Coefficient.

HELMINTH SPECIES GROUP	Duck Group									
	1	2	3	4	5	6	7	8	9	10
A	66.7	51.3	42.5	64.1	36.1	26.5	20.8	55.5	35.0	35.4
B	3.2	1.3	6.4	2.6	8.2	8.6	1.0	11.1	28.4	12.9
C	3.8	0	4.3	2.6	3.1	45.8	17.9	0	8.3	22.6
D	1.9	0	38.3	0	2.1	5.8	1.0	0	1.7	0
E	1.9	0	0	10.2	0	3.4	0	0	3.3	0
F	1.9	0	2.1	0	0	1.7	1.0	5.5	6.7	6.5
G	6.4	2.6	2.1	7.8	1.0	1.0	1.0	22.2	14.9	9.7
H	0	0	0	0	0	3.4	0	0	0	0
I	7.7	1.3	2.1	2.6	17.5	2.7	59.2	0	0	9.7
J	1.9	40.8	0	0	5.5	1.0	0	0	0	0
K	0	2.6	0	0	25.8	0	0	0	0	0
L	4.5	0	2.1	10.2	1.0	0	0	5.5	1.6	3.2
	100									

The proportion of each helminth species group in all duck groups derived by cluster analysis using Jaccard's Coefficient.

HELMINTH SPECIES GROUP	Duck Group 1	2	3	4	5	6	7	8	8	10
A	18.6	11.6	8.9	13.4	9.4	10.9	10.1	5.4	8.0	3.7
B	4.9	1.7	7.5	2.9	11.9	19.7	1.1	5.9	36.4	7.5
C	3.1	0	2.5	1.5	2.3	53.6	24.7	0	5.5	6.7
D	4.4	0	66.4	0	4.4	19.8	1.7	0	3.2	0
E	11.0	0	0	44.1	0	29.0	0	0	15.8	0
F	11.1	0	9.1	0	0	14.6	8.5	11.1	31.6	13.8
G	15.0	4.9	3.7	13.5	2.2	3.5	1.7	17.9	28.8	8.4
H	0	0	0	0	0	100.0	0	0	0	0
I	5.5	1.0	1.1	1.4	11.7	2.9	73.9	0	0	2.6
J	4.7	81.5	0	0	11.8	2.5	0	0	0	0
K	0	8.1	0	0	91.8	0	0	0	0	0
L	23.3	0	8.3	40.0	5.0	0	0	10.0	7.1	6.2

FINE PRINT

The proportion of each helminth species group in all duck groups derived by cluster analysis using Euclidean distance.

HELMINTH SPECIES GROUP	DUCK GROUP													
	1	2	3	4	6	6	7	8	9	10	11	12	13	14
AA	4.3	2.8	2.7	1.9	3.1	5.1	2.2	3.7	17.3	12.9	9.3	11.9	13.9	8.8
BB	1.5	1.0	1.0	1.1	1.0	4.4	24.5	1.2	2.5	0	1.4	7.6	38.0	15.7
CC	2.2	2.5	1.2	2.3	27.7	1.0	0	44.3	5.0	2.7	1.9	3.2	3.7	2.5
DD	1.2	8.2	8.2	2.4	1.5	1.0	0	8.8	3.0	59.5	1.9	1.1	3.0	1.0
EE	4.1	30.6	8.7	2.6	2.6	20.3	0	4.1	13.0	3.8	3.3	4.4	1.0	1.8
FF	5.7	10.6	2.9	15.9	1.5	7.3	0	4.6	8.9	6.7	6.1	17.6	0	11.9
GG	15.1	7.0	0	0	0	0	0	0	0	0	0	64.6	0	13.2
HH	0	42.2	0	0	0	6.3	0	0	0	0	0	42.9	0	8.6
II	0	0	0	71.2	0	8.1	0	0	3.5	0	0	7.1	10.1	0
JJ	0	1.3	1.0	0	2.1	77.0	0	0	4.1	0	6.7	7.1	1.0	0
KK	0	0	0	3.7	3.0	0	24.7	0	9.8	0	0	0	58.6	0
LL	0	0	0	0	0	2.6	0	0	1.6	0	0	0	95.7	0
MM	19.4	23.7	1.7	2.5	3.6	6.7	0	9.8	10.6	2.8	1.9	14.4	1.0	2.1
NN	3.0	3.9	1.3	6.5	2.9	3.4	0	0	1.9	1.8	3.7	28.4	2.7	40.3
OO	5.9	0	0	7.8	0	0	0	0	0	0	73.8	9.4	0	2.9
PP	1.0	1.0	0	0	2.0	1.0	15.1	18.5	1.0	1.0	1.0	1.0	59.9	1.9
QQ	1.0	0	0	0	0	1.0	1.0	0	1.0	0	0	22.7	14.7	59.7

FINE PRINT

The proportion of each helminth species group in each duck group derived by cluster analysis using Euclidean distance.

HELMINTH SPECIES GROUP	DUCK GROUP 1	2	3	4	5	6	7	8	9	10	11	12	13	14
AA	20.6	10.3	30.5	8.6	13.4	17.6	6.5	7.1	49.5	39.4	27.1	17.2	11.0	9.4
BB	3.3	1.3	2.9	2.3	1.5	6.9	33.1	1.1	3.2	0	1.8	4.9	13.7	7.7
CC	4.8	4.2	6.1	4.8	55.2	1.2	0	39.4	6.6	3.9	2.5	2.1	1.4	1.2
DD	1.3	7.1	22.0	2.6	1.5	1.0	0	3.9	2.1	42.9	1.3	1.0	1.0	1.0
EE	2.6	15.2	13.5	1.6	1.5	9.7	0	1.1	5.1	1.6	1.3	1.0	1.0	1.0
FF	6.2	8.7	7.6	16.5	1.5	5.8	0	2.0	5.8	4.6	4.0	5.7	0	2.9
GG	3.6	1.3	0	0	0	0	0	0	0	0	0	4.6	0	1.0
HH	0	6.8	0	0	0	1.0	0	0	0	0	0	2.7	0	1.0
II	0	0	0	32.5	0	2.8	0	0	1.0	0	0	1.0	1.0	0
JJ	0	1.0	1.5	0	1.2	36.2	0	0	1.6	0	2.6	1.4	1.0	0
KK	0	0	0	2.6	1.9	0	10.9	0	4.2	0	0	0	6.9	0
LL	0	0	0	0	0	1.0	0	0	1.0	0	0	0	4.9	0
MM	39.0	36.4	8.4	4.8	6.6	9.9	0	7.9	12.8	3.6	2.4	8.7	1.0	1.0
NN	7.3	7.4	7.4	15.1	6.4	6.0	0	0	2.8	2.8	5.4	20.6	1.1	21.8
OO	6.7	0	0	8.4	0	0	0	0	0	0	50.6	3.2	0	1.0
PP	1.3	1.0	0	0	9.1	1.0	46.9	37.4	3.0	1.0	1.0	1.0	49.8	2.2
QQ	3.2	0	0	0	0	1.0	2.5	0	1.9	0	0	26.3	9.4	51.6

The proportion of each helminth species group (Jaccard's Coefficient) within each duck species.

	MAL	WID	GAD	BWT	RUD	BUF	CAN	RIN	WWS	SCA
	1	2	3	4	5	6	7	8	9	10
A	66	60	52	36	42	40	39	37	21	23
B	2	0	2	8	6	13	18	35	1	5
C	3	2	0	3	4	19	19	5	18	53
D	2	2	0	2	38	0	5	0	1	6
E	6	0	0	0	0	0	5	0	0	2
F	1	0	0	0	2	8	7	2	1	1
G	9	7	2	1	2	8	1	19	1	1
H	0	0	0	0	0	0	1	0	0	4
I	7	0	16	17	2	8	3	0	59	3
J	0	2	41	5	0	0	2	0	0	0
K	0	2	2	26	0	0	0	0	0	0
L	3	12	0	1	2	3	1	2	0	0
	100%									

The proportion of each helminth species group (Jaccard's Coefficient) in each duck species.

	MAL	WID	GAD	BWT	RUD	BUF	CAN	RIN	WWS	SCA
	1	2	3	4	5	6	7	8	9	10
A	15	7	11	8	8	6	18	7	9	8 / 100%
B	3	0	2	9	5	9	35	28	1	8
C	2	1	0	2	2	7	22	2	19	44
D	2	2	0	4	58	0	16	0	2	16
E	33	0	0	0	0	0	49	0	0	18
F	2	0	0	0	7	20	53	7	6	5
G	22	9	4	2	4	13	4	34	2	5
H	0	0	0	0	0	0	23	0	0	77
I	5	0	1	11	1	3	3	0	72	3
J	0	16	68	9	0	0	6	0	0	0
K	0	3	5	92	0	0	0	0	0	0
L	15	38	0	6	10	10	10	10	0	0

The proportion of each helminth species group (Euclidean distance) within each duck species.

	MAL	WID	GAD	BWT	RUD	BUF	CAN	RIN	WWS	SCA
	1	2	3	4	5	6	7	8	9	10
AA	34	53	37	11	28	6	17	23	11	10
BB	2	1	0	1	2	2	4	0	14	7
CC	5	10	3	45	3	3	3	1	1	1
DD	2	18	44	4	1	6	1	0	1	1
EE	8	8	2	2	1	12	2	10	1	1
FF	4	6	7	2	4	1	12	13	0	3
GG	1	0	0	0	0	0	1	0	0	1
HH	3	0	0	0	0	0	4	0	0	1
II	1	0	0	0	0	18	3	2	1	0
JJ	4	0	0	1	3	14	2	3	1	0
KK	3	0	0	1	0	2	0	0	7	0
LL	1	0	0	0	0	1	0	0	5	0
MM	23	2	3	9	2	16	16	13	1	2
NN	5	2	3	3	6	5	17	8	1	22
OO	0	0	0	0	50	0	4	0	0	2
PP	3	0	1	23	1	2	1	0	50	2
QQ	6	0	0	0	0	0	15	0	9	47
	100%									

The proportion of each helminth species group (Euclidean distance) in each duck species.

	MAL	WID	GAD	BWT	RUD	BUF	CAN	RIN	WWS	SCA
	1	2	3	4	5	6	7	8	9	10
AA	13	9	13	4	12	1	1	5	16	11 / 100%
BB	2	5	0	1	2	9	9	0	55	20
CC	7	6	3	60	4	2	7	1	6	4
DD	3	14	64	6	2	5	2	0	3	1
EE	23	11	4	5	4	20	10	18	1	3
FF	6	5	10	3	7	1	42	12	0	13
GG	16	0	0	0	0	0	7	0	0	8
HH	23	0	0	0	0	0	70	0	0	7
II	3	0	0	0	0	49	29	5	13	0
JJ	11	0	0	2	8	21	11	47	1	0
KK	10	0	0	3	0	3	0	0	85	0
LL	11	0	0	0	0	3	0	0	96	0
MM	24	1	3	9	3	9	36	8	1	5
NN	4	1	2	2	5	2	29	4	3	47
OO	0	0	0	0	80	0	12	0	0	7
PP	1	0	1	1	1	1	1	0	84	2
QQ	1	0	0	0	0	0	16	0	17	66

Appendix 7. Data matrix of parasite species and waterfowl used in this study.

Appendix 7 (continued)

Key to Appendix 7. (Numeric Codes)

Column 1 (2 digits) Duck Codes

01 - Mallard
02 - Widgeon
03 - Gadwall
04 - Blue-winged teal
05 - Ruddy
06 - Bufflehead
07 - Canvasback
08 - Ring-necked duck
09 - White-winged scoter
10 - Lesser scaup

Column 2 (2 digits) Bird number

Column 3 (5 digits) Lake, month, year

Lake Codes

01 - Charron
02 - Bellshill
03 - Wadlin
04 - Chip
05 - Cowoki
06 - Bistcho
07 - Lanes
08 - Dusty
09 - Cow
10 - Wolf
11 - Fleeinghorse
12 - Rattlesnake

Appendix 7 (continued)

Column 4 (2 digits) Sex

01 - male

02 - female

-0 - unknown

Column 5 (3 digits) Length of small intestine (cm)

Column 6 (4 digits) Parasite species codes

(as listed in Appendix 2)

Column 7 (2 digits) Gut section number

01-20 - Five percent sections of small intestine (01 - anterior end)

21 - large intestine

22 - caeca

Column 8 (5 digits) Number of mature parasites per section

Column 9 (5 digits) Number of immature parasites per section

Column 10 (5 digits) Total numbers of parasites per section

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01 01 01679 02   154 0016 01 00000 00001 00001
01 01 01679 02   154 0016 02 00000 00001 00001
01 01 01679 02   154 0016 03 00002 00003 00005
01 01 01679 02   154 0016 04 00011 00012 00023
01 01 01679 02   154 0016 05 00008 00008 00016
01 01 01679 02   154 0016 06 00008 00007 00016
01 01 01679 02   154 0016 07 00001 00005 00006
01 01 01679 02   154 0016 08 00000 00001 00001
01 01 01679 02   154 0002 04 00001 00000 00001
01 01 01679 02   154 0007 04 00000 00002 00002
01 01 01679 02   154 0007 06 00000 00001 00001
01 01 01679 02   154 0025 07 00000 00001 00001
01 01 01679 02   154 0025 08 00000 00002 00002
01 01 01679 02   154 0025 09 00000 00005 00005
01 01 01679 02   154 0025 10 00000 00007 00007
01 01 01679 02   154 0025 11 00000 00010 00010
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01 01 01679 02   154 0019 22 00001 00000 00001
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01 02 01679 02   148 0001 02 00000 00017 00017
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01 02 01679 02   148 0007 07 00000 00001 00001
01 02 01679 02   148 0007 08 00000 00001 00001
01 02 01679 02   148 0016 03 00000 00001 00001
01 02 01679 02   148 0016 04 00000 00001 00001
01 02 01679 02   148 0016 05 00005 00011 00016
01 02 01679 02   148 0016 06 00002 00009 00011
01 02 01679 02   148 0016 07 00000 00002 00002
01 02 01679 02   148 0016 08 00000 00002 00002
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01 02 01679 02   148 0074 03 00000 00001 00001
01 02 01679 02   148 0031 04 00000 00001 00001
01 02 01679 02   148 0031 05 00000 00001 00001
01 02 01679 02   148 0031 06 00001 00000 00001
01 02 01679 02   148 0031 07 00000 00003 00003
01 02 01679 02   148 0031 08 00000 00007 00007
01 02 01679 02   148 0055 05 00003 00001 00004
01 02 01679 02   148 0055 06 00005 00000 00005
01 02 01679 02   148 0055 07 00003 00001 00004
01 02 01679 02   148 0055 08 00000 00003 00003
01 02 01679 02   148 0055 09 00000 00002 00002
01 02 01679 02   148 0012 06 00000 00001 00001
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01 02 01679 02   148 0012 10 00000 00002 00002
01 02 01679 02   148 0025 09 00000 00006 00006
01 02 01679 02   148 0025 10 00000 00014 00014
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01 02 01679 02   148 0027 14 00008 00000 00008
01 02 01679 02   148 0027 15 00011 00000 00011
01 02 01679 02   148 0027 16 00012 00000 00012
01 02 01679 02   148 0027 17 00010 00000 00010
01 02 01679 02   148 0027 18 00008 00001 00009
01 02 01679 02   148 0027 19 00007 00000 00007
01 02 01679 02   148 0027 20 00003 00000 00003
01 02 01679 02   148 0003 14 00000 00001 00001
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01 02 01679 02  148 0003 19 00001 00000 00001
01 02 01679 02  148 0003 20 00001 00000 00001
01 02 01679 02  148 0103 18 00000 00003 00003
01 02 01679 02  148 0103 19 00000 00007 00007
01 02 01679 02  148 0103 20 00000 00006 00006
01 02 01679 02  148 0046 19 00001 00000 00001
01 02 01679 02  148 0006 21 00029 00016 00035
01 02 01679 02  148 0004 22 00110 00081 00191
01 02 01679 02  148 0028 22 00000 00001 00001
01 02 01679 02  148 0015 22 00001 00000 00001
01 02 01679 02  148 0014 22 00001 00000 00001
01 03 01577 02  158 0001 01 00000 00002 00002
01 03 01577 02  158 0001 02 00000 00008 00008
01 03 01577 02  158 0001 03 00000 00002 00002
01 03 01577 02  158 0001 04 00000 00002 00002
01 03 01577 02  158 0016 02 00000 00004 00004
01 03 01577 02  158 0016 03 00001 00001 00002
01 03 01577 02  158 0016 04 00000 00013 00013
01 03 01577 02  158 0016 05 00000 00006 00006
01 03 01577 02  158 0016 06 00000 00001 00001
01 03 01577 02  158 0074 02 00000 00004 00004
01 03 01577 02  158 0074 04 00000 00003 00003
01 03 01577 02  158 0074 05 00000 00003 00003
01 03 01577 02  158 0074 06 00000 00004 00004
01 03 01577 02  158 0074 07 00000 00004 00004
01 03 01577 02  158 0002 03 00000 00003 00003
01 03 01577 02  158 0002 04 00010 00005 00015
01 03 01577 02  158 0002 05 00001 00000 00001
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01 03 01577 02  158 0002 07 00001 00001 00002
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01 03 01577 02  158 0025 06 00000 00002 00002
01 03 01577 02  158 0025 07 00000 00001 00001
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01 03 01577 02  158 0025 09 00000 00011 00011
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