THE UNIVERSITY OF ALBERTA

ECOLOGY OF THE HELMINTHS OF THREE SPECIES OF ARCTIC - NESTING GEESE WITH PARTICULAR REFERENCE TO THE LESSER SNOW GOOSE (CHEN CAERULESCENS CAERULESCENS): A COMMUNITY ANALYSIS

by

© TERRENCE GENE NERAASEN

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

FALL, 1970

UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled Ecology of the Helminths of Three Species of Arctic-Nesting Geese with particular reference to the Lesser Snow Goose (Chen caerulescens caerulescens): A Community Analysis submitted by Terrence Gene Neraasen in partial fulfilment of the requirements for the degree of Master of Science.

ABSTRACT

The helminths of adult lesser snow geese (Chen caerulescens caerulescens), white-fronted geese (Anser albifrons) and Pacific brant (Branta bernicla nigricans) from the Anderson River Delta, N.W.T. were reported. Thirty-two species of helminths were recovered with 15 species being reported for the first time from snow geese, 4 reported for the first time from white-fronted geese and 16 for the first time from brant. Fifteen species were "common" (present in all species or in at least 25% of at least one species) in the geese. The effect of the grazing habits of the geese on their helminth faunas was discussed.

Seasonal variations in the abundance, structure and diversity of the community of helminths in adult snow geese were examined. Included in this portion of the study were breeding, migrating and wintering birds. The community was dynamic; most species were "ubiquists" or "migration" forms but showed various patterns of variation in abundance with season. Factors important in determining the various patterns of seasonal abundance were discussed. Nematodes dominated the community at all times of the year. Cestodes were found in significant numbers only on the breeding

grounds. Trematodes were poorly represented but were most prominent in migrating birds.

The acquisition of a community of helminths by young snow geese was followed by sampling young birds on the breeding grounds, on the fall migration route and on the wintering grounds. They began to acquire helminths in their first week of life and continued to do so until mid-winter when the last samples (from the wintering grounds) were examined. Their fauna of helminths became more similar to that of breeding adults as the young approached the wintering grounds. A major factor in this convergence was the acquisition of a nematode fauna characteristic of the adults. Young birds were not generally more heavily infected with helminths than were adults, nor did they acquire many parasites not recovered from adults.

The majority of the exchange of helminths among anseriformes on the Anderson River Delta occurred between geese and involved common species which may be considered typical of geese. Snow geese and their young, as the most abundant host groups, played central roles in the circulation of helminths. Brant were important in introducing species of helminths to the delta which were thereafter circulated through snow geese. The importance of the degree of association between host groups on the delta, and on migrations, and the influence of habitat preferences of the geese on the exchange of helminths between them and other host groups was discussed.

ACKNOWLEDGEMENTS

I wish to express my sincerest thanks to Dr. J. C. Holmes, Chairman of my committee, for suggesting the study and for his guidance and encouragement during the course of the work and in preparation of the manuscript.

I am grateful to Dr. T. W. Barry, Canadian Wildlife Service, Inuvik, for logistical and financial support for the field portion of the study, and to Patricia Barry for welcoming me to their home upon my stays in Inuvik.

Thanks are also due the personnel of the Inuvik Research Laboratory for much help and consideration given a greenhorn from "outside".

Mr. S. M. Hodgson, Commissioner of the Northwest Territories kindly granted the necessary permits for the summer work at the Anderson River Delta. Scientific Kill Permits for the collection of Migratory Birds were granted by the Canadian Wildlife Service.

I wish to thank Messrs. Alex Dzubin, Canadian Wildlife Service, Saskatoon, Robert G. Jeffrey, Washington Department of Game and Frank M. Kozlik, California Department of Fish and Game, for collecting fall and winter samples of geese.

Mr. Billy Jacobson, Tuktoyaktuk, introduced me to

the Arctic and taught me much about the Anderson River in the first summer of the study. For this, and his help and companionship, I am grateful. Mr. William Glasgow provided invaluable assistance and companionship in the summer of 1968. His cheerful disposition and enthusiastic hunting prowess were much appreciated.

Special thanks are due my wife, Cheryl, for her many sacrifices and constant encouragement throughout the study and preparation of the manuscript.

To my friends and colleagues who provided assistance in the field and laboratory, I express sincere thanks. In particular, I wish to thank Jona Samuel, who did a fine job on some difficult figures, and Dr. Bill Samuel and Messrs. Rory McLachlin, Ron Podesta and Jim Wolford, who were constant sources of help and/or constructive criticism.

This study was supported by the University of Alberta Boreal Institute, the Department of Zoology through Teaching Assistantships and summer assistance, the Canadian Wildlife Service and by NRC operating grant A-1464 to Dr. J. C. Holmes.

TABLE OF CONTENTS

CHAPTER PAGE

LIST OF TABLES

LIST OF FIGURES

FIGURE PAGE

FIGURE		PAGE

FIGURE PAGE

INTRODUCTION

The parasites of anseriformes are numerous and extensively studied (McDonald, 1969a,b). In recent years, a few authors have studied the helminth populations of particular waterfowl species, or groups of species using the same area to breed and raise their young, as a unit, recognizing at the same time that parasites exhibit varying degrees of specificity to their hosts and that host and environmental factors affect the success of particular parasites differently (Wisniewski, 1958; Cornwell and Cowan, 1963; Buscher, 1965, 1966; *inter alia*). A complex of interacting factors have been implicated in determining the nature of the helminth faunas. Such factors as the age or sex of the host, food habits, variation in the abundance or nature of invertebrate populations, and the season of the year have been considered to be particularly important. Bykhovskaya-Pavlovskaya (1962), Dogiel (1964), and Buscher (1965) have shown, mostly in general terms, that migration is a significant factor. Only Buscher (1965) has characterized the helminth faunas of specific hosts on the breeding grounds, migration route and wintering area.

Further studies, which could provide comprehensive data about the parasites of a population of birds whose breeding, wintering and migratory distributions could be delimited and the changes in parasitism with age, season and location could be monitored, are needed. Arctic-nesting geese provide such populations. This study was undertaken in the spring of 1967 in an attempt to provide that type of data. The first objective of the study was to survey the helminths of geese breeding at Anderson River, N.W.T. The lesser snow goose (*Chen caerulescens caerulescens*) was the major host considered, but the white-fronted goose (*Anser albifrons*) and Pacific brant (*Branta bernicla nigricans*) breed there in substantial numbers and were included in the study as well. Other objectives were to characterize the seasonal variation of the helminths in lesser snow geese (considering the effects of migration and wintering as well), to follow the acquisition of helminths by young snow geese, and finally, to investigate the degree of exchange of helminths among the geese (and other anseriformes) on the Anderson River breeding grounds.

Methods of community analysis used extensively in other branches of ecology (cf. Macfadyen, 1964), have been used infrequently in ecological parasitology. Only Holmes and Podesta (1968) have considered the entire

helminth community of a group of hosts (wolves and coyotes) as something other than a set of independent populations of different species of helminths. Populations of different helminths coexisting in a host can be expected to make up a community having a measureable structure and diversity, properties which are nonexistent in populations of a single species. The great majority of parasitological investigations have provided inadequate data on abundance, even for populations of individual species, have entirely ignored community structure and have used the number of species of parasites present as the only measure of diversity. An analysis of the helminth faunas of geese with an emphasis on the overall faunas (regarded as communities) would be particularly instructive, in that comparisons of the faunas of different hosts, or of the fauna of one host at different times of the year, would be more meaningful than a simple comparison of lists of species.

II. HELMINTHS OF ADULT GEESE AT THE ANDERSON RIVER DELTA, N.W.T.

Introduction

Little is known about the parasites of natural populations of geese. In North America, only the Canada goose (*Branta canadensis*) has received much attention, mostly in work done on wintering populations (Herman and Wehr, 1954; Herman, Steenis and Wehr, 1955; Hanson, Levine and Kantor, 1956; Hansen, McNeil and Priebe, 1957; Hanson and Gilford, 1961). Most of these authors were concerned with specific parasites (primarily *Amidostomum anseris*) and do not provide data concerning the entire populations of helminths in the geese. Nevertheless, this work, and that of others (Schiller, 1954; Wehr and Herman, 1954; Leiby and Olsen, 1965), has raised the question of the loci of transmission of parasites of geese (and migratory birds in general). It was the opinion of most of these authors that parasites were probably contracted in northern breeding areas, the arctic or sub-arctic regions in particular, as opposed to the wintering grounds. However, only Schiller (1952, 1954) and Holmes and Colbo

(1970) have provided information as to some of the parasites which infect geese in arctic breeding areas.

Records of parasites occurring in snow geese, white-fronted geese and brant are scattered throughout the literature, representing records from few birds taken over widely separated geographic areas. As a result of Asian or European work, white-fronted geese are recorded as hosts of 41 species of helminths (14 trematodes, 13 cestodes, 14 nematodes) (McDonald, 1969b). Snow geese and brant, on the other hand, have been studied only rarely, and are hosts of 22 (8 trematodes, 3 cestodes, 11 nematodes) (McDonald, 1969b; Holmes and Colbo, 1970) and 12 (7 trematodes, 4 cestodes, 1 acanthocephalan) (McDonald 1969b) species of parasites respectively. This study provided an opportunity to obtain adequate samples of these geese from their arctic nesting grounds on the Anderson River Delta.

The Study Area

The Anderson River Delta (69° 40' N, 129° 00' W) supports large populations of lesser snow geese, Pacific brant, white-fronted geese, whistling swans (*Olor columbianus*) and various ducks and shorebirds. The Anderson River Migratory Bird Sanctuary was established

there in 1960 and the Canadian Wildlife Service has maintained a well appointed field station on the east bank at Krekovik Landing ever since. The delta has served as the study area for long term studies of the general biology of the geese nesting there (Barry, 1967).

The northern limit of the treeline extends a considerable distance downstream in a narrow band along the banks of the Anderson River, so that subarctic taiga exists only forty-four miles upstream from the mouth. Extensive willow flats are found along the banks (and on upstream islands) from here northwards to the mouth of the river. These flats afford abundant nesting cover for white-fronted geese. As a result, snow geese and brant, nesting at the mouth of the river, are in close contact with nesting white-fronts (Barry, 1967).

The geography, flora and fauna, and history of prior study at the Anderson River Delta have been described in detail by Barry (1967). He divided the delta into ten geographical-floristic zones, of which four are of major importance to the geese nesting there. Figure 1 is a map of the delta delimiting these areas. The outer delta consists of a number of islands and mud bars constituting the newest and lowest part of the delta. It is frequently inundated with brackish water during storm tides; its flora consists of the salt-tolerant, pioneering

species of plants. Pacific brant nest in this zone, with some snow geese using the higher portions.

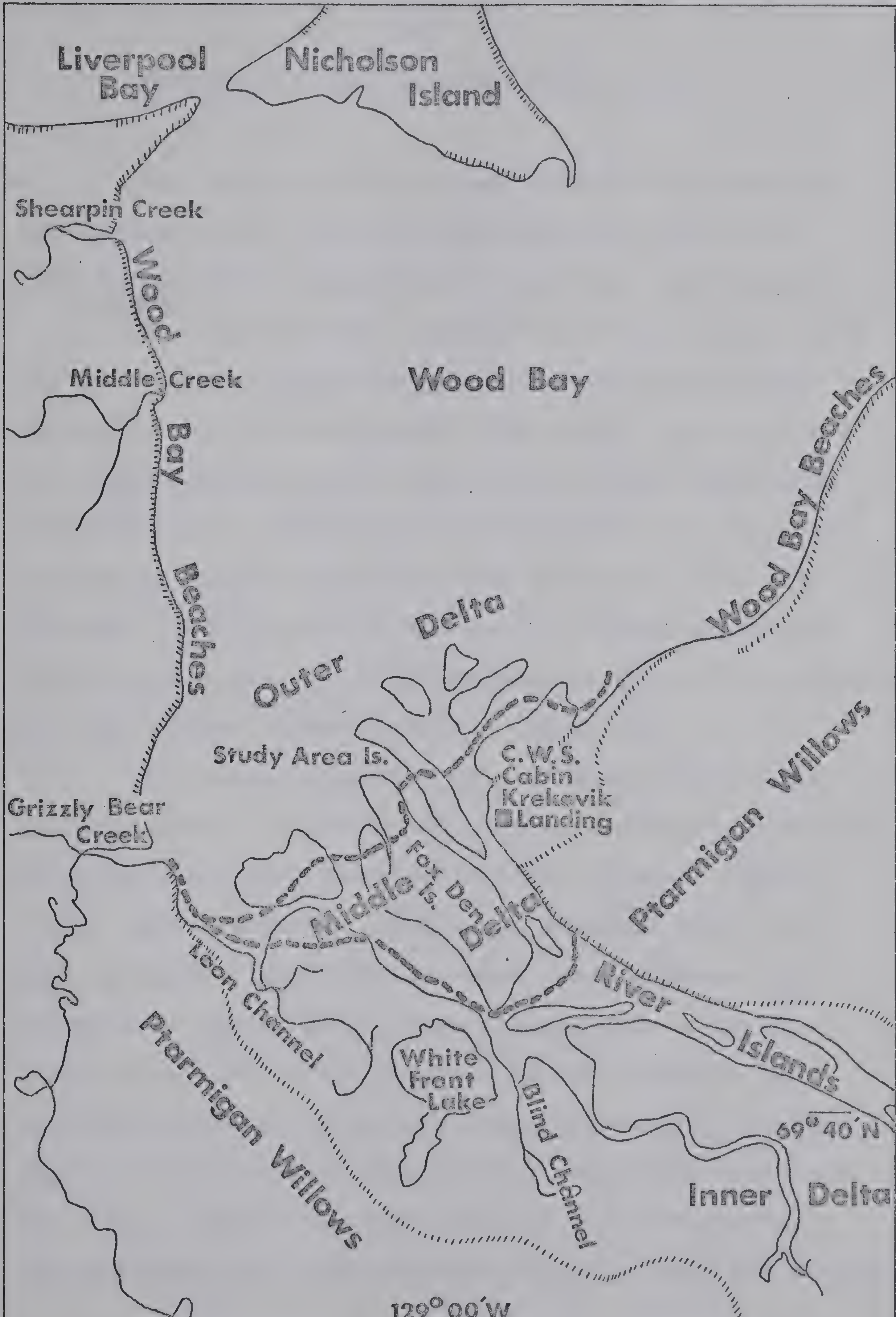
The middle delta is composed of the older, higher, drier, more southerly parts of the delta islands, which are characterized by low cutbanks rather than the marshy or muddy flats of the outer delta. Nests of the snow geese are concentrated in this area.

The inner delta consists mostly of the flat marshy prairie of the mainland. It is characterized by its many lakes, ponds, sloughs and poorly drained marshes, and has a lush vegetation. This area (and areas further upstream) are favored by nesting white-fronts. Moulting snow geese and brant (and their young) also use this zone, particularly the area around Loon Channel.

The tributary streams draining into Wood Bay are used to a certain extent by nesting white-fronted geese, but primarily as moulting and feeding places by all three species of geese after the young have hatched.

In general, the circumscribed area, the concentrations of three species of geese in relatively close association, the availability of the field station, and the prior study of the geese in the area, made it an ideal location for a parasitological investigation of arctic-nesting geese.

Figure 1. Map of the Anderson River Delta [reproduced from Barry (1967)]


Liverpool Bay
Nicholson Island
Shearpin Creek
Wood Bay Beaches
Middle Creek
Wood Bay
Wood Bay Beaches
Outer Delta
Study Area Is.
C.W.S. Cabin
Krekovik Landing
Ptarmigan Willows
Grizzly Bear Creek
Fox Den Is.
Middle Is.
Delta
Loon Channel
River Islands
White Front Lake
Blind Channel
Ptarmigan Willows
69° 40′N
Inner Delta
129° 00′W

The Geese of the Anderson River Delta

The following notes concerning the distribution and biology of the geese of Anderson River are taken from Barry (1967), supplemented by my own observations.

The Anderson River population of snow geese forms one of two major satellite colonies of the large Banks Island colony (150,000 birds). The latter is one of the two major contributors to the Pacific Flyway population of snow geese. The other major contributor is the colony on Wrangel Island (350,000 birds) in the U.S.S.R. The Anderson River portion of the Pacific Flyway population of snow geese winters in the Sacramento Valley of California and the western states of Mexico (Figure 2).

The spring migration of snow geese begins at a leisurely pace, following the northward advance of the 40° isotherm until they reach central and northern Alberta, about April twentieth. Their pace quickens after this and, in their final push northward, they overtake the progress of spring thaw. They use Hay Lakes, the Slave River Delta, and runoff channels on the Mackenzie and Anderson Rivers as favorite staging areas before continuing on to the Anderson River Delta. When they arrive on the delta, between the fifteenth and twentieth of May, their nesting sites are not yet cleared of snow and little

Figure 2. Distribution and migratory routes of the geese of Anderson River, N.W.T.

Snow geese: wintering area;

migratory route.

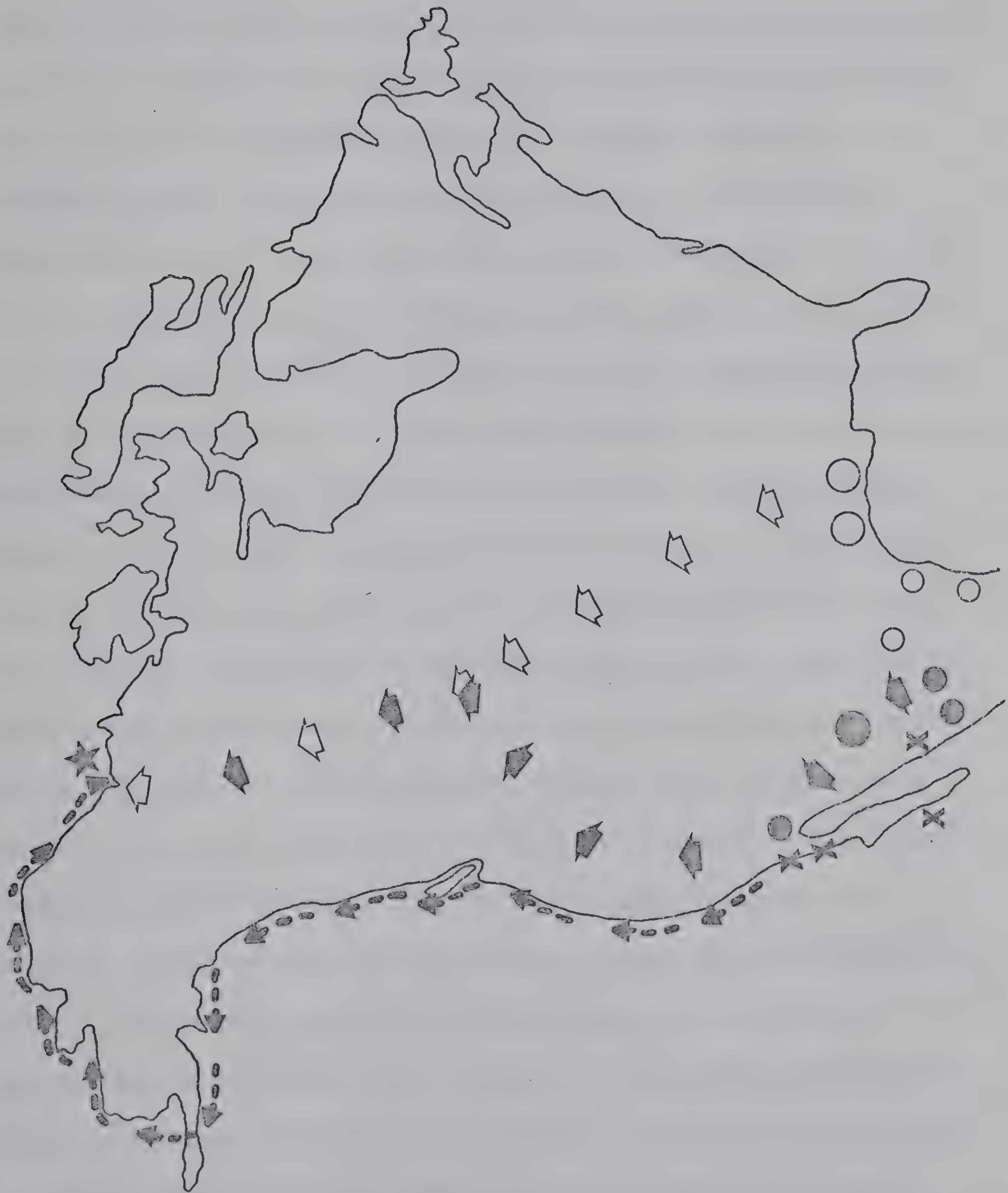
White-fronted geese: wintering area;

migratory route

Pacific brant: wintering area;

migratory route

(reproduced from Barry (1967))



food is available. The metabolic demands of waiting around on the snow until nest sites become available, of nest initiation, territorial defense and egg-laying are met by mobilization of the extensive fat reserves acquired during migration. (They are in the best condition of the year upon arrival at Anderson River.) Weight losses are incurred by both sexes during this period. This loss continues in the females until after the hatch at the end of June and early July. Males regain some weight during the latter half of the incubation period, when they feed on new plant material. After the hatch, the geese abandon the nesting islands for favorite feeding and moulting areas in the inner and outer delta. They are in frequent close contact with other geese, particularly brant and their young, during this period. Males lose some weight during the early part of the brood rearing period. However, all geese, including the young, gain weight very rapidly and are flying by about August twentieth. They soon leave the Anderson River Delta for feeding and staging areas on the north-western edge of the Mackenzie Delta. The length of their stay there is variable, depending on the weather. Migration southward basically is a retracing of the spring route. Although they spend a fair amount of time feeding in the fields of central and southern Alberta and Saskatchewan, they move southward

much more rapidly than they move northward in the spring.

The Anderson River population of white-fronted geese are part of the Central Flyway population, wintering along the Gulf of Mexico in coastal areas of Louisiana, Texas and east central Mexico (Figure 2). Their distribution in winter overlaps that of snow geese from the Eastern Arctic, but not that of snow geese from the Western Arctic. Their spring migration follows the Great Plains east of the Mississippi to west-central Saskatchewan and eastern Alberta, which they reach by early May. From here northward, their route overlaps that of the Anderson River population of snow geese. They use many of the same staging areas. From these areas the white-fronts fan out over the willow tundra north of treeline to nest. The Anderson River-Liverpool Bay white-fronts seem to be separated from other nesting concentrations of white-fronts by extensive stretches of unsuitable habitat. They are the most numerous goose at Anderson River (about 25,000 birds) but they nest in scattered groups so their population is not the most dense. Their nests are scattered in the heavy willow cover of the inner and middle delta and upstream on the Anderson River. The details of their nesting activities are similar to those of snow geese. They are ready to leave the nesting grounds at about the same time. Their southward

migration retraces the spring one except that the Kindersley, Saskatchewan area is the only major staging area used in the fall.

Pacific brant winter in coastal California and Mexico (Figure 2). The coastal location of brant would preclude any extensive contact with snow geese. In the spring they migrate at a leisurely pace along the Pacific Coast to Vancouver Island. From here they either skirt the Alaskan coast or cross the North Pacific and the Gulf of Alaska to Izembek Bay, where the entire Pacific brant population gathers by early May. Some of them nest on the Yukon-Kuskokwim Delta, while others go along the Arctic Coast to Anderson River and points as far east as Queen Maud Gulf. They nest on the low islands of the outer delta at Anderson River, mingling with a few nesting snow geese. They begin nesting somewhat later than do snow geese and, because of the uncertain condition of their nesting habitat, are somewhat less synchronous in their breeding activities. After the hatch (which may be spread out over ten or more days for the whole population) brant move to the outlying creeks and channels where they mix extensively with moulting snow geese and their young. Fall migration is a reversal of the spring route. The entirely coastal migration pattern of brant enables them to take advantage of the food and shelter afforded by open bays on the Arctic and Pacific Coasts.

Materials and Methods

Complete necropsies were performed on 177 adult lesser snow geese, 41 adult white-fronted geese and 65 adult Pacific brant, all collected on the Anderson River Delta. All birds were shot; all were examined within eight hours of death. Birds were usually collected in lots of eight so that those not examined immediately were either placed outside (where it was usually very cool) or in barrels dug into the permafrost. Conventional methods of examination were used.

Trematodes and cestodes were relaxed in cold water and fixed in alcohol-formol-acetic acid (A.F.A.). Nematodes were fixed in hot 5% glycerine in 70% ethyl alcohol. Tissue to be sectioned was fixed in Bouins' fluid.

Conventional methods of preparation and examination of specimens were used. Blachin's lactic acid carmine stain (Reichenow, et al., 1952) (used with unfixed material) stained the genitalia and ducts with a clarity given by no other method. It was especially useful for large, heavy-bodied cestodes or large trematodes such as Zygocotyle lunata, but was unsatisfactory for small, thin worms due to excessive shrinkage and curling of the strobila and loss of rostellar hooks or collar spines.

The nomenclature of McDonald (1969b) has been adopted, using Spasskaya's (1966) nomenclature for the Hymenolepididae. The monotypic genus Anserilepis has not been used; instead, I have used Drepanidotaenia barrowensis.

In computing indexes of similarity, the number of worms of each species of helminth recovered from a sample of geese was converted to a percentage of the total number of worms of all species. (This percentage is termed the "importance value".) This was done separately for each species of goose. An index of similarity of the helminth faunas of two species of geese was calculated as follows: the "importance values" for each species of helminth common to both geese are compared and the lower of the two values taken; the sum of these values is the index of similarity.

Results

A total of 32 species of helminths (7 trematodes, 15 cestodes, 10 nematodes) were recovered from adult geese at the Anderson River Delta. Twenty-four species (4 trematodes, 11 cestodes, 9 nematodes) were recovered from lesser snow geese, 15 (2 trematodes, 6 cestodes, 7 nematodes) from white-fronted geese and 22 species (4 trematodes, 12 cestodes, 6 nematodes) from Pacific brant.

Table 1 summarizes the data and gives taxonomic citations for each species of helminth recovered. Fifteen species of helminths from snow geese, four from white-fronted geese and sixteen from brant constitute new host records. Three species of helminths are reported from North America for the first time.

Capillaria sp. and *Tetrameres sp.* provisionally are considered new and will be described elsewhere.

Retinometra longivaginata was considered to be insufficiently described by Joyeux and Baer (1936); material from this study agrees with the fragmentary published descriptions (see Spasskaya, 1966). A more complete description of this worm will be presented elsewhere. Worms designated *Hymenolepis sp.* could not be identified further, since no mature specimens were available. This species was present only in brant and only in the first few weeks after their arrival at Anderson River. Ten rostellar hooks of the "diorchoid" type, 0.029 mm in length, were present but are insufficient to identify the species.

A single specimen of *Ornithobilharzia pricei* was recovered from a Pacific brant. The characteristics of the worm agree in most respects with Wetzel's (1930) original description. In view of the variability noted by Ulmer and Vande Vusse (1970) in *Dendritobilharzia*

Table 1. Helminths recovered from adult geese at the Anderson River Delta, N.W.T.

Host	Snow geese	White-fronts	Brant
Number examined	177	41	65
Helminth	Prevalence % - Mean Intensity /(range)		
TREMATODA			
Echinostoma revolutum+ (Froelich, 1802)	* 7-3.5 (1-16)	27-2.9 (1-10)	
Catatropis pricei (Harwood, 1939)			*17-15.8 (1-50)
Notocotylus attenuatus+ (Rudolphi, 1809)	9-2.8 (1-8)	10-7.8 (1-15)	1.5-4.0 (4)
Paramonostomum sp.			1.5-18.0 (18)
Zygocotyle lunata (Diesing, 1836)	*8-1.4 (1-3)		
Ornithobilharzia pricei (Wetzel, 1930)			*1.5-1.0 (1)
*Apatemon anseris*** (Dubois, 1964)	*<1-19.0 (19)		
CESTODA			
Anomotaenia ciliata (Fuhrmann, 1913)	*3-1.0 (1)		*1.5-1.0 (1)
Cloacotaenia megalops (Nitzsch, 1829)	*<1-2.0 (2)		
*Diorchis stefanskii*** (Czaplinski, 1956)	*<1-1.0 (1)		*8-1.2 (1-2)

Table 1 continued

Host Number examined Helminth	Snow geese 177	White-fronts 41 Prevalence % - Mean Intensity /(range)	Brant 65
Drepanidotaenia barrowensis+ (Schiller, 1952)	*3-2.3 (1-5)	29-3.8 (1-10)	34-12.0 (1-123)
Drepanidotaenia lanceolata+ (Bloch, 1782)	14-3.3 (1-19)		26-3.0 (1-9)
Fimbriaria fasciolaris (Pallas, 1781)	*<1-1.0 (1)		
Parabisaccanthes philactes (Schiller, 1951)	*1-1.0 (1)		*8-3.4 (1-9)
Retinometra longivaginata+ (Fuhrmann, 1906)	*45-3.9 (1-16)	*2-1.0 (1)	*35-3.4 (1-9)
*Retinometra venusta*** (Rosseter, 1897)		*15-3.0 (1-7)	
Sobolevicanthus gracilis (Zeder, 1803)			*1.5-1.0 (1)
Tschertkovilepis krabbei+ (Kowalewski, 1895)	48-2.3 (1-10)	85-3.5 (1-12)	*37-4.0 (1-10)
Tschert. setigera+ (Froelich, 1789)	5-2.2 (1-9)	2-1.0 (1)	68-22.1 (1-156)
Wardium creplini (Krabbe, 1869)		2-1.0 (1)	*3-1.5 (1-2)
Wardoides nyrocae (Yamaguti, 1935)	*1-1.0 (1)		*1.5-1.0 (1)
Hymenolepis sp.			9-1.8 (1-2)

Table 1 continued

Host / Number examined / Helminth	Snow geese 177	White-fronts 41	Brant 65
	Prevalence % - Mean Intensity /(range)		
NEMATODA			
Sarconema eurycerca+ (Wehr, 1939)	*3-2.4 (1-3)	46-4.7 (1-18)	
Heterakis dispar+ (Schrank, 1790)	14-2.3 (1-9)		*49-18.4 (1-77)
Tetrameres fissispina+ (Diesing, 1861)			*31-4.2 (1-28)
Tetrameres sp.+	*15-3.1 (1-13)	*34-3.5 (1-16)	
Amidostomum anseris+ (Zeder, 1800)	2-2.8 (1-3)	10-2.3 (1-3)	*3-2.5 (1-4)
A. spatulatum+ (Baylis, 1932)	93-12.8 (1-100)	51-4.1 (1-14)	*1.5-1.0 (1)
Epomidiostomum crami+ (Wetzel, 1931)	94-6.8 (1-30)	100-15.3 (3-33)	*65-6.7 (1-24)
Trichostrongylus tenuis+ (Mehlis, 1846)	71-11.2 (1-85)	17-10.0 (1-23)	*66-27.0 (1-150)
Capillaria obsignata (Madsen, 1945)	*1-1.0 (1)	*2-1.0 (1)	
Capillaria sp.	*9-1.1 (1-2)		

+ = "common" species

* = new host record

** = new North American record

pulverulenta (Braun, 1901), the smaller size (3.1x 0.26 mm compared to 5.3 - 6.2 x 0.6 - 0.625 mm in the original material) and the slightly greater distance between suckers (0.42 mm, compared with 0.232 - 0.300 mm) in this specimen are considered to be within the normal range of variation in the species.

Table 2 gives the proportions of trematodes, cestodes and nematodes in the entire sample of worms from each host species. Nematodes made up the greatest proportion in all three geese but were least predominant in brant. Brant had the greatest proportion of cestodes. Trematodes made up very low percentages of the total in all hosts.

Nine species of helminths (1 trematode, 4 cestodes, 4 nematodes) were present in all three geese although not in equal numbers (Table 1). Another eleven species (1 trematode, 6 cestodes, 4 nematodes) were recovered from two of the three geese. All but one of the latter group (Wardium creplini) were present in snow geese, seven were found in brant, and four were recovered from white-fronted geese. These shared species of helminths were the basis of the indexes of similarity, which compare the total helminth fauna of one goose species to that of the others. These measures showed that the fauna of lesser snow geese was similar to that of the other host

Table 2. Composition of the helminth fauna of geese at Anderson River.

Host N	Snow geese 177	White-fronts 41	Brant 65
Number of species	24	15	22
Total no. of worms	5554	1170	3822
Percent of total comprised by:			
trematodes	2	5	5
cestodes	11	16	39
nematodes	87	79	56

species (41% similar to the fauna of white-fronts, with 13 shared species; 40% similar to the fauna of brant, with 15 shared species), but that the faunas of brant and white-fronts were relatively dissimilar (20% similarity, 10 shared species). The greatest contributors to the indexes of similarity were the nematodes (e.g., 36% out of the 41% similarity between the faunas of the snow geese and white-fronted geese was contributed by the nematodes they shared).

Fifteen species of helminths (14 in snow geese, 11 in white-fronts, 13 in brant) were "common", that is, were found in all three species of geese and/or were present in more than twenty-five percent of at least one species of host (Table 1, indicated by the symbol, +). Two of these species were found in more than twenty-five percent of all three hosts, four were in more than twenty-five percent of two of the hosts, and seven were in more than twenty-five percent of one of the species of geese. These species of helminths made up ninety-nine percent of the total number of worms in snow geese and white-fronted geese, and ninety-six percent of the total in brant. The other ten species of helminths in snow geese, four species in white-fronts and nine species in brant made up the remainder.

Five species of helminths were restricted to snow geese, one was recovered only from white-fronts, and five species were restricted to brant. Only one of these species (*Tetrameres fissispina*, in brant) was very common; most were found in less than ten percent of their hosts.

Discussion

Many of the "common" species of helminths recovered from geese at Anderson River are characteristic parasites of geese or of waterfowl in general (McDonald,

1969b). The prevalence of some of these species in this study (*Sarconema eurycerca*, *Tetrameres* sp., *Retinometra longivaginata*, *Tschertkovilepis krabbei*) suggests that they are more common in geese than previously recognized. Most of the other species recovered, although relatively uncommon, are also typically found in anseriformes, particularly ducks. The exceptions are *Capillaria obsignata*, which occurs typically in galliformes, and only accidentally in anseriformes, and *Capillaria* sp. and *Apatemon anseris*, about which little is known.

There are no studies of the parasites of geese from other areas which can be treated in a comparable way. Schiller (1952, 1954) and Holmes and Colbo (1970) are the only authors who have considered the parasites of North American arctic-nesting geese. However, Schiller's work, on a variety of geese from Alaska, dealt only with cestodes and gives no data on prevalence or abundance for individual species. Holmes and Colbo (1970) reported 10 species of helminths from five greater snow geese (*Chen caerulescens atlantica*) from Hazen Camp, Ellesmere Island, N.W.T. The sample of geese was too small to permit a comparison with the present study. However, only one species of helminth (*Apatemon gracilis* Rudolphi, 1819) recovered in that study was not found in the geese at Anderson River.

Two studies, dealing with the parasites of Canada geese in Illinois (Hanson and Gilford, 1961) and the helminths of grey geese (Anser anser) in northern Kazakhstan (Zaskind, 1963), involve large enough samples and provide enough data to be useful. Ten species of helminths were reported from the geese in Illinois; all but two (which are not identified beyond the generic level) were found in the geese at Anderson River. One of the unidentified species was of a genus recovered from geese at Anderson River and may have been the same species as well. In the geese from Kazakhstan, thirteen species (two of which were found only in young birds) were reported; five of these were also found in geese at Anderson River. Four species of helminths (Echinostoma revolutum, Notocotylus attenuatus, Drepanidotaenia lanceolata and Amidostomum anseris) were "common" in geese from all three studies. In addition, Tschertkovilepis setigera was very common in birds from Anderson River and Kazakhstan, while S. eurycerca was common in geese from Anderson River and Illinois.

Despite these similarities in species compositions, the helminth faunas of geese at Anderson River were relatively dissimilar (measured by indexes of similarity) to the fauna of geese from Illinois. The similarity of the latter to the helminth fauna of Anderson River

white-fronts was 11%, to that of snow geese was 5%, and to that of brant was 10%. The absence of Amidostomum spatulatum, Epomidiostomum crami and Heterakis dispar, and the low number of Trichostrongylus tenuis in the geese from Illinois are the main reasons for the lack of similarities. Indexes of similarities with the helminth fauna of geese from Kazakhstan could not be derived from the data presented.

From the limited data available, it would seem that geese in general are infected with characteristic species of helminths but that the helminth faunas as a whole, when considered as communities, show a great deal of variability.

The indexes of similarity between the helminth faunas of the three species of geese at Anderson River reflect the relative degrees of association of the geese on migration routes and on the breeding grounds. The fauna of snow geese can be considered intermediate between those of white-fronts and brant. The faunas of the latter two were almost equally similar to that of the snow geese, but were much less similar to one another. White-fronts and snow geese have at least partially overlapping spring migration routes, where the parasites responsible for some of the similarity of their faunas could be acquired. There is only minimal overlap between them on the breeding

grounds. There is considerable mixing of snow geese and brant on the Anderson River Delta, particularly after the hatch. The geese use many of the same feeding and moulting areas so that there is ample opportunity for the acquisition of similar helminths. Brant and white-fronts do not overlap at all on migration and mix very infrequently at Anderson River.

Geese, in general, are grazers (Cooch, 1964; Dzubin, Miller and Schildman, 1964; Hansen and Nelson, 1964, in Linduska, 1964). Barry (1967) found only plant material in the proventricular and gizzard contents of geese at Anderson River. I did not make systematic food sample analyses in this study, but only plant material was noted in the proventriculi and gizzards examined even though animal material was specifically looked for. According to Dillon (1959) and Sugden (1969), the inclusion of gizzard contents in food analyses tends to bias the data in favour of harder material which is retained in the gizzard for a longer time than is softer material. Sugden (1969) also pointed out that birds collected for the purpose of food analysis should be collected only during peak feeding periods. Food materials are then in the esophagus and proventriculus and are not so subject to differential rates of passage. It was recommended that gizzard contents be ignored. None of these

requirements were met in this study. However, Barry's (1967) data, and my observations indicate that geese at Anderson River are similar to other geese in being almost entirely grazers.

This grazing habit has obvious effects on the composition of the helminth fauna. Most of the worms in each species of goose (85% of the total number of helminths in snow geese, 66% in white-fronts, 53% in brant) have direct life cycles. Metacercariae of the most common trematode in geese from Anderson River (*N. attenuatus*) encyst on debris or vegetation (McDonald, 1969b) and would be ingested frequently by grazing geese. The more common cestodes utilize limnetic or littoral copepods which could easily be ingested accidentally as the geese feed in and around ponds (Dubinina, 1953; Kotecki, 1964; Czaplinski and Jarecka, 1967; McDonald, 1969b). It is significant that forms such as *Anomotaenia ciliata* and *Diorchis stefanskii* which utilize more benthic ostracods or cladocerans, which would be less likely to be ingested accidentally, were uncommon in the geese.

III. SEASONAL VARIATION OF THE COMMUNITY OF HELMINTHS IN ADULT SNOW GEESE

Introduction

Seasonal variations in the populations of helminths of waterbirds, mostly on their breeding grounds, have received considerable attention in recent years (Gower, 1938; Oschmarin, 1950; Dubinina, 1953; Bezubik, 1956; Okorokov, 1957; Sulgostowska, 1958; Wisniewski, 1958; Busa, 1964; Gallimore, 1964; Shevtsov, 1964; Colbo, 1965; Graham, 1966). The original source or "nucleus" of infections (brought to the breeding grounds by the host, transferred from other hosts or from over-wintered infections in intermediate hosts) was considered to be an important factor in the generation of different patterns of seasonal variation (Buscher, 1965; Graham, 1966). The early events of the breeding period (egg-laying, territorial defense and incubation) were shown to have important effects as well (Gallimore, 1964; Colbo, 1965). Superimposed upon these effects and often indistinguishable from them were others, such as the effects of changes in food habits with season, or changes in distribution or abundance of populations of intermediate hosts.

There has been little work concerning the effects of migration on the abundance and diversity of helminths although migrations over considerable distances through a wide range of geographic regions are characteristic of waterfowl. A good deal of general information on the effects of migration is available in summarized form in the books by Bykhovskaya-Pavlovskaya (1962) and Dogiel (1964). These authors indicated that migratory birds had different faunas of helminths on the breeding and wintering areas. The length of the migration between these areas influenced the degree of difference; the greater the separation (in terms of distance or ecology), the greater the differences in the helminths. Dogiel (1964) proposed four broad categories for the helminths of migratory birds based on where transmission of the parasite occurred. "Ubiquists" were parasites transmitted throughout the range of the host. "Northern" parasites were those transmitted only on the northern breeding grounds while "southern" species were forms transmitted on the more southerly wintering grounds. "Migration" parasites were those present in the birds only along their migratory route.

In general, these authors, and others (Ryzhikov, 1956; Cornwell and Cowan, 1963; Buscher, 1965), have indicated that breeding birds are more heavily infected

with a greater variety of helminths than are wintering or migrating birds. Most of the cestodes and trematodes of birds in the U.S.S.R. were "northern" parasites. The impoverishment in the abundance and variety of helminths in migrating and wintering birds has been attributed to a variety of factors, including a loss of worms due to a reduction in food intake or changes in the character of the foods available, and reduced possibilities of re-infection (Bykhovskaya-Pavlovskaya, 1962; Buscher, 1965). Intestinal cestodes and trematodes were particularly susceptible to loss (Dogiel, 1964). On the other hand, migrations provided opportunities for at least partial replenishment of the helminth fauna (with "ubiquists" and "migration" species) depending on where and for what length of time birds stopped along the route (Belopolskaya, 1956; Bykhovskaya-Pavlovskaya, 1962; Cornwell and Cowan, 1963).

Lesser snow geese have an extensive migration between their breeding grounds on the Anderson River Delta and their wintering grounds in the central valley in California. Conditions they encounter in the two areas are very different. They also encounter a great variety of ecological conditions on their migrations. Even though the same general route is followed in the spring and fall, climatic and biotic conditions are very

different. The variety of conditions the birds encounter throughout the year could be expected to have significant effects on their helminth faunas.

Materials and Methods

A sample of geese was collected as they arrived at the Anderson River Delta in the last week of May. This sample will be referred to as the "arrival" sample. Thereafter, approximately fifteen geese were collected every two weeks, with attempts being made to collect equal numbers of each sex. Five samples were taken in the ten week period from June first to August fifteenth. For most analyses of the data, the points on graphs and tables represent the means, medians, etc. for these two-week periods. However, in calculating Simpson's indexes, rarefaction indexes and indexes of similarity between the faunas of geese from different periods, the two samples taken in June, and those taken in July, were combined. The June samples represent geese taken during the egg-laying and incubation period, and are collectively designated the "nesting" sample. The two July samples represent geese collected after they moved away from the nesting areas to feeding and moulting areas, and are collectively called the "mid-summer" sample. The "late-summer" sample was taken in the last two-week period

before the geese were ready to leave the delta (August 1-15). These periods (arrival, nesting, mid-summer and late-summer) are natural divisions of the time spent on the breeding grounds.

The fall sample was collected in late October and early November in Alberta and Saskatchewan. The winter sample was taken in late December, 1968 and early January, 1969 in Washington and California. The spring birds were collected at Beaverhill Lake, Alberta in late April of 1968 and 1969.

Medians, rather than the means were used as measures of central tendency because the former are more robust, not overly influenced by extreme values (Uemura, 1964). Ninety-five percent confidence limits were determined for the medians of large samples (Campbell, 1967).

The prevalence (percent of the birds infected) times the median intensity was used as a measure of the size of the populations of individual species of helminths. This combination gives a better picture of the abundance of a helminth than either the prevalence or the intensity of infection alone, particularly when prevalence and intensity varied in opposite directions. In effect, the measure represents an estimate of the number of worms per hundred birds.

Indexes of similarity between the faunas of helminths from birds collected at different times were calculated as above (p. 15). A method of easily visualizing the degree of similarity between several samples is the "trellis" diagram developed by the Uppsala school of plant sociologists and used recently by Holmes and Podesta (1968) to compare the helminth faunas of wolves and coyotes from various regions of North America. It is usual practice to arrange the samples along the ordinate and abscissa so that maximum values appear along the principle diagonal. However, in this section, samples of geese have been arranged in chronological order beginning with the "arrival" sample.

Measures of faunal diversity are basically of two kinds. Those which measure how equitably the individuals of a sample are divided among the species present (the MacArthur "broken-stick" model (1957), the Preston log-normal distribution (1948), and the Simpson index (1949)) measure what Whittaker (1965) called dominance-diversity. Those which depend upon the number of species present (d values of Margalef (1957), α values of Fischer, Corbet and Williams (1943) and the rarefaction index of Sanders (1968)) measure species-diversity (Whittaker, 1965).

According to Sanders (1968) the species-diversity and dominance-diversity measures are only weakly correlated,

with the degree of correlation being dependent on sample size. A strong correlation is found with small sample sizes while no significant correlation, or only a weak one, exists with large sample sizes. This relationship is apparently due to the fact that species-diversity measures are affected by how a sample is divided among the species present. There is always a dominance diversity component in all species-diversity measures which is most strongly expressed with small sample sizes, where only the more common species (those which affect the dominance-diversity measures most) would be present.

Several measures of faunal diversity were used in this study. The mean number of species per bird and Simpson's index were used as measures of dominance-diversity. Both of these measures are relatively independent of sample size. Simpson's index is defined by the equation $c=\Sigma(Y/N)^2$ where c is the concentration of dominance, Y is the "importance value" of the species, and N is the sum of the importance values for all species in the sample. In this paper, Y is the number of worms of each species and N is the total number of worms of all species in the sample. High indexes suggest faunas dominated by a few very common species while low indexes indicate equitably distributed faunas. Since most other indexes of diversity give high values for diverse faunas,

the scale for Simpson's index in Figure 5 is reversed to make it directly comparable to the other measures.

The total number of species per sample and the rarefaction index of Sanders (1968) were used as measures of species-diversity. The former is strongly dependent on sample size, while according to Sanders (1968), the rarefaction index is not. The rarefaction procedure required taking the total number of species in a given sample represented by "X" number of worms, and then arranging them in order of decreasing abundance. The number of species one would expect to find in a decreasing number of worms could then be calculated, keeping the proportions of the total represented by each of the species the same as those in the original sample (see Sanders (1968) for details). The species-diversity of the samples in this study could be compared at the 200 worm level, since each sample had over 200 worms.

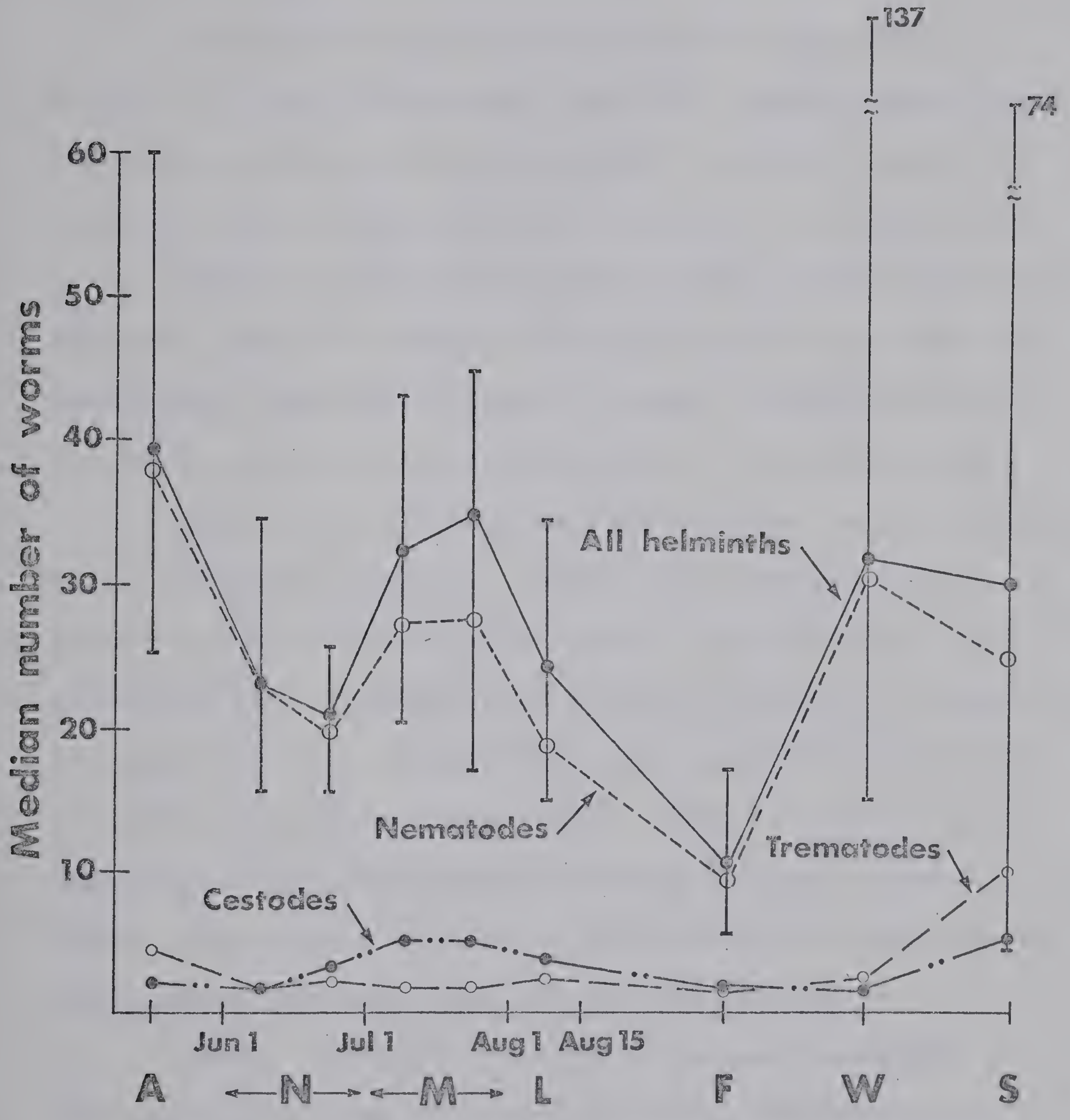
Results

All birds examined were infected with nematodes; the proportions of the birds infected with cestodes and trematodes varied from 16-100% and 13-40% respectively (Table 3). The median number of worms per bird varied with season (Table 3, Figure 3). The number of species of helminths recovered from geese showed some change

Number examined	32	59	55	31	19	23	7
Total Helminths							
Median intensity	39.5	23.0	33.0	24.0	11.0	32.0	30.0
Confidence limits*	26-60	18-26	28-41	15-34	6-17	15-137	4-74
Number of species	15	14	18	13	13	12	14
Mean no. species/bird	4.2	3.7	5.5	5.3	2.8	4.3	4.3
Simpson's index	.46	.32	.22	.26	.52	.50	.21
No. species/200 worms	9.8	11.2	13.0	12.0	12.4	9.2	13.6
Trematodes							
Prevalence (%)	31	31	20	19	21	40	28
Median intensity	4.0	1.0	1.0	2.0	1.0	2.0	10.0
Percent of total	4.0	3.0	1.0	2.0	4.5	1.0	8.0
Number of species	4	3	2	2	4	2	4
Simpson's index	.40	.35	.50	.71	.30	.51	.42
Cestodes							
Prevalence (%)	65	34	93	94	16	43	57
Median intensity	2.0	2.0	5.0	3.5	1.5	1.0	5.0
Percent of total	5.0	4.0	18.0	19.0	1.5	1.0	5.0
Number of species	4	4	9	4	1	2	1
Simpson's index	.48	.48	.35	.35	1.00	.89	1.00
Nematodes							
Median intensity	38.0	22.0	27.0	18.0	9.0	31.0	25.0
Confidence limits	20-52	17-24	21-30	9-26	6-17	13-134	4-50
Percent of total	91	93	81	79	94	98	87
Number of species	7	7	7	7	8	8	9
Simpson's index	.54	.37	.33	.39	.58	.52	.27

* P 95%

Figure 3. Seasonal variation in intensities of infection with helminths in adult snow geese.



137
74
60
50
40
30
20
10
Median number of worms
All helminths
Nematodes
Trematodes
Cestodes
Jun 1
Jul 1
Aug 1
Aug 15
A
N
M
L
F
W
S

with season (12-18 species out of a total of 26) but other measures of faunal diversity were more variable (Figures 4 & 5).

Lesser snow geese on arrival at the Anderson River Delta had the heaviest helminth burdens encountered (median intensity 39.5 worms/bird). Fifteen species of helminths were recovered with a mean of 4.2 species per bird. However, the high Simpson's index (0.46) indicated that the fauna was dominated by few species and the low rarefaction index (9.8 spp./200 worms) indicated that the rare species were present in very low proportions.

During the nesting period, populations of helminths were drastically reduced. There was a reduction in the proportion of birds infected and/or the intensity of infection with each group of helminths (Table 3, Figure 3). Although the total number of species per bird decreased slightly, Simpson's index (0.32) and the rarefaction index (11.2 spp./200 worms) indicated a more diverse fauna, with a more equitable distribution of worms among the species present, than in the arrival sample.

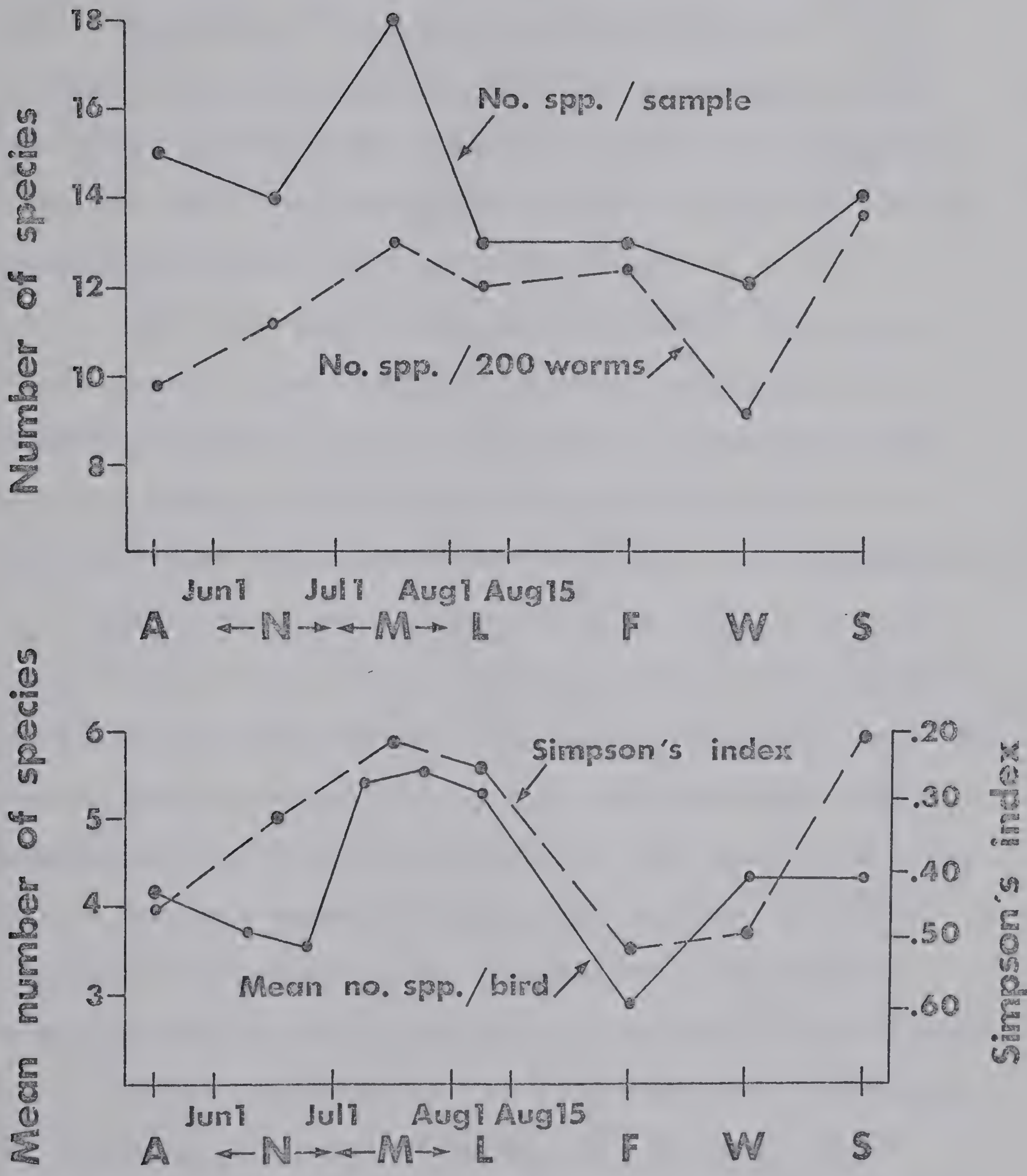
After the hatch and the subsequent movement of the geese away from the nesting areas, populations of helminths began to increase rapidly so that in "mid-summer", the intensity of infection averaged 33.0 worms per bird. Only the trematodes did not show an increase.

Figure 4. Seasonal variation in the total number of species per sample and the rarefaction index (no. spp./200 worms) for the helminth fauna of adult snow geese.

A = Arrival sample, N = Nesting sample,
M = Mid-summer sample, L = Late-summer sample,
F = Fall sample, W = Winter sample, S = Spring sample.

Figure 5. Seasonal variation in the mean number of species per bird and Simpson's index for the helminth fauna of adult snow geese.

A = Arrival sample, N = Nesting sample,
M = Mid-summer sample, L = Late-summer sample,
F = Fall sample, W = Winter sample, S = Spring sample.


Number of species
18
16
14
12
10
8
No. spp. / sample
No. spp. / 200 worms
Jun1
Jul1
Aug1
Aug15
A
N
M
L
F
W
S
Mean number of species
6
5
4
3
Simpson's index
.20
.30
.40
.50
.60
Simpson's index
Mean no. spp. / bird
Jun1
Jul1
Aug1
Aug15
A
N
M
L
F
W
S

Cestode infection levels were the highest of the year (up to 100% infected (av. 93%), 5.0 worms/bird) at this time. Measures of diversity indicated that the fauna was very equitably distributed (Simpson's index 0.22), that birds had frequent multiple infections (5.5 spp./bird) and that very few species were exceptionally rare (rarefaction index 13.0 spp./200 worms).

The infection levels at the end of the summer ("late-summer") were sharply reduced (intensity 24.0 worms/bird) from those prevailing during the mid-summer period. Decreases in the populations of cestodes and nematodes were responsible for this drop, with intensities of nematodes dropping to 18.0 worms per bird and intensities of cestodes to 3.5 worms per bird. The prevalence of infection with cestodes also dropped somewhat from the maximum during the latter part of the mid-summer period. Measurements of diversity suggested that there was little change from mid-summer although the species diversity measures (13 species in the sample, 12.0 species/200 worms) indicated that the fauna was slightly less diverse.

Birds collected on the fall migration route had the lowest populations of helminths recorded. The prevalence and intensity of infection with each group of helminths was very low. Thirteen species of helminths were present, but Simpson's index (0.52) and the mean

number of species per bird (2.8) indicated that the fauna was the least diverse encountered. However, the rarefaction index (12.4 spp./200 worms) and the total number of species present showed that there was no lack of variety in the helminths. The few species that were abundant were present in a large proportion of the birds and dominated the fauna numerically, while the other species were present at low, but equitable levels.

Geese collected from the wintering grounds had regained relatively heavy helminth burdens (intensity 32.0 worms/bird). Only twelve species were recovered from wintering geese, but the mean number of species per bird (4.3) indicated that several were present in a high proportion of the birds. Simpson's index (0.50) indicated that the fauna was dominated by a few species. The fauna was also low in species-diversity (9.2 spp./200 worms) indicating that several species were very rare.

Lesser snow geese collected on their northward migration ("spring") had helminth loads comparable to those in wintering birds but with fewer nematodes and more cestodes and trematodes. This was also the most diverse fauna in terms of Simpson's index (0.21) and the rarefaction index (13.6 spp./200 worms), and was also amongst the most diverse in terms of the total number of species present (14) and mean number of species per bird

(4.3). Most species were present at moderate, equitably-distributed levels, few being very rare.

Table 4 gives the species composition of the helminth fauna of adult snow geese and the importance value of each species in each collecting period. Indexes of similarity comparing the faunas of the various periods were computed from these data and a trellis diagram was constructed for easy visual comparison of degrees of similarity of the faunas in different seasons (Figure 6). Data on the prevalence and intensity of infection with each species of helminth in each season are presented in Appendix 1.

Figure 6 indicates that the total helminth fauna of snow geese was a dynamic entity with the faunas of particular periods showing high degrees of similarity to those of the periods immediately preceding and following them, but showing less similarity to the faunas from periods further removed in time and/or location. The greatest degrees of similarity were between periods on the breeding grounds, but even here the end points (arrival and late-summer) were much less similar to each other than they were to the faunas of intermediate periods. This situation is illustrated by the string of high values along the principle diagonal which compare the periods in a chronological sequence, and the lower

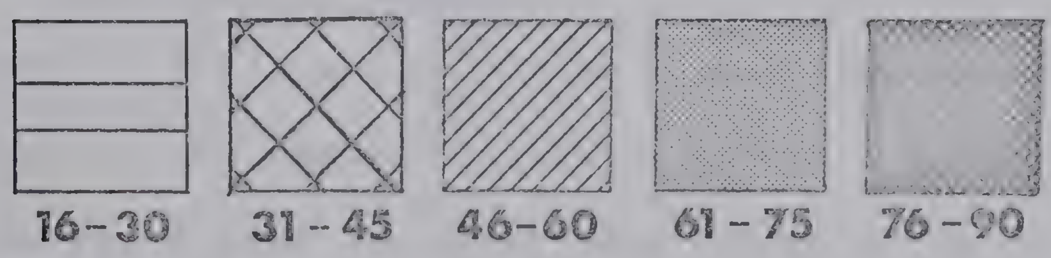
Period		Arrival	Nesting	Mid	Late	Fall	Winter	Spring
Number of geese		32	59	55	31	19	23	7
Total number of worms		1499	1323	1836	813	225	1874	247
Percent of total represented by:	*Category of helminth							
Echinoparyphium sp.	M					0.4		
Echinostoma revolutum	M	1.8	1.0			0.9		0.4
Notocotylus attenuatus	U	0.4	1.2	0.4	1.7		0.5	4.0
Zygocotyle lunata	U	0.1	0.7	0.3	0.4	1.3		0.4
Apatemon anseris	M	1.2				1.8	0.6	3.3
Anomotoenia ciliata	N		0.2	0.1				
Cloacotaenia megalops	N			0.1				
Dicranotaenia multistriata	W						0.9	
Diorchis stefanskii	N		0.1					
Drepanidotaenia barrowensis	N			0.4				
D. lanceolata	N			2.0	5.4			
Fimbriaria fasciolaris	N			0.1				
Parabisaccanthes philactes	N			0.1				
Retinometra longivaginata	N	2.3	2.5	9.0	8.5			
Tschertkovilepis krabbei	U	2.7	1.2	5.5	4.4	1.3	0.1	4.9
Tschertkovilepis setigera	N	0.1		1.0	0.2			
Wardoides nyrocae	N	0.1						
Sarconema eurycerca	N			0.3	0.4	0.4		1.2
Heterakis dispar	U		0.8	0.6	4.1	0.9	68.6	31.2
Tetrameres sp.	U	0.4	2.6	1.8	0.8	4.4	1.1	4.0
Amidostomum anseris	U	0.5	0.1			0.5	0.2	0.4
A. spatulatum	U	64.8	49.2	20.1	11.3	3.1	0.4	29.6
Epomidiostomum crami	U	18.3	20.5	22.8	17.2	70.2	12.7	13.3
Trichostrongylus tenuis	U	7.5	19.5	35.1	44.8	13.8	12.5	5.6
Capillaria obsignata	M	0.1					2.4	1.2
Capillaria sp.	U	0.1	0.3	0.3	0.7	0.9	0.1	0.4

* U = ubiquist
N = northern
M = migration
W = wintering ground

Figure 6. Trellis diagram showing similarities of the helminth faunas of adult snow geese at different seasons.

W = Winter sample, S = Spring sample, A = Arrival sample, N = Nesting sample, M = Mid-summer sample, L = Late-summer sample, F = Fall sample.

	A	N	M	L	F	W	S
A		74	52	42	33	22	54
N			67	55	44	28	56
M				82	44	28	48
L					39	31	43
F						28	32
W							54
S							



values in the rest of the columns and rows which compare each period to all other periods. For instance, the "arrival" fauna showed the greatest similarities to the spring and nesting faunas with a steady decrease in similarity to the faunas of other periods. The fall and winter faunas were the least diverse (in terms of Simpson's indexes) and showed the least similarity to the faunas of other periods. The faunas of these two periods were not very similar to one another, indicating that the species dominating them were different.

Trematodes were of little consequence to the helminth fauna as a whole, comprising a maximum of eight percent of the total number of worms in any collecting period (Table 3). They did contribute to the species-diversity of the fauna, particularly to the faunas of migrating geese. Migrating geese and those arriving at Anderson River had the greatest number of trematode species (4). *Echinostoma revolutum*, *Notocotylus attenuatus* and *Zygocotyle lunata* were present in geese throughout much of their range but were more important and abundant in the spring or early summer. *Apatemon anseris* also showed a peak in importance value on spring migration. *Echinostoma revolutum* and *Apatemon anseris* were lost soon after the geese began nesting and were not picked up again until the fall. *Echinoparyphium sp.* was picked up then also.

Cestodes were of greatest significance to the helminth fauna during mid- and late-summer when they became sufficiently abundant to comprise almost 20% of the total number of worms. Only four of the eleven species of cestodes encountered on the breeding grounds were very abundant. Two (Tschertkovilepis krabbei and Retinometra longivaginata) were brought into the area by snow geese, while the other two (Drepanidotaenia lanceolata and Tschertkovilepis setigera) were encountered only after the hatch (one immature worm, tentatively identified as Tschert. setigera, was found in a bird on arrival). The variations in abundance of these cestodes with season are presented in Figure 7. The rapid increases in abundance in mid-summer are notable. All decreased in abundance by late-summer and (except Tschert. krabbei) were absent by the time the geese reached Alberta and Saskatchewan during fall migration. Tschertkovilepis krabbei and Dicranotaenia multistriata were the only cestodes in wintering geese.

As pointed out earlier, nematodes were present in all geese regardless of season, and comprised 79-98% of the total number of worms recovered from geese in each period (Table 3). At least seven of the nine nematodes were present in each period. Obviously, the characteristics of the fauna of adult snow geese in each season was

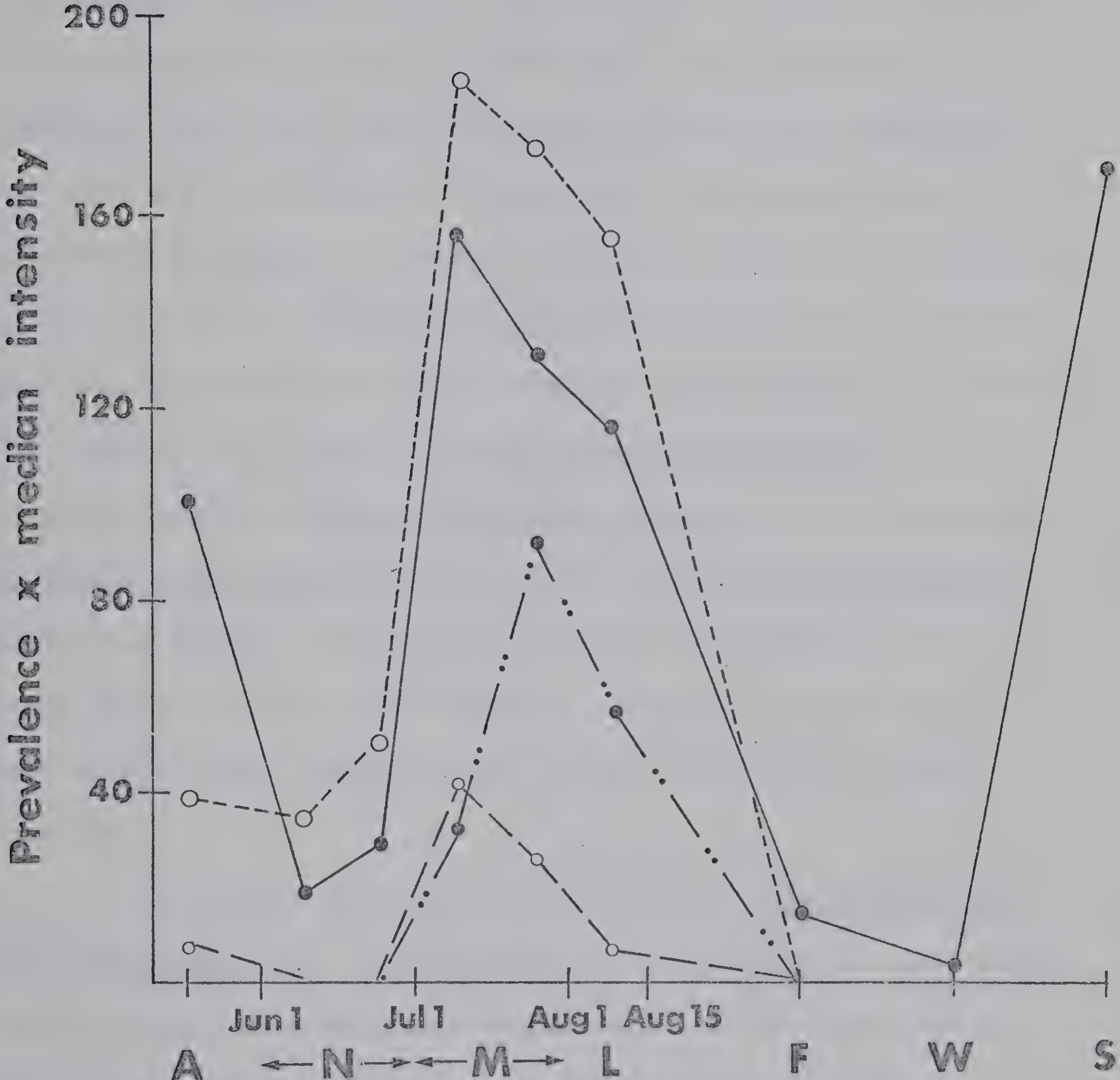
Figure 7. Seasonal variation in the abundance of the major cestodes of adult snow geese.

Drepanidotaenia lanceolata

Retinometra longivaginata

Tschertkovilepis krabbei

Tschertkovilepis setigera


Prevalence x median intensity
200
160
120
80
40
Jun 1
Jul 1
Aug 1
Aug 15
A
N
M
L
F
W
S

determined to a great extent by the nematodes.

Seasonal variations in abundance (prevalence times median intensity) for the four most common nematodes are presented in Figure 8. Together, these four represented 77-88% of the total number of worms present in each sampling period (Table 4). It is readily apparent that they were the major factors determining the overall abundance of helminths, the dominance-diversity (Simpson's index), and the indexes of similarity between periods. Each species had a different seasonal pattern of abundance and dominated the fauna at a different time of the year: Amidostomum spatulatum in the arrival sample, Trichostrongylus tenuis at late-summer, Epomidiostomum crami in the fall and Heterakis dispar in wintering birds. Periods in which the faunas of the geese were diverse (in terms of Simpson's index) had relatively equal proportions of all or most of these species.

Two other species of nematodes (Capillaria sp. and Tetrameres sp.) were present in all samples but were neither very abundant nor important to the fauna as a whole (Appendix 1, Table 4). They were consistent factors in determining the species-diversity (rarefaction index) within periods. The other nematodes were sporadic in their appearance, but were most important

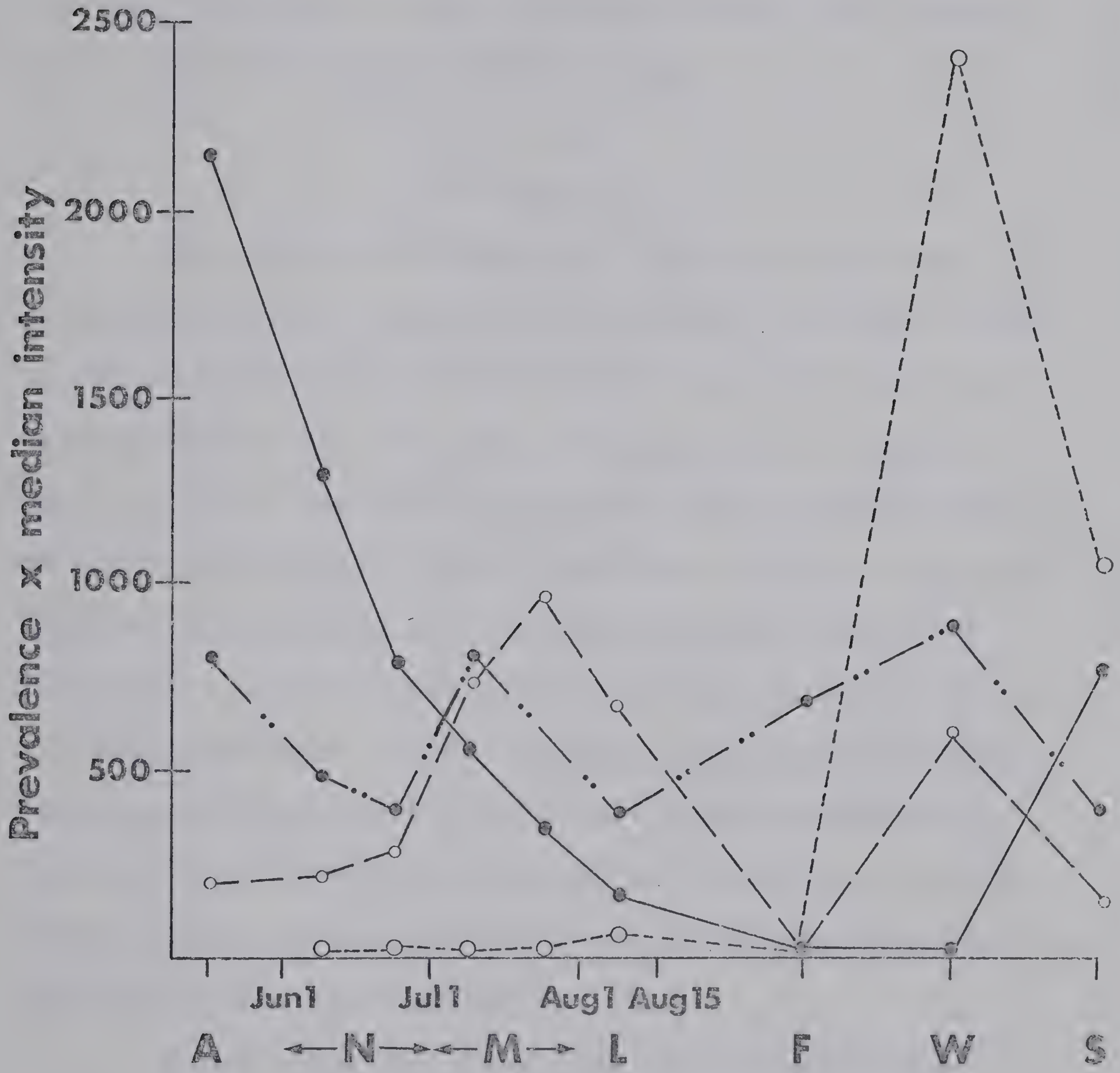
Figure 8. Seasonal variation in the abundance of the major nematodes of adult snow geese.

Amidostomum spatulatum

Epomidiostomum crami

Heterakis dispar

Trichostrongylus tenuis



Prevalence x median intensity
2500
2000
1500
1000
500
Jun1
Jul1
Aug1
Aug15
A
N
M
L
F
W
S

and abundant on migration or during the winter. They were very minor contributors to the indexes of dominance-diversity and the indexes of similarity between some periods, but were of some significance to the species-diversity of the faunas when present.

Discussion

The paucity of trematode infections in snow geese was probably due to a combination of restrictions in the distributions of requisite snail hosts and the grazing habits of the geese. Trematodes as a group were basically migratory parasites and were most abundant on spring migration. Infections were probably picked up from infective pools established in areas along the migratory route by other birds breeding in those regions. All the trematodes (except Apatemon anseris) have been reported at relatively high levels from various water-birds in the Beaverhill--Cooking Lakes drainage system (Colbo, 1965; Graham, 1966) where all spring birds and some fall birds were collected.

Other waterfowl have also been shown to have greater trematode burdens in the spring (Buscher, 1965; Graham, 1966) due perhaps to the early shedding of cercariae from over-wintered infections in snails or to over-wintered metacercariae. With snow geese, the

leisurely pace of spring migration and the greater time spent feeding in or near melt-water ponds in the spring, (relative to the fall migration) may have been important factors as well.

The trematodes found in snow geese over much of their range (_N. attenuatus_, _Z. lunata_) utilize a wide variety of almost cosmopolitan intermediate hosts and encyst as metacercariae on vegetation or debris. Because of these conditions, both were probably readily available to geese grazing near bodies of water. They can be considered ubiquists.

Ten of the twelve cestodes can be considered northern parasites, characteristic of the tundra breeding grounds. Although _Tschert. krabbei_ can be considered a ubiquist, it also reached a peak in abundance on the breeding grounds. The only other cestode in wintering birds, _D. multistriata_, is normally found in grebes, which are abundant on the wintering grounds. No mature worms of this species were found, and their presence in snow geese was probably accidental.

The findings of this study were in general agreement with those of Schiller (1954), Bykhovskaya-Pavlovskaya (1962), Dogiel (1964) and Buscher (1965) who suggested that cestodes were predominantly parasites of northern breeding areas, and that the coincidence in time and place

of large populations of intermediate and definitive hosts on the breeding grounds was particularly conducive to the transmission of cestodes. Ponds teeming with invertebrates are abundant in areas of the Anderson River Delta used extensively by the geese during the brood-rearing period. A few sweeps of a plankton net through any of these ponds yielded a collecting bottle full of invertebrates. Life cycles are known for three of the four most abundant cestodes (all except R. longivaginata). All three utilize limnetic or littoral copepods as intermediate hosts. These forms would be readily available to geese grazing in or near the ponds.

Most of the nematodes of lesser snow geese (all except Sarconema eurycerca and Tetrameres sp.) belong to groups which have direct life cycles. Most (all except S. eurycerca, and perhaps Capillaria obsignata) could be considered ubiquists. However, the patterns of the seasonal variation in abundance and importance values for each species indicated that the requirements for optimum transmission of each species were obviously different. A classification of these helminths with reference to times when they were most abundant or when they were most rapidly acquired would be more useful than one which relies only on the presence of the helminth or the possibility of transmission in an area.

The gizzard nematodes were basically migration parasites (*Amidostomum anseris* and *A. spatulatum*) or were almost equally abundant in all sampling periods (*E. crami*). All were apparently transmitted to geese along the spring migration route. Other species of *Amidostomum* and *Epomidiostomum* have a short developmental time outside the host (6-11 days at approximately 20 C) (Leiby and Olsen, 1965). Rapid development to the infective stage would be a distinct advantage to worms living in migratory hosts. The species found in this study probably have similar developmental characteristics, which could account for the build-up of their populations in the spring. Snow geese migrate northward following the 40^{o} isotherm until their last big push from northern Alberta to the Anderson River Delta (Barry, 1967). Even in areas where the clearance of snow and ice was not complete, the warmed microclimate of melt-water pools and open areas along the banks of rivers and streams could have provided suitable conditions for development of the larvae. Because successive flocks of geese use the same resting and staging areas, the possibilities of picking up infections of gizzard nematodes derived from eggs shed the same spring are very good. A combination of activity patterns of the geese and developmental characteristics of the parasites seem to have produced high

populations of gizzard nematodes in the spring and arrival samples.

Epomidiostomum crami seems to be particularly well adapted to the environment of its host and the changes that occur with the seasons. The seasonal pattern of abundance (Figure 8) indicated that at least three different but overlapping generations of worms were encountered and that transmission occurred in all areas from the Arctic tundra to southern California. In view of the rather extensive pathology associated with this worm (p.113), the low intensities of infection encountered would be advantageous to both host and parasite. The prevalence of infection was always high, ensuring a steady rate of egg dispersal and completion of the worm's life cycle, while the low number of worms per bird would have no deleterious effect on the host.

Larvae of Trichostrongylus tenuis also reach the infective stage in a very short time (8-9 days) (Cram and Cuvillier, 1934). Third stage larvae migrate up onto vegetation and would be readily available to grazing geese. New infections mature in 4-7 days allowing the quick build-up in the population noted in mid- and late-summer in this study. Infections were present in arriving geese so that a pool of infective larvae was probably well developed by the time geese began extensive feeding after

broods were produced. The constant use of favored feeding areas by the geese, and the short life cycle of the worm would have enabled several generations of worms to have infected the geese on the breeding grounds.

Heterakis dispar has a much longer generation time (30-48 days) than the other nematodes discussed (McDonald, 1969b). This may explain why H. dispar was relatively uncommon in geese except on the wintering areas. Heterakid eggs can survive up to eight months in the soil so that infections on the wintering area could have been the result of an extensive pool of infective stages built up in the warm southern region over a long period of time. Geese in Czechoslovakia, when penned in the same area every winter, were heavily infected with H. dispar (Busa, 1964). Snow geese using the same wintering areas each year may be duplicating that situation.

Only two species of helminths can be considered southern parasites (D. multistriata and C. obsignata) (Table 4). However, this classification is inexact since neither is a characteristic parasite of waterfowl and C. obsignata, although most abundant on the wintering grounds was also present in the "spring" and "arrival" samples. Three species (all trematodes) are migration parasites and (except for Apatemon anseris) were found

nowhere but on migratory routes or in the early part of the summer. The majority of the helminths of snow geese are ubiquists (2 trematodes, 1 cestode, 7 nematodes) or northern parasites (10 cestodes, 1 nematode). As pointed out above, several of the ubiquists were abundant the year round or in the spring or summer. Only one species (H. dispar)was most abundant in the winter. When one considers that the migration parasites were most abundant in the spring as well, the fall and winter periods were devoid of "characteristic" species of helminths.

In general, the results of this study support the findings of other workers who have studied the effects of migration on the parasites of birds. The helminth fauna of lesser snow geese on the Anderson River Delta breeding grounds was most diverse in terms of the total number of species and mean number of species per bird. This was due to the large number of ubiquists and to the acquisition of the northern species, especially ten species of cestodes. In addition, the populations of most of the species of helminths were greatest during the summer.

The general reduction in parasite numbers from arrival to the end of the nesting period was associated with two factors: the stress of nest initiation, territorial defense and incubation (a similar situation was recorded for grebes and coots in Alberta by Gallimore

(1964) and Colbo (1965)) and inadequate (and generally ignored) food resources throughout most of the nesting period.

The rapid accumulation of cestodes and the increases in populations of T. tenuis, E. crami and H. dispar after the hatch was associated with extensive feeding by the geese, and with the continued use of favored areas which had been seeded previously with helminth eggs or were seeded soon after the hatch.

A number of factors could have been responsible for the reductions in many helminths during the late-summer. Late in the summer, geese began feeding extensively along major channels of the river where low water levels had exposed submergent vegetation. This shift from the meadows and ponds of the moulting and feeding areas may have removed the birds from sources of infection.

The complete loss of all cestodes except Tschert. krabbei and the reduction in most other helminths (except E. crami) during fall migration was probably due to a complex of factors affecting the availability of infective material. The reduced fauna in the fall was numerically sparse, but had a relatively high degree of species-diversity. This, and the fact that new species were acquired in the fall, suggests that the availability of infective material was a more important factor in the

reduction of helminth burdens than were changes in gut physiology.

The generally low numbers of helminths (except *E. crami* and *H. dispar*) and low diversity of the helminth fauna of wintering birds is in agreement with the findings of other authors. Only one species (*D. multistriata*) was found only on the wintering area, and except for *H. dispar*, none of the helminths were more abundant there than elsewhere. There was no appreciable acquisition of parasites characteristic of the wintering area. Indexes of similarity between the fauna of wintering birds and those of birds from other periods (except the spring period) were low, indicating that the faunas were different. However, these differences were not due to the acquisition of new species of helminths (except for the faunas of birds on the breeding grounds where the northern parasites were acquired) but to the presence of helminths in different proportions in each period.

The diverse helminth fauna (in terms of both dominance-diversity and species-diversity) of geese in the spring, and the similarities of that fauna and the faunas of geese of other periods is indicative of the transitional nature of the spring fauna. As indicated earlier, many of the nematodes and trematodes were acquired on spring migration, and worms such as *H. dispar*,

C. obsignata and Apatemon anseris were well represented in the spring fauna as well as being abundant on the wintering grounds. The latter group are characteristic of the geese on the southern portion of their range. These forms and the ubiquists bridged the gap between the wintering and breeding areas.

The community of helminths in adult snow geese was characterized by the dynamic nature of its abundance, structure, and diversity. Stability was provided by the presence of many ubiquists, but the acquisition and loss of northern and migration parasites provided for variety in species composition of the fauna. Above all, the population dynamics of individual species of helminths (particularly the ubiquists) did much to produce the dynamic nature of the entire community.

IV. THE ACQUISITION OF HELMINTHS BY YOUNG LESSER SNOW GEESE

Introduction

The rate and order of acquisition of helminths by young water birds have been studied by several workers (Bykhovskaya-Pavlovskaya, 1962; Cornwell and Cowan, 1963; Gallimore, 1964; Colbo, 1965; Graham, 1966). Dogiel (1964) proposed the idea that precocious young were more likely to acquire parasites with complex life-cycles than were altricial nestlings. Work on a variety of water birds has shown that trematodes, cestodes, nematodes and acanthocephalans may be acquired in any order, depending on the species of host, but that generally, helminths with complex life cycles were acquired first (the above authors; Wehr and Herman, 1954).

Wehr and Herman (1954) studied the effect of age on the acquisition of parasites by young Canada geese (Branta canadensis) in Michigan and Utah. They calculated that many parasites were acquired in the first week or two of life. Cestodes were acquired first followed closely by trematodes and then nematodes.

Young water birds often harbour greater parasite

loads than adults and are susceptible to certain parasites to which adults are refractile (Ginetsinskaya, 1952; Hanson, Levine and Kantor, 1956; Bykhovskaya-Pavlovskaya, 1962; Cornwell and Cowan, 1963; Buscher, 1965; Colbo, 1965; Graham, 1966). On the other hand, Gallimore (1964) found little difference between the numbers of helminths in adult and immature grebes, and Threlfall (1967) found that young herring gulls (*Larus argentatus*) in Wales never acquired as varied or extensive parasite loads as adults.

Schiller (1954), Hansen et al. (1956), and Shevtsov (1964) reported that young geese (*Philacte canagica*, *Branta canadensis* and *Anser anser*) were more heavily infected with helminths, particularly cestodes and trematodes, than were adults taken in the same areas. Holmes (in Barry, 1967) recorded much greater cestode burdens in young than in adult lesser snow geese and Pacific brant at Anderson River, N.W.T. Infections with some nematodes were also more common in young brant than in adults.

Bykhovskaya-Pavlovskaya (1962) pointed out that adult birds generally had a more diverse trematode fauna than their young, but that the young of migratory birds acquired a species composition approaching the adult condition by the time they left the breeding grounds in

the fall. Gallimore (1964) and Graham (1966) supported this idea in their work with grebes and scaup in Alberta. They were cognizant of the fact that adult birds were more apt to have a variety of helminths because they had been exposed to the ecological variety of migrations.

Schiller (1952), Herman and Wehr (1954), Hanson and Gilford (1961) and Leiby and Olsen (1965) have proposed that most of the parasites of northern or arctic-nesting birds are contracted on the breeding grounds. Schiller (1952, 1954) reported the cestodes of young geese and ducks in Alaska, while Holmes (op. cit.) recorded at least nine helminth species (one trematode, at least 5 cestodes, 3 nematodes) from young geese at Anderson River. Their studies provided information concerning some of the species that infect young waterfowl in the arctic but were not extensive enough to give a picture of the dynamics of the helminth populations in young birds.

The present study provided an opportunity for an extensive survey, over two summers, of the parasites of young lesser snow geese on the Anderson River breeding grounds. Birds of the year were also collected on the fall migration route and the wintering grounds, so that the acquisition, and population levels, of helminths in young geese could be followed through their first migration.

Materials and Methods

In each year of the study, approximately eight young lesser snow geese were collected every week between the hatch (at the end of June) and late August when geese began flocking up before leaving the delta. This enabled me to follow the acquisition of species of helminths and the build up of populations of helminths at weekly intervals. Collections on fall migration and the wintering grounds were done in conjunction with collections of adults (p. 32).

The hatch of snow geese is relatively synchronous, with most clutches hatching within a period of three or four days (Barry, 1967; personal observations). Therefore, ages of young geese could be estimated with a good deal of precision. In addition, Southwick's (1953) waterfowl brood classification based on characteristics of the plumage was used to supplement estimates of age, so that birds could be placed in weekly age classes. The terminology used for birds in their first, second, ..., sixth week was 0+ weeks, 1+ weeks, ..., 5+ weeks respectively. The ages of geese (young or adult) from areas other than the breeding grounds were determined by characteristics of the plumage.

Samples of adult geese were collected every two weeks on the breeding grounds and it was not possible to

break the data down into weekly intervals. Therefore, it was necessary to pool the data from two successive samples of young geese, in order to compare the prevalence and intensity of infection with helminths, trematodes, cestodes and nematodes in young and adult geese collected during the same periods. The fall and winter samples could be compared directly since the birds were collected at the same times and places. For a comparison of the numbers of specific helminths in the two age groups on the breeding grounds, the data from all young geese over two weeks of age (2+ to 5+ weeks) (when the populations of helminths had reached relatively high levels) were pooled and compared to the pooled data from adults collected during the same period (July 16 to August 15). Prevalences were compared using the Chi-squared test, while differences between median intensities were tested for statistical significance using a Mann-Whitney U test (see Campbell, 1967).

Simpson's indexes, rarefaction indexes (no. spp/200 worms) and indexes of similarity were determined as above (pp.15,34). Indexes of similarity comparing the faunas of the entire sample of young geese on the breeding grounds, fall migration and the wintering grounds to those of breeding adults (June 1 to August 15), adults on fall and spring migration and the wintering grounds, were

calculated. The samples were arranged along the ordinate and abscissa of a trellis diagram to place maximum values along the principle diagonal.

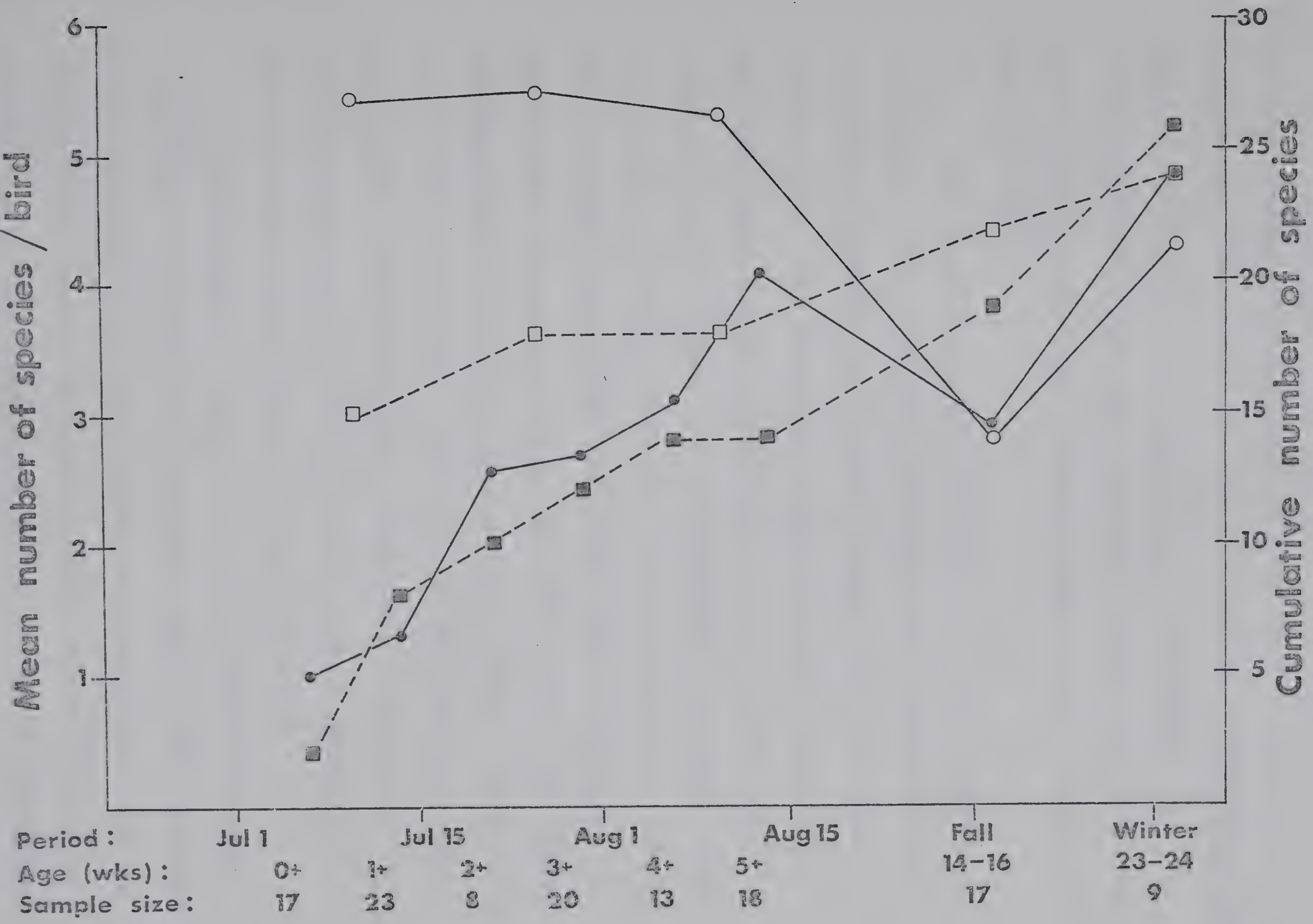
Results

Young snow geese began to acquire helminths within their first week and continued to add new species until shortly before they left the breeding grounds. Eight species were acquired in the first two weeks and by the end of the fifth week, all 14 species recovered from young geese on the breeding grounds had been encountered in at least some of the young (Figure 9). The mean number of species per bird also increased steadily over the summer period to a high of 4.1 species per bird during the sixth week. In comparison, adults were infected with 18 species and had a mean of 5.3-5.5 species per bird during the same period (July 1 to August 15).

The cestodes, Tschertkovilepis krabbei and Parabisaccanthes philactes, were the first helminths acquired; each was found in goslings less than a week after the hatch. Young geese taken early in the second week harbored the cestodes, Retinometra longivaginata and Tschertkovilepis setigera. By the end of their second week, the young geese were infected with seven of

Figure 9. The acquisition of species of helminths by young and adult lesser snow geese.

Adults:	mean no. spp./bird	○
	cumulative no. spp.	□
Young:	mean no. spp./bird	●
	cumulative no. spp.	■



Mean number of species / bird
Cumulative number of species
6
5
4
3
2
1
30
25
20
15
10
5
Period :
Jul 1
Jul 15
Aug 1
Aug 15
Fall
Winter
Age (wks) :
0+
1+
2+
3+
4+
5+
14–16
23–24
Sample size :
17
23
8
20
13
18
17
9

the ten cestodes encountered in them on the breeding grounds and harbored their first nematode, *Trichostrongylus tenuis*. The trematode, *Notocotylus attenuatus*, was recovered from young geese in their fourth week (3+) and was the only species of trematode encountered in them at Anderson River.

The population of helminths built up rapidly in young geese with both the prevalence and intensity of infection reaching peak levels during the fifth week (Figure 10). The prevalence of infection remained at the same level (100%) during the sixth week but the intensity of infection (22.0 worms/bird) declined somewhat, to 15.5 worms per bird. The prevalence of infection in young geese from the third week on was not significantly different from that of adults. The median intensity of infection in young birds during their fifth week (22.0 worms/bird), and that of the combined fifth and sixth week samples (16.0 worms/bird) (Table 5) were essentially equal to that of adults (24.0 worms/bird) collected in August (Figure 10 and Table 5).

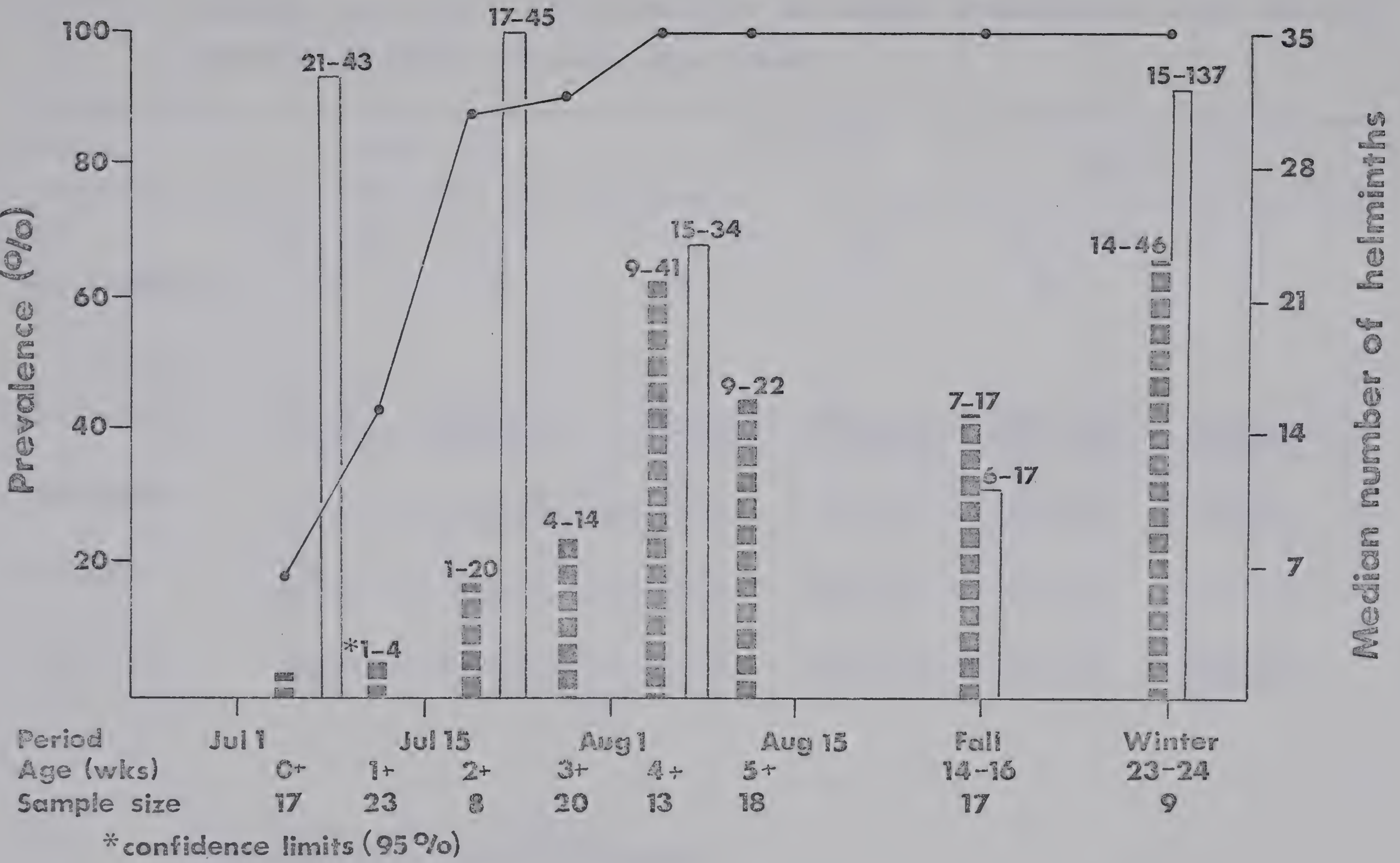
Prevalences and intensities of infection with trematodes were very low in young geese on the breeding grounds (Figure 11) with trematodes comprising only 3% of the total number of worms. There was no significant difference in the prevalence or intensity of infection

Figure 10. Acquisition of populations of helminths by young and adult snow geese.

Prevalence in the young

Median no. worms/adult bird

Median no. worms/young bird



Prevalence (%)
100
80
60
40
20
Median number of helminths
35
28
21
14
7
21-43
*1-4
1-20
17-45
4-14
9-41
15-34
9-22
7-17
6-17
14-46
15-137
Period
Jul 1
Jul 15
Aug 1
Aug 15
Fall
Winter
Age (wks)
0+
1+
2+
3+
4+
5+
14-16
23-24
Sample size
17
23
8
20
13
18
17
9
*confidence limits (95 %)

Table 5. Seasonal variation in the prevalence and median intensity of infection with helminths in young and adult snow geese.

Period	July 1-15		July 16-31		August 1-15	
Age	0-1+ wks*	Adult	2+-3+ wks	Adult	4+-5+ wks	Adult
No. examined	40	32	38	23	31	31
Helminths	**33-1.0 (1-9)	100-32.5 (9-85)	89-8.0 (1-52)	100-35.0 (8-68)	100-16.0 (1-52)	100-24.0 (3-98)
Trematodes		25-1.0 (1-2)	4-1.0 (1)	13-1.0 (1-2)	32-1.5 (1-12)	19-2.0 (1-8)
Cestodes	33-1.0 (1-9)	88-5.0 (1-24)	79-3.0 (1-52)	100-5.0 (1-22)	97-8.5 (1-50)	90-3.5 (1-19)
Nematodes	3-1.0 (1)	100-27.0 (7-72)	54-5.0 (2-16)	100-28.0 (4-64)	68-5.0 (1-32)	100-18.0 (1-39)

* = two weekly samples combined

** = Prevalence (%) - Median Intensity / (Range)

Table 5. Seasonal variation in the prevalence and median intensity of infection with helminths in young and adult snow geese (Cont.)

Period	Fall		Winter	
Age	14-16 wks	Adult	23-24 wks	Adult
No. examined	17	19	9	23
Helminths	100-15.0 (2-75)	100-11.0 (4-25)	100-23.0 (11-85)	100-32.0 (5-370)
Trematodes	29-2.0 (1-3)	21-1.0 (1-7)	33-2.0 (2-10)	40-2.0 (1-3)
Cestodes	76-2.0 (1-8)	16-1.5 (1-2)	67-1.0 (1-11)	43-1.0 (1-5)
Nematodes	94-13.0 (1-73)	100-9.0 (3-24)	100-18.0 (10-72)	100-31.0 (5-370)

between the combined samples of young geese taken in August (4+ and 5+ weeks) and the sample of adults collected in the same period.

Cestodes were the most abundant group of helminths in young geese on the breeding grounds. The prevalence of infection reached a maximum (100%) during the sixth week while the median intensity peaked during the fifth week (17.5 worms/bird) and then declined by the end of the summer (5.0 worms/bird) (Figure 11). The intensity of infection with cestodes in the combined samples of young geese collected in August was significantly greater ($p < .01$) than that of adults collected in the same period. Sixty-seven percent of the worms recovered from young geese were cestodes while only 18% of the worms in adults collected from July 1 to August 15 were cestodes.

Nematode infections were acquired more slowly than cestodes but did build up over the summer period (Figure 11). Populations of nematodes in young geese on the breeding grounds did not approach those of adults (Table 5). Thirty percent of the worms recovered from young geese were nematodes while 80% of those from adults collected in the same period were nematodes.

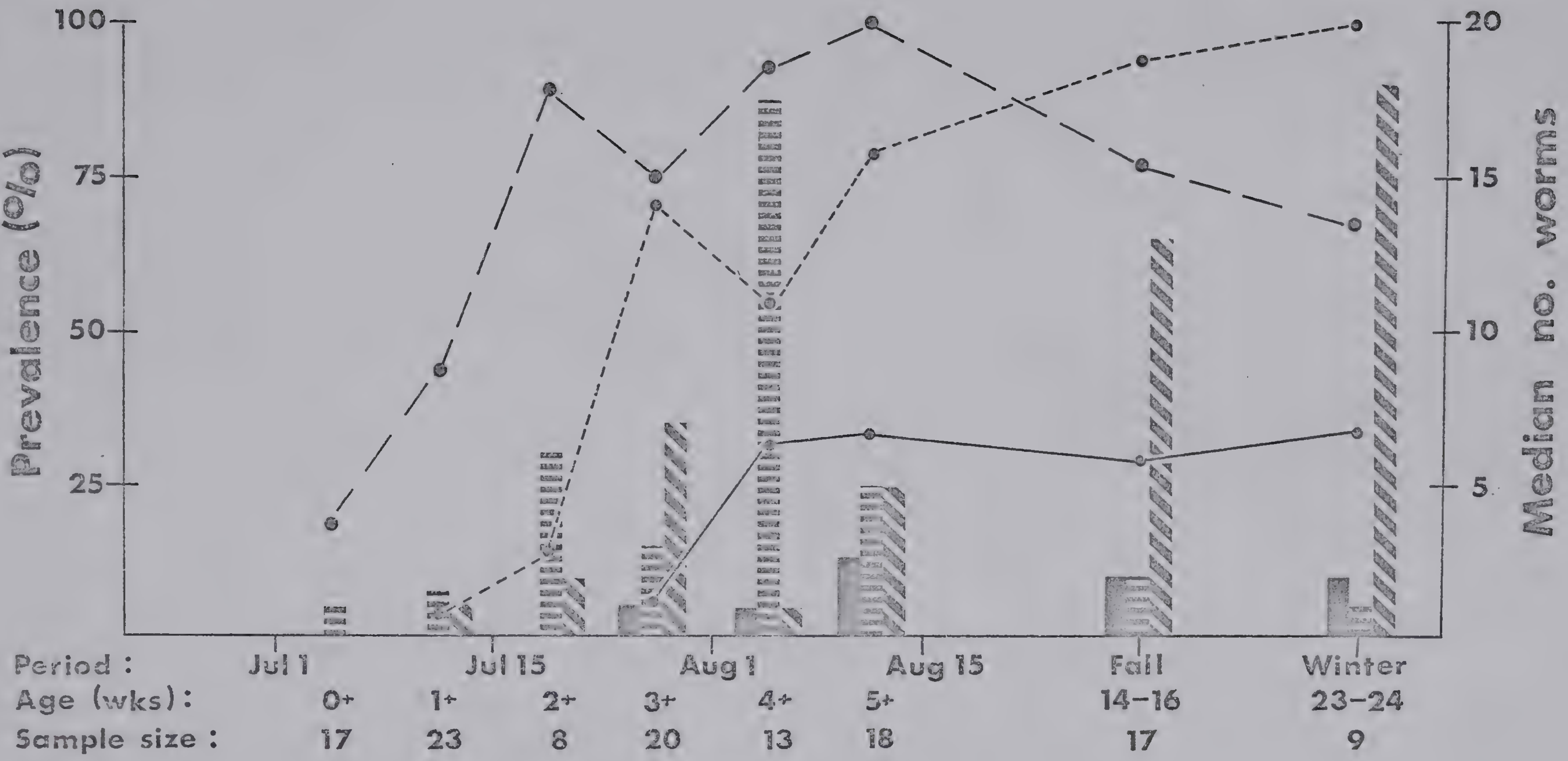
The rates of acquisition of specific helminths are presented in Table 6. Of the 14 species recovered on the breeding grounds, Dicranotaenia coronula, Diorchis

Figure 11. Acquisition of trematodes, cestodes and nematodes by young lesser snow geese.

Prevalence trematodes -- Worms/bird

Prevalence cestodes -- Worms/bird

Prevalence nematodes -- Worms/bird


Prevalence (%)
100
75
50
25
Median no. worms
20
15
10
5
Period :
Jul 1
Jul 15
Aug 1
Aug 15
Fall
Winter
Age (wks) :
0+
1+
2+
3+
4+
5+
14-16
23-24
Sample size :
17
23
8
20
13
18
17
9

Age (weeks)	0+	1+	2+	3+	4+	5+	14-16 Fall	23-24 Winter
Number examined	17	23	8	20	13	18	17	9
Number of species	2	7	9	11	10	11	12	15
Helminth								
TREMATODA								
<u>Echinoparyphium</u> <u>sp</u>.							*12-1.5 (1-2)	
<u>Echinostoma</u> <u>revolutum</u>							18-2.0 (1-2)	
<u>Notocotylus</u> <u>attenuatus</u>				5-1.0 (1)	31-1.0 (1-3)	33-2.5 (1-12)		11-10.0 (10)
<u>Apatemon</u> <u>anseris</u>							6-1.0 (1)	22-2.0 (2)
CESTODA								
<u>Anomotaenia</u> <u>ciliata</u>								22-1.0 (1)
<u>Dicranotaenia</u> <u>coronula</u>					8-1.0 (1)		6-1.0 (1)	
<u>Dicranotaenia</u> <u>multistriata</u>								22-1.5 (1-2)
<u>Diorchis</u> <u>stefanskii</u>				5-1.0 (1)		6-1.0 (1)	6-1.0 (1)	11-1.0 (1)
<u>Drepanidotaenia</u> <u>barrowensis</u>		9-1.0 (1)	25-1.0 (1)	20-1.0 (1-3)	8-2.0 (2)	67-2.5 (1-14)		
<u>D</u>. <u>lanceolata</u>		4-1.0 (1)	50-14.0 (3-50)	15-1.0 (1-3)	76-8.5 (1-18)	28-10.0 (1-40)	18-1.0 (1)	
<u>Fimbriaria</u> <u>fasciolaris</u>		4-2.0 (2)	13-1.0 (1)					
<u>Parabisaccanthes</u> <u>philactes</u>	6-1.0 (1)		13-1.0 (1)	10-1.0 (1)				
<u>Retinometra</u> <u>longivaginata</u>		4-1.0 (1)	13-1.0 (1)	5-1.0 (1)	23-3.0 (1-4)	11-1.0 (1)		
<u>Retinometra</u> <u>sp</u>.								11-1.0 (1)
<u>Sobolevicanthus</u> <u>gracilis</u>			13-1.0 (1)	5-1.0 (1)		17-1.0 (1-2)		

Age (weeks)	0+	1+	2+	3+	4+	5+	14-16 Fall	23-24 Winter
Number examined	17	23	8	20	13	18	17	9
Number of species	2	7	9	11	10	11	12	15
Helminth								
Tschertkovilepis krabbei	12-1.5 (1-2)	13-2.0 (1-3)	63-1.0 (1-2)	50-1.5 (1-7)	23-1.0 (1-2)	78-2.0 (1-5)	65-2.0 (1-5)	22-5.5 (5-6)
Tschert. setigera		13-2.0 (1-9)	25-1.0 (1)	40-3.0 (1-11)	69-4.0 (1-41)	28-1.0 (1-5)		
NEMATODA								
Sarconema eurycerca								11-6.0 (6)
Heterakis dispar			13-2.0 (2)	20-6.0 (1-16)	23-1.0 (1)	28-3.0 (1-14)	6-1.0 (1)	33-4.0 (3-10)
Tetrameres sp.								22-1.0 (1)
Amidostomum anseris							18-1.0 (1)	55-2.0 (1-4)
A. spatulatum								11-1.0 (1)
Epomidiostomum crami					15-1.0 (1)	17-1.0 (1)	53-4.0 (1-33)	88-6.5 (3-38)
Trichostrongylus tenuis		4-1.0 (1)		65-4.0 (1-16)	31-4.0 (1-29)	72-5.0 (1-18)	82-10.5 (1-62)	88-11.5 (9-17)
Capillaria obsignata								22-4.0 (4)
ACANTHOCEPHALA								
Polymorphus contortus							6-1.0 (1)	

*Prevalence (%) - Median Intensity
Range

stefanskii, Fimbriaria fasciolaris, P. philactes and Sobolevicanthus gracilis were present only sporadically or in low numbers. Drepanidotaenia lanceolata, R. longivaginata and Tschert. setigera reached a peak abundance when the young geese were in their fifth week and then declined by the summer's end. The other species reached peak levels in the last week spent on the breeding grounds. Only two species (D. coronula, and S. gracilis) were not found in adult snow geese. Six species (Drepanidotaenia barrowensis, D. lanceolata, Tschert. krabbei, Tschert. setigera, Heterakis dispar and T. tenuis) made up 93% of the total number of worms recovered from young geese.

Young geese over two weeks of age (combined samples of geese 2+ to 5+ weeks of age) were more often infected with D. barrowensis and Tschert. setigera ($p < .001$, Table 7) than were adults collected in the same period (July 16 to August 15). The intensities of Tschert. setigera and D. lanceolata infections were also greater ($p < .01$ and $p < .05$ respectively) in young birds. Retinometra longivaginata, Epomidiostomum crami and T. tenuis were found in a greater proportion of adults ($p < .001$) and in higher numbers ($p < .05$) than in young geese. There were no significant differences in the prevalence or intensity of infection with other species of helminths found in both adults and young.

Area	Breeding Grounds				Fall				Winter			
Age	Young (2+-5+wk)	Adult			Young (14-16 wk)	Adult			Young (23-24 wk)	Adult		
No. examined	59	54			17	19			9	23		
Parasite	Prev.(%) / Md.	Prev.(%) / Md.	χ^2	U or x(1)	Prev.(%) / Md.	Prev.(%) / Md.	χ^2	U or x	Prev.(%) / Md.	Prev.(%) / Md.	χ^2	U or x
N. attenuatus	19/1.0	11/2.0	1.23	16.5					11/10.0	13/3.0	.02	1
D. barrowensis	36/1.0	6/2.0	46.14*	25								
D. lanceolata	39/6.0	35/2.0	0.17	2.52*								
P. philactes	5/1.0	2/1.0	0.86	--								
R. longivaginata	19/1.0	59/2.5	19.75*	2.53*								
Tschert. krabbei	53/2.0	61/2.0	0.84	--	62/2.0	10/1.5	11.41*	--	22/5.5	4/1.0	2.43	8.5
Tschert. setigera	41/2.0	11/1.0	12.63*	2.64*								
E. crami	8/1.0	87/5.0	70.05*	3.40*	53/4.0	100/7.0	11.49*	51.5	88/6.5	100/9.0	2.63	0.72
H. dispar	22/2.0	33/1.0	1.80	89	6/1.0	5/2.0	.01	--	33/4.0	78/31.0	5.79*	15.5
T. tenuis	53/5.0	96/10.0	27.67*	2.27*	82/10.5	47/1.0	4.75*	20.5*	88/11.5	74/8.0	0.84	51

Prev.(%) = prevalence

Md. = median intensity

(1) The values of U or x are derived from the Mann-Whitney U test for differences between sample medians. U is used with samples of 20 or less, x is used if one or both samples are greater than 20 (Campbell, 1967).

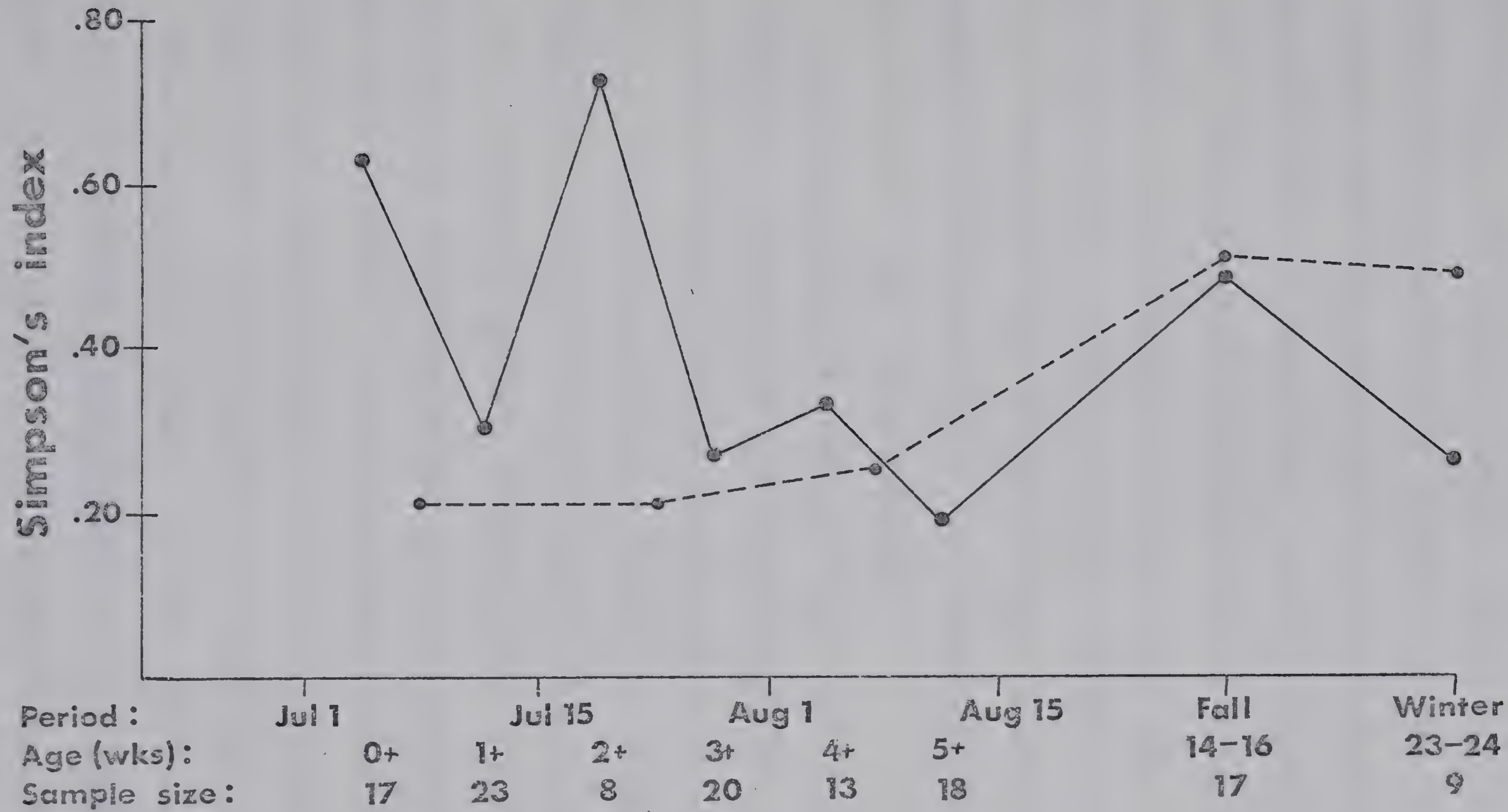
* Significant at 5% level.

The helminth fauna of young snow geese gradually became more diverse (in terms of cumulative number of species and mean number of species per bird). The number of species per sample increased from two species during the first week to 11 during the fourth week and then remained stable until the geese were ready to leave the breeding grounds (Table 6). The number of species in the combined samples of young geese taken in August (4+ and 5+ weeks) (12 species) compared favourably with the number of species (13) in the sample of adults collected then. In terms of Simpson's indexes, the diversity of the fauna of young geese fluctuated erratically until after the third week (Figure 12). After that, the indexes (.19-.34) were comparable to those of the faunas of adults (.22-.26) taken in July and August. The combined samples of young geese over two weeks of age had a Simpson's index of 0.19. This compared with an index of 0.23 for the fauna of adults during the same period. These values were the same for the fauna of the total sample of young geese and that of adults collected from June to August 15. The rarefaction indexes (p. 35) for the same combined samples of young geese were 11.2 spp./200 worms and 11.4 spp./200 worms respectively. Rarefaction indexes for the faunas of adults collected over the period from June to August 15 varied from 11.2-13.0 spp./200 worms.

Figure 12. Variation of Simpson's index for the helminth fauna of young snow geese.

Young ●————●

Adults ●- - - - - -●


Simpson's index
.80
.60
.40
.20
Period : Jul 1 Jul 15 Aug 1 Aug 15 Fall Winter
Age (wks) : 0+ 1+ 2+ 3+ 4+ 5+ 14–16 23–24
Sample size : 17 23 8 20 13 18 17 9

Although these measures of diversity indicated that the faunas of young and adult snow geese on the breeding grounds were similar in terms of how the worms in the samples were apportioned among the species present, the species most responsible for the diversities were different. Cestodes were the major factors determining the diversity of the fauna of young geese, with nematodes of lesser importance (only 3 species of nematodes were present in young geese). Cestodes were of some importance in determining the diversity of the fauna of adults, but the major factors were the nematodes.

As young geese encountered fall migration and their wintering grounds for the first time, the rate of accumulation of new species of helminths accelerated (Figure 9). The mean number of species per bird dropped to 2.9 species in the fall, but rose to 4.8 species per bird on the wintering grounds. Adults had a mean of 2.8 species per bird in the fall and 4.3 species per bird on the wintering grounds. Young geese had 12 and 15 species in the fall and winter respectively, while adults had 13 species in the fall and 12 on the wintering grounds.

Five new parasites were acquired by young geese in the fall, including Echinoparyphium sp., Echinostoma revolutum, Apatemon anseris, Amidostomum anseris and one specimen of an acanthocephalan, Polymorphus contortus.

All except the latter were picked up by the adults in the fall as well. Seven more species, *Anomotaenia ciliata*, *Dicranotaenia multistriata*, *Retinometra sp.*, *Sarconema eurycerca*, *Amidostomum spatulatum*, *Capillaria obsignata* and *Tetrameres sp.*, were recovered for the first time from young geese on the wintering grounds. Seven helminths contracted on the breeding grounds were present in young geese in the fall; five of these species were present on the wintering grounds as well (Table 6).

Nematodes were the most abundant group of helminths in young geese on the fall migration and the wintering grounds, comprising 87 and 88% of the total number of worms in those periods respectively. Cestodes made up only 10% of the total in the fall and 7% in the winter. This compares with the faunas of adults which were composed of 94% nematodes and 2% cestodes in the fall, and 98% nematodes and 1% cestodes in the winter.

The intensity of infection with helminths remained at about the same level on fall migration as that encountered in young geese just before they left the breeding grounds, but increased to a peak (23.0 worms/bird) on the wintering grounds (Figure 10, Table 5). In the adults, the intensity of infection dropped abruptly in the fall (11.0 worms/bird) but rose again in the winter (32.0 worms/bird). There were no significant

differences between the median intensities in young and adult birds in either of these periods although the data from the wintering grounds may be unreliable in view of the small sample of young geese (9), and the range in 95% confidence limits (Figure 10) for the median intensities.

The prevalence and intensity of nematode infections in young geese increased through the fall and winter. Both measures decreased for cestodes while trematode burdens remained at about the same level. The intensity of infection with nematodes was comparable to that in adults for both the fall and winter although the winter data are again unreliable. However, the important point is that the nematode populations of young and adults were comparable by fall. The prevalence of infection with cestodes was significantly greater ($p < .001$) in young birds in the fall but was essentially the same as that of adults by the time the wintering grounds were reached.

The prevalence of infection with Tschert. krabbei and the prevalence and intensity of infection with T. tenuis in young geese in the fall were significantly greater than those in adults (Table 7). By the time the wintering grounds were reached, these measures were not significantly different. The median intensities of infection with E. crami were not significantly different

in the fall but the prevalence of infection was greater in adults. By the time the wintering grounds were encountered, the prevalences in young and adults were also essentially equal. On the wintering grounds, the prevalence of infection with *Amidostomum anseris* in young geese was greater than that in adults while *H. dispar* was found in a greater proportion of adults and in higher numbers.

Three species, *Tschert. krabbei*, *E. crami* and *T. tenuis* made up 90% of the total number of worms in young geese in the fall. Those three species and *N. attenuatus*, *Amidostomum anseris* and *H. dispar* comprised approximately 90% of the total number of worms in wintering young.

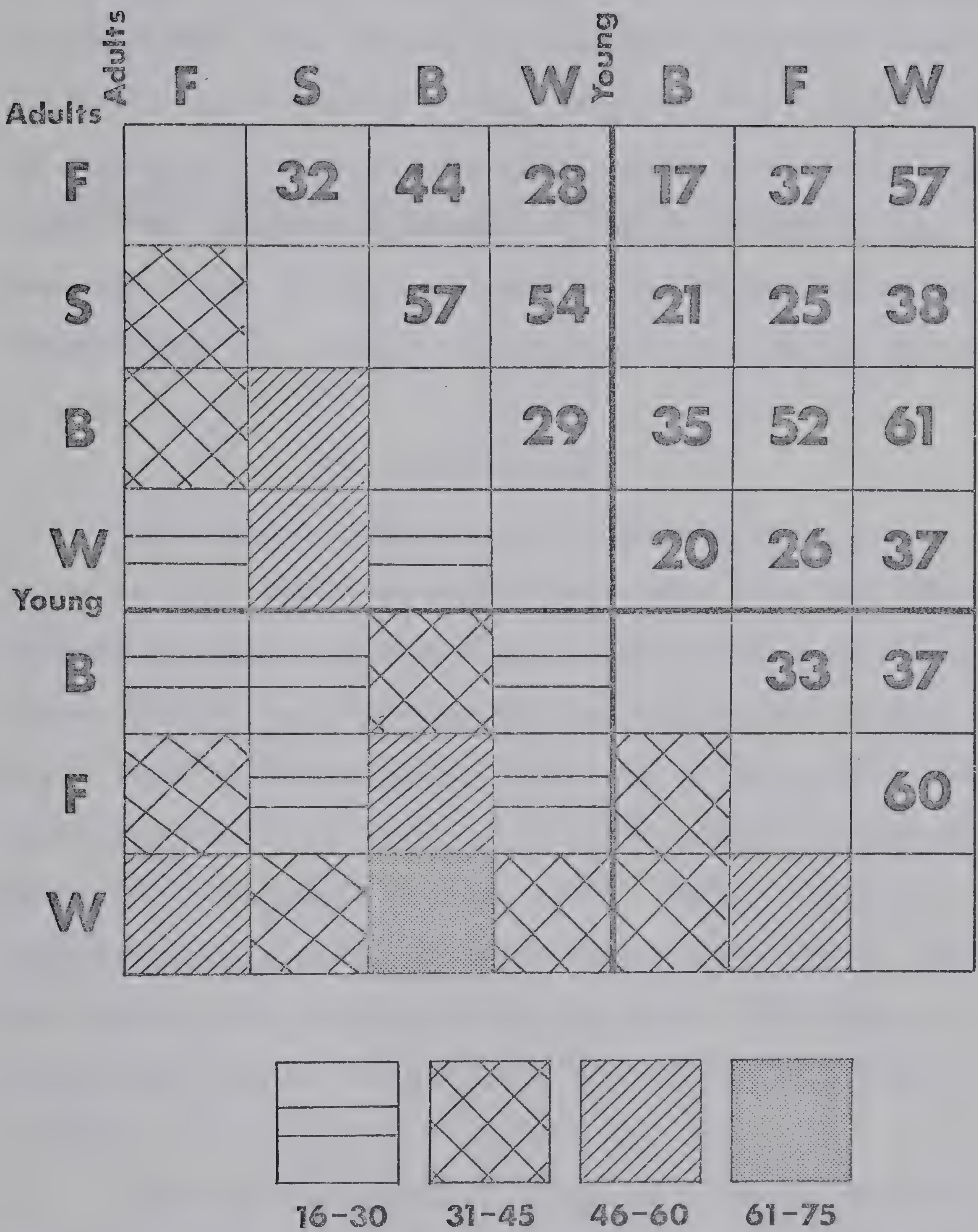
The diversity of the fauna of young snow geese was somewhat reduced on fall migration from the condition on the breeding grounds. Simpson's index (0.49) and the mean number of species per bird (2.9) indicated that the fauna was dominated by only a few species (the 3 above). Both these measures and the number of species present (12) were comparable to those of the fauna of adults (Simpson's index 0.52, 2.8 spp./bird, 13 species). The rarefaction index (10.6 spp./200 worms) was lower than that of the fauna of adults (12.4 spp./200 worms). By the time the wintering grounds were reached, all the measures of diversity for the fauna of young geese indicated a more

diverse fauna than those for the fauna of adults. Young geese had 15 species as opposed to 12 in adults, 4.8 species per bird as opposed to 4.3 in adults, Simpson's index 0.27 as opposed to 0.50 for adults and 14.8 spp./200 worms as opposed to 9.2 spp./200 worms in adults. The most important factor in the increased diversity of the fauna of young geese was the acquisition of a diverse nematode fauna and the presence of a more diverse cestode fauna. The young geese began acquiring new species of nematodes on fall migration, and by the time the wintering grounds were encountered, they had eight of the nine species of nematodes encountered in adults (p. 43). Simpson's index for the nematode fauna of wintering young (0.34) indicated that it was more equitably distributed than the nematode fauna of adults (Simpson's index 0.52).

The helminth faunas of young and adult geese were compared by means of indexes of similarity between all combinations of breeding ground, fall, winter and spring faunas. The results are summarized in a trellis diagram (Figure 13). The most obvious conclusion to be drawn from this information is that as the young geese approached the wintering grounds their helminth fauna became more similar to that of breeding adults. The greatest similarity of faunas (61% similar) was between that of adults on the breeding grounds (combined June to August 15 samples) and

Figure 13. Trellis diagram showing indexes of similarity between the helminth faunas of young and adult snow geese from different periods.

F = Fall migration, S = Spring migration, B = Breeding grounds, W = Wintering grounds.


Adults
F S B W
Young
B F W
Adults
F 32 44 28 17 37 57
S 57 54 21 25 38
B 29 35 52 61
W 20 26 37
Young
B 33 37
F 60
W
16–30
31–45
46–60
61–75

that of wintering young. Indexes of similarity between the faunas of birds taken at the same time were consistently about 40%. The increasing similarity of the faunas parallels the tendency of the fauna of young geese towards an abundance and diversity approaching the adults' condition. The increasing abundance and diversity of the nematode fauna of young geese was the major factor in determining the greater similarity of the helminth faunas.

Discussion

The rapid accumulation of parasites by young birds in this study compares favourably with the findings of Wehr and Herman (1954), which indicated that young Canada geese acquired many of their parasites within the first week or two of life. The same situation has been described for other young anatids (Cornwell and Cowan, 1963; Buscher, 1965; Graham, 1966). There is general support in this study as well for Dogiel's (1964) idea that precocious young pick up helminths with complex life-cycles first, rather than ones with direct life-cycles.

Two of the cestodes acquired by young geese in their first ten days of life (Tschert. krabbei and R. longivaginata) and the first nematode acquired (T. tenuis), were present in adult geese throughout the nesting period

and were the most common cestodes and nematode in adults after mid-summer. Young geese were undoubtedly infected on the nesting area from cysticercoids and larvae that originated from infections in adults. Other workers have shown a similar situation, where young waterbirds they examined were infected initially with parasites specific to, or very common in, the adults (Ginetsinskaya, 1952; Gallimore, 1964; Graham, 1966). The infective pool or "nucleus" established by infections in adults in areas where the young began feeding after hatching was probably the important factor.

Heavy burdens of cestodes have been reported previously from young geese (Schiller, 1954; Zaskind, 1963; Shevtsov, 1964; Holmes, in Barry, 1967). According to Schiller (1954) and Barry (1967), young geese generally eat more animal food than do adults. My own observations, though not quantified, support this view. Cestodes, of course, are biohelminths and would be expected to reflect the amount of animal food in the diet. Cestodes were also more important in the helminth fauna of adult geese on the breeding grounds (p. 51) than elsewhere, so it is not surprising that they would be the most common group of helminths in young geese on the breeding area. The nuclei of infection for _Tschert_. _krabbei_ and _R_. _longi-vaginata_ were supplied predominantly by adult snow geese,

while other cestodes abundant in young geese (D. barrowensis, D. lanceolata and Tschert. setigera) probably originated from extensive infections in brant arriving at Anderson River in the spring (p. 115).

An important factor in the production of high populations of cestodes in young geese was the rapid maturation of many of the cestodes. The finding of mature, egg producing infections of D. barrowensis, D. lanceolata and Tschert. setigera in young geese less than two weeks of age in this study suggests that prepatent periods for some of them may be even shorter than those reported (15-25 days and 13-14 days for D. lanceolata and Tschert. setigera respectively) (McDonald, 1969b). Rapid maturation of worms in the large population of young geese at Anderson River would have ensured an early dispersal of large numbers of cestode eggs into the environment and widespread infection of intermediate hosts. The development of the cysticercoid of D. lanceolata to infectivity takes 10-18 days at 18-20 C (McDonald, 1969b) which means that the generation time of this species is relatively short. In the six weeks spent on the breeding grounds, young geese could have been infected with several generations of worms, allowing the accumulation of large populations. Similar developmental characteristics for the other

cestodes could help to explain their abundance as well.

Schiller (1954) proposed a relationship between the rapid maturation of cestodes in large populations of young geese on the Yukon-Kuskokwim Delta, and the density of cestode eggs (his Figure 6, p. 197) which could have been instrumental in the production of heavy cestode burdens. The scheme proposed there is generally adequate for a description of the build up in egg density at Anderson River. However, recent evidence has indicated that Cyclophyllidean eggs are susceptible to freezing (Kisielewska, 1957) so that egg density on the arctic breeding grounds would be nil at the time geese began arriving in the spring. In addition the number of viable eggs would probably decline very abruptly to zero with the onset of freezing temperatures in the fall. This does not preclude the possibility of the occurrence of over-wintering infections in intermediate hosts, so that some infective material may be available to birds arriving in the spring.

Two of the three nematodes encountered in young geese on the breeding grounds (E. crami and T. tenuis) showed definite peaks in abundance in the adults during the summer. As indicated earlier (p. 52) both were considered true ubiquists and were present in adult snow geese upon arrival at Anderson River at sufficient levels

to have produced adequate nuclei of infection for the young. Considering the probable short developmental period outside the host required for both species (p. 53), they seemed rather late in appearing in young geese, particularly E. crami. In addition to feeding on more animal material, young geese may feed on different plant material than adults at least until late in the summer. This could explain the delay in appearance of the two nematodes. It may also help to explain the greater prevalence and intensity of infection in adults once the worms were acquired by the young.

The paucity of trematodes and nematodes in young geese on the breeding area made their fauna different than that of adults, even though the various indexes indicated that their fauna was approaching that of adults in diversity. The increase in similarity of the helminth fauna of young snow geese in the fall and winter to that of breeding adults was due to the acquisition of the characteristic nematode fauna after the breeding area was abandoned for points further south. The time spent on the fall migration and wintering grounds was very important in the characterization of the helminth fauna of young snow geese. The helminths acquired by young geese on those areas were present in adults in the spring, lost on the breeding grounds and reacquired again in the fall

or winter. *Amidostomum spatulatum*, which was considered earlier to be a spring parasite of adults (p. 53) was not acquired by young geese even on the wintering area (except for one worm in one bird). In all probability, this parasite would be acquired when the young geese make their first northward migration.

The environment within the gut during long migration flights may not be as important a factor as previously considered in the general loss of worms that occurred on fall migration. The greater number of species of cestodes (some of which were also found on the breeding grounds) in young geese as compared to the adults, and the increased burdens of *Tschert. krabbei* and *T. tenuis* in young geese (they decreased in adults) on fall migration suggests that a variety of factors which influence the availability of infective stages may be more important.

Generally, the parasites of young lesser snow geese were acquired throughout the range of the bird and no single area can be singled out as the region in which helminths were acquired. Obviously, the cestodes were primarily breeding ground forms. Trematodes, generally parasites of migrating adults and more characteristic of geese on southern portions of their range, were predictably acquired by young geese after they left the breeding

grounds. The exception (N. attenuatus) was a ubiquist in adults. Two of the nematodes (E. crami and T. tenuis) were acquired steadily throughout the range of the host. Both were true ubiquists in adults. H. dispar, most prominent in wintering adults, showed basically the same pattern in young geese. The other species did not show up until the wintering grounds were reached. One of them (S. eurycerca) was a northern parasite of adults. Another (A. spatulatum) was basically a spring parasite of adults and was very rare in young geese. It would seem that a bird must complete an entire yearly cycle and pass through the entire circuit of ecologico-geographical areas before its characteristic fauna of helminths has been acquired.

V. THE CIRCULATION OF HELMINTHS AMONG THE GEESE AT ANDERSON RIVER

Introduction

The overlap in species reported from various waterfowl (references in McDonald (1969a)) suggests that there is a considerable circulation of helminths among them, particularly among those breeding in the same area. Wisniewski (1958) and his co-workers in Poland have provided some evidence for the extent of that exchange. Sulgostowska (1963) concluded that the most abundant host on a given lake is responsible for the characterization of the trematode fauna of birds ecologically associated with it, a generalization which can be extended to entire helminth faunas (Graham, 1966).

Lesser snow geese are the most abundant of the geese in the Anderson River Delta, with progressively lower populations of brant and white-fronts. Under these conditions, snow geese could be expected to occupy a central role in the circulation and maintenance of the helminths found there. Large numbers of other waterfowl, particularly ducks and swans, use the delta and might play some role in the circulation of helminths of the geese.

The degree of association of the geese with each other might also affect the exchange of helminths. The geese are separated geographically on their wintering grounds and use at least partially different migratory routes to the Anderson River Delta; this probably influences the kinds of helminths which they bring to the breeding grounds. There is little contact between white-fronts and the other geese on the breeding grounds, but snow geese and brant are frequently in close contact during the brood-rearing period.

The helminths recovered from adult geese at Anderson River have been surveyed in Section II, and the seasonal changes in the communities of helminths in adult and young snow geese were examined in detail in Sections III and IV. The purpose of this section is to examine the interactions between the communities of helminths of the geese at Anderson River.

Materials and Methods

Geese were collected as they arrived at the delta in the spring, when the geese had left the nesting areas and had begun to frequent favored feeding areas (approximately two weeks after the hatch), and just before they were ready to leave the delta in mid-August. These collections were designated as "arrival", "mid-summer", and "late-summer" samples, respectively. The timing of these collections for

snow geese has been defined (p. 31). Other geese were taken to correspond as closely as possible to the snow geese.

The mid-summer sample of brant was taken during the third week of July; the late summer sample from August 8-15. White-fronted geese were collected whenever possible; the mid-summer sample includes all geese collected in July, the late-summer sample those collected in the first week of August. Most of these birds were taken from upstream locations.

Indexes of similarity were calculated as above (p. 15). Species overlap indexes (Jaccard's Coefficients) were calculated from the formula 100 X C/(a+b-c) where c = the number of species common to the two samples, a = the number of species in one sample and b = the number of species in the other sample. For the purposes of these two comparisons, samples of young geese have been combined within each species.

Differences between groups of indexes were tested for significance by the Mann-Whitney U test (two sample rank comparison test), the same as that used above (p. 65) for testing for the significance of differences between medians.

Results and Discussion

Thirty-three species of helminths were recovered from young and adult geese. The relative prevalences of

infection with each helminth in each host group are presented in Table 8. Complete data on prevalence and median intensity of infection are presented in Appendices II and III.

Eighteen species were "common" (present in 25% or more of at least one sample of a host group) (Table 8). Most of these species were abundant in several host groups over much of the summer. The other 15 species were rarely present in more than 10% of any sample of geese and were usually present in low numbers.

Young geese were infected with 18 species of helminths, only one of which (Dicranotaenia coronula) was not recovered from adult geese. Fourteen of these helminths were common species (Table 8). In effect, young geese acquired the same helminths as those present in adults.

Species overlap indexes (Jaccard's Coefficients) and indexes of similarity were calculated and arranged in trellis diagrams (Figures 14 and 15). Samples were arranged along the axes of the diagrams in species groups and in chronological order. These indexes provided different measures of the degree of exchange of helminths among host groups.

In general, intraspecific overlap indexes and indexes of similarity between samples of adult geese were significantly greater than interspecific ones (Mann-Whitney U test, $p < .001$). Samples of white-fronts and brant had

Table 8. Seasonal changes in relative prevalences of infection with helminths in geese at the Anderson River Delta, N.W.T.

Host	Snow Geese					White-fronts					Brant		
Age	Adults			Young		Adults			Young		Adults		
Sample / Helminth	*A	M	L	M	L	A	M	L	M	L	A	M	L
TREMATODA													
Echinostoma revolutum+	**x					xx	xx						
Catatropis pricei+											xxx		
Notocotylus attenuatus+	x	x	x	o	xx	o	x	xx	xxx	xxx	o		
Paramonostomum sp.											o		
Zygocotyle lunata	o	x	x										
Ornithobilharzia pricei												o	
Apatemon anseris+	x												
CESTODA													
Anomotaenia ciliata		o										o	
Cloacotaenia megalops		o											
Dicranotaenia coronula					o								
Diorchis stefanskii				o	o						o	x	x
Drepanidotaenia barrowensis+		x		x	xxx	xx	xx			xx	xx	xx	xx
Drepanidotaenia lanceolata+		x	xx	x	xxx			xx			x	xxx	
Fimbriaria fasciolaris		o		x									
Parabisaccanthes philactes+		o		x						xxx	x	o	x
Retinometra longivaginata+	xx	xxx	xxx	x	x		o				xxx	xx	xx
Retinometra venusta+						o	xx	xx		x			
Sobolevicanthus gracilis				x	x							o	
Tschertkovilepis krabbei+	xxx	xxx	xxx	xx	xxx	xxx	xxx	x		xxx	xxx	xxx	xx
Tschertkovilepis setigera+	o	x	x	x	xxx			o		x	xxx	xxx	xx
Wardium creplini							o						
Wardoides nyrocae	o										x		o
Hymenolepis sp.											x	o	
NEMATODA													
Sarconema eurycerca+		x	o			xxx	xxx	o					
Heterakis dispar+		x	xxx	x	xx						xx	xxx	xx
Tetrameres fissispina+											xx	xx	xx
Tetrameres sp.+	x	xx	x			xx	x	xxx					
Amidostomum anseris+	xx					x	xx			x	o	o	
Amidostomum spatulatum+	xxx	xxx	xxx			xxx	xx	xxx		o	o		
Epomidiostomum crami+	xxx	xxx	xxx		x	xxx	xxx	xxx		xx	xxx	xxx	xx
Trichostrongylus tenuis+	x	xxx	xxx	x	xxx	x	x	xx	x	xx	xxx	xxx	xx
Capillaria obsignata	o						o						
Capillaria sp.	x	x	x										

+ = "common" species

* A= Arrival sample, M= Mid-summer sample, L= Late-summer sample.

**o = present in a single bird, x= in 25% of a sample, xx= in 25-40%, xxx= in

Figure 14. Trellis diagram showing species overlap indexes (Jaccard's Coefficients) between the helminth faunas of samples of geese at Anderson River, N.W.T.

A = Arrival sample, M = Mid-summer sample, L = Late-summer sample, Y = Young geese.

		White-fronts A 11	White-fronts M 14	White-fronts L 9	White-fronts Y 10	Snows A 15	Snows M 18	Snows L 13	Snows Y 14	Brant A 18	Brant M 16	Brant L 13	Brant Y 16
White-fronts	A 11*		78	67	62	44	38	41	25	32	23	20	29
	M 14			53	50	53	39	42	27	37	25	29	30
	L 9				58	41	42	69	28	29	19	22	25
	Y 10					39	40	35	41	47	37	35	44
Snows	A 15						43	56	32	38	24	27	35
	M 18							72	52	44	42	35	48
	L 13								42	41	32	37	38
	Y 14									45	58	50	88
Brant	A 18										62	55	62
	M 16											53	60
	L 13												53
	Y 16												

16-30 31-45 46-60 61-75 76-90

*number of species

Figure 15. Trellis diagram showing indexes of similarity between the helminth faunas of samples of geese at Anderson River, N.W.T.
A = Arrival sample, M = Mid-summer sample,
L = Late-summer sample, Y = Young geese.

		White-fronts A	White-fronts M	White-fronts L	White-fronts Y	Snows A	Snows M	Snows L	Snows Y	Brant A	Brant M	Brant L	Brant Y
White-fronts	A		81	74	11	34	41	33	19	21	20	13	12
	M			72	18	36	43	36	19	18	19	13	11
	L				15	39	56	52	26	29	26	25	24
	Y					7	9	9	15	13	12	11	13
Snows	A						52	42	13	19	21	17	12
	M							82	36	41	40	48	33
	L								40	43	43	60	39
	Y									65	63	54	55
Brant	A										77	68	51
	M											73	55
	L												58
	Y												

0–15 | 16–30 | 31–45 | 46–60 | 61–75 | 76–90

significantly higher intraspecific indexes ($p < .05$) than interspecific ones with one exception; there was no significant difference in species overlap between the intraspecific white-front indexes and the white-front-snow goose indexes. Intraspecific snow goose indexes were not generally greater than interspecific ones except that species overlap between snow goose samples was significantly greater than the overlap between the samples of snow geese and brant.

These relationships suggest that white-fronts and brant had relatively distinct communities of helminths while that of snow geese was intermediate between the two but tending toward white-fronts in species composition. Species overlap between snow geese and white-fronts was significantly greater ($p < .05$) than that between snow geese and brant. This relationship is further supported by the fact that the faunas of white-fronts and brant had greater overlap and similarity to the fauna of snow geese than they had to each other ($p < .05$ in both cases).

Young white-fronts and young brant had greater species overlap and similarity with their respective adults than with the adults of other species ($p < .05$ in all cases). Young snow geese, on the other hand, overlapped with adult snows and brant equally and had a fauna more similar to that of brant than to that of their parents.

Young white-fronts overlapped relatively strongly

with all host groups (Figure 14) but showed very little similarity to any of them (Figure 15). They had few helminths, most of which were common species (Table 8) (thus the high overlap) but none of these were abundant (Appendix III) (thus the low similarities). Those helminths which were abundant in young white-fronts were not present or not abundant in other geese.

The communities of helminths in young snows and brant were most strongly influenced by those of adult geese (particularly adult brant). This was apparently not true of young white-fronts.

Changes in both overlap and similarity between samples of geese occurred over the summer. These changes were of different magnitudes depending on the samples comparied but none were testable for significant differences. However, general trends could be outlined. Hereafter references to specific host groups will refer to their helminth faunas.

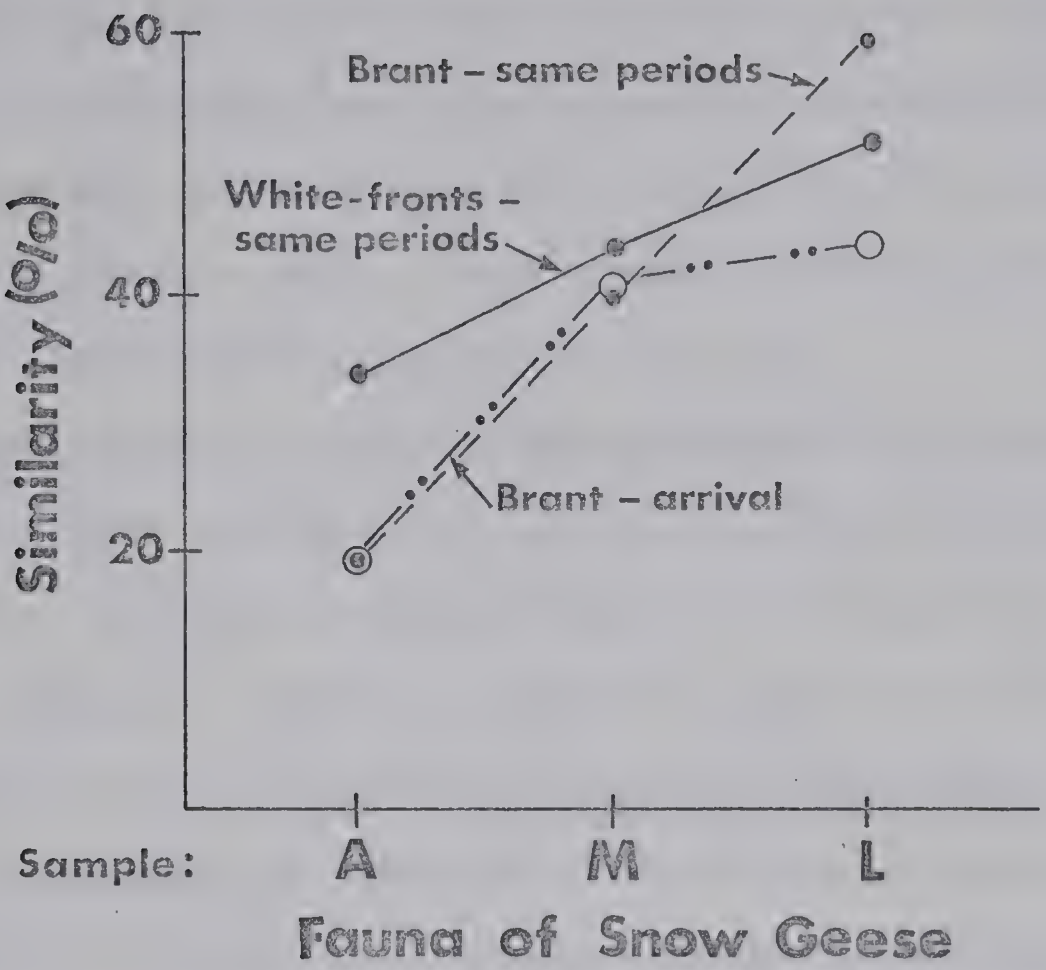
Snow geese and white-fronts overlapped strongly and were relatively similar upon arrival. The overlap between arrival samples of snow geese and brant was of the same magnitude but their similarity was much lower. Snow geese and white-fronts increased in overlap and similarity as the summer passed. The latter of these trends is illustrated in Figure 16 (white-fronts-same periods). The similarity of snow geese and brant also increased with time (Figure 16,

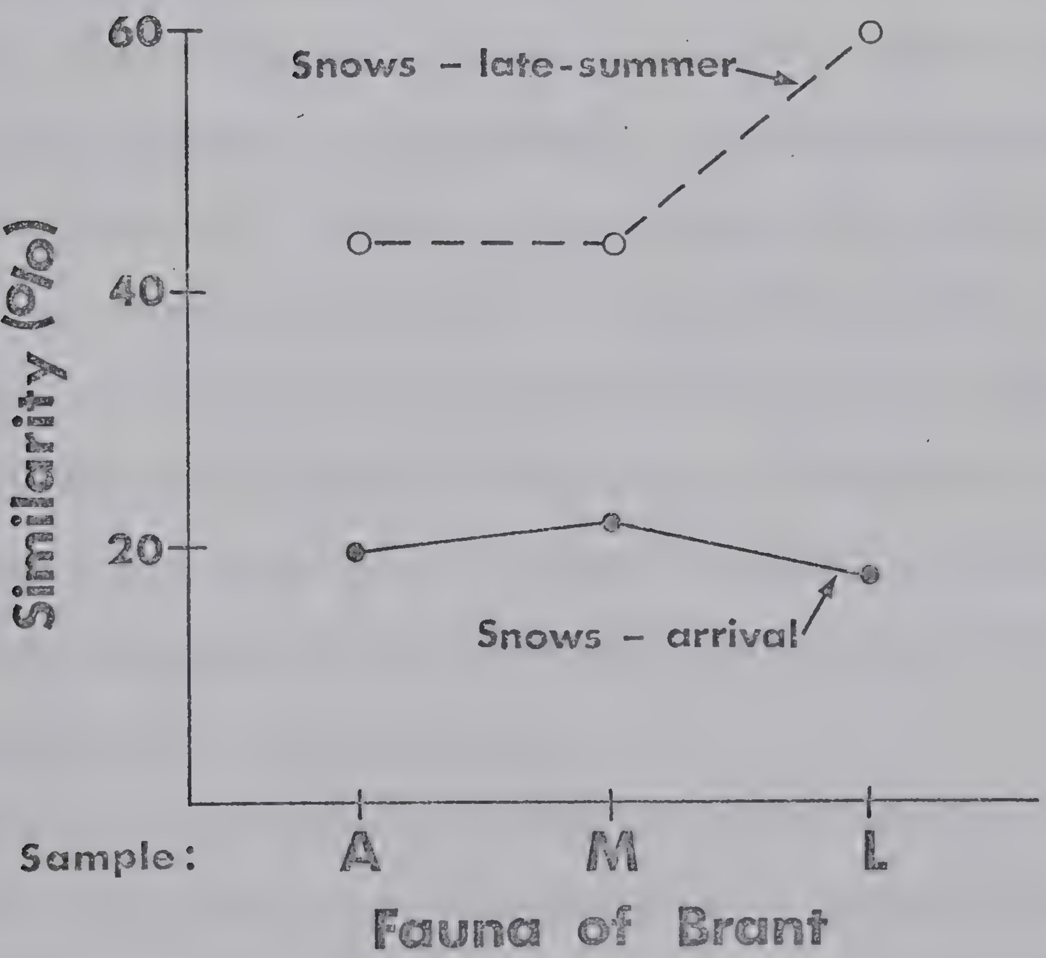
Figure 16. Similarity of the faunas of selected samples of white-fronts and brant to the faunas of all samples of snow geese.

A = Arrival sample, M = Mid-summer sample,
L = Late-summer sample.

Figure 17. Similarity of the faunas of the arrival and late-summer samples of snow geese to the faunas of all samples of brant.

A = Arrival sample, M = Mid-summer sample,
L = Late-summer sample.


60
40
20
Similarity (%)
Brant – same periods
White-fronts – same periods
Brant – arrival
Sample: A M L
Fauna of Snow Geese


60
40
20
Similarity (%)
Snows – late-summer
Snows – arrival
Sample: A M L
Fauna of Brant

Brant-same periods) while their species overlap did not change. White-fronts and brant showed relatively little overlap and even less similarity. Their species overlap decreased with time while their similarity remained essentially unchanged (Figures 14 and 15).

The increase in species overlap between snow geese and white-fronts was not due to an extensive exchange of helminths. They consistently shared 8 to 9 species from sample to sample. Only two species acquired by white-fronts after they arrived (Retinometra longivaginata and Capillaria obsignata) could be traced to snow geese (Table 8); both were present in one white-front in mid-summer. Sarconema eurycerca was the only helminth acquired by snow geese which was traceable to white-fronts. When their overlap was greatest (late-summer), they had minimum numbers of species. Changes in overlap were probably due to a loss of unshared species of helminths rather than the acquisition of new species by either, or both. This suggests that there was little exchange of helminths between white-fronts and snow geese on the breeding grounds. The nature of the community of helminths in young white-fronts also supports this contention.

There was a greater exchange of helminths between snow geese and brant than indicated by changes in overlap indexes. Several species brought to the area by brant were acquired by snow geese and both picked up some

cestodes which neither brought to the delta in the spring (Table 8). However, one or the other host lost species they had shared previously and gained others not acquired by the other host. As a result, their species overlap indexes changed little.

The snow geese became more similar to the arrival sample of brant as the summer passed. This is demonstrated in Figure 16 where all the samples of snow geese were compared to the arrival sample of brant. Figure 17 (Snows-late-summer) shows essentially the same thing. That the converse was not true is shown by Figure 17 (snows-arrival).

The convergence of the community of helminths in snow geese toward the community brought to the area by brant was due to two main factors, 1) snow geese acquired parasites introduced to the area by brant and 2) snow geese lost their heavy population of Amidostomum spatulatum as time went on (Figure 8, p. 49). The latter factor had the effect of equalizing the importance of other shared species in the two communities in the absence of any change in their numbers.

What species of helminths were most important in the exchange among geese at Anderson River? None of the "uncommon" species were abundant enough to have influenced their helminth communities. Eight species (Zygocotyle lunata, Anomotaenia ciliata, Cloacotaenia megalops, Diorchis stefanskii, Fimbriaria fasciolaris, Sobolevicanthus gracilis

and *Wardoides nyrocae*) are common parasites of ducks and all but the latter were recovered from ducks there. They probably formed a large segment of duck to geese exchange. *Wardium creplini* is a relatively common cestode of swans and may have been acquired by white-fronts from swans. Two other uncommon species (*Hymenolepis* sp. and *C. obsignata*) were found only in adult brant and snow geese respectively and were not exchanged. *Capillaria obsignata* may have been acquired from galliformes on areas other than the breeding grounds since it is a characteristic parasite of galliformes (McDonald, 1969b).

Four typical goose parasites were not exchanged (*Ornithobilharzia pricei* and *Capillaria* sp.) or were not transmitted at all at Anderson River (*Apatemon anseris* and *Paramonostomum* sp.).

Four of the common species were either not transmitted on the breeding grounds (*Catatropis pricei*) or were not exchanged between geese (*Echinostoma revolutum*, *Retinometra venusta* and *Tetrameres fissispina*). The latter group may have been exchanged to some degree with ducks. The remaining 14 common species were present in at least two host groups for most of the summer and comprised 86-99% of the total number of worms in each sample. These 14 species were the major determinants of the species overlap indexes and the indexes of similarity covered above. The description of the patterns of exchange of these helminths among

the geese entailed measuring their populations in the geese (Appendices II and III) and considering the concept of an "infective pool".

Mature helminths release preproductive products (eggs, larvae) into the environment (or to vectors). This shedding of reproductive products builds up a "pool" of infective stages which may provide, directly or indirectly, a source of infection to the same or other hosts using the area. The development of an infective pool is necessary for the transmission and exchange of helminths. Definitive hosts contribute to this pool and draw from it for new infections. The only available estimate of the magnitude of each host group's contribution to the pool was an indirect one, namely, the number of mature worms in the population.

An estimate of the number of each species of helminth per hundred birds (prevalence times median intensity) was calculated. This was done for each of the helminths in each host group during each of the collection periods. These estimates were multiplied by a weighting factor, which is a subjective estimate of the relative abundance of each host group and the degree of association of that group with the others. This weighting factor which can be called the "effective density" was assigned as follows: adult snow geese 1.0, young snow geese 2.0, adult brant 0.25, young brant 0.50, adult white-fronts 0.10, young

white-fronts 0.20. The timing of the samples made three estimates of the status of each pool possible. The results are presented in pie diagrams (Figures 18 and 19) where the diameter of each pie is proportional to the total number of mature worms in all host groups.

Figure 18a represents the number of infective pools (of the 14 species) established and then maintained by each of the host groups. It was derived by converting the contribution of each host group to a proportion of the total infective pool for each of the 14 helminths. This was done separately for each sample. These proportions were then summed for each host group in each sample, thereby arriving at a value which was equivalent to the number of species out of 14 that were established (in the arrival sample) or maintained (mid- and late-summer samples) by each host group. The diameter of each pie in Figure 18a is constant because the total number of species considered was constant.

Adult snow geese and brant brought about equal proportions of the initial pools or nuclei of infection to the delta in the spring. Each established the nucleus for the equivalent of about six species. White-fronts contributed the nucleus for the equivalent of two species.

Snow geese and white-fronts (including their young) became more important in the maintenance of the pool of infective stages over the summer while the role of brant diminished (Figure 18a mid- and late-summer). In all cases,

Figure 18. Diagrammatic representation of the roles played by various host groups in the establishment and maintenance of pools of infective stages for some "common" helminths exchanged among the geese at Anderson River, N.W.T.

A. Combined pool for the 14 "common" species

B. *Retinometra longivaginata*

C. *Epomidiostomum crami*

D. *Amidostomum spatulatum*

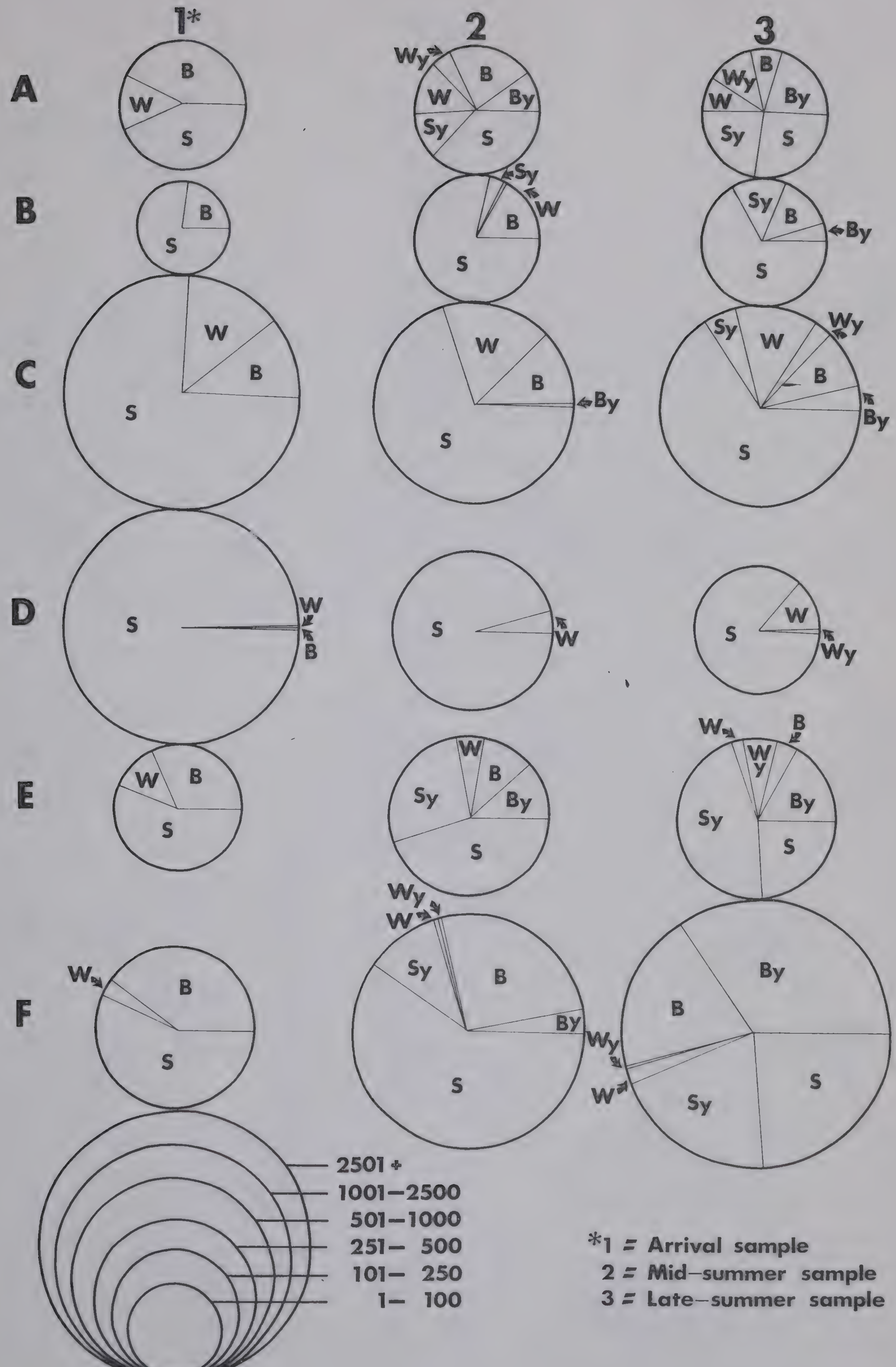
E. *Tschertkovilepis krabbei*

F. *Trichostrongylus tenuis*

S = Snow adults, Sy = Snow young,

W = White-front adults, Wy = White-front young,

B = Brant adults, By = Brant young.



1*
2
3
A
B
C
D
E
F
W
B
S
Wy
By
Sy
2501 +
1001–2500
501–1000
251– 500
101– 250
1– 100
*1 = Arrival sample
2 = Mid–summer sample
3 = Late–summer sample

Figure 19. Diagrammatic representation of the roles played by various host groups in the establishment and maintenance of pools of infective stages for some "common" helminths exchanged among the geese at Anderson River, N.W.T.

A. *Drepanidotaenia barrowensis*

B. *Drepanidotaenia lanceolata*

C. *Tschertkovilepis setigera*

D. *Heterakis dispar*

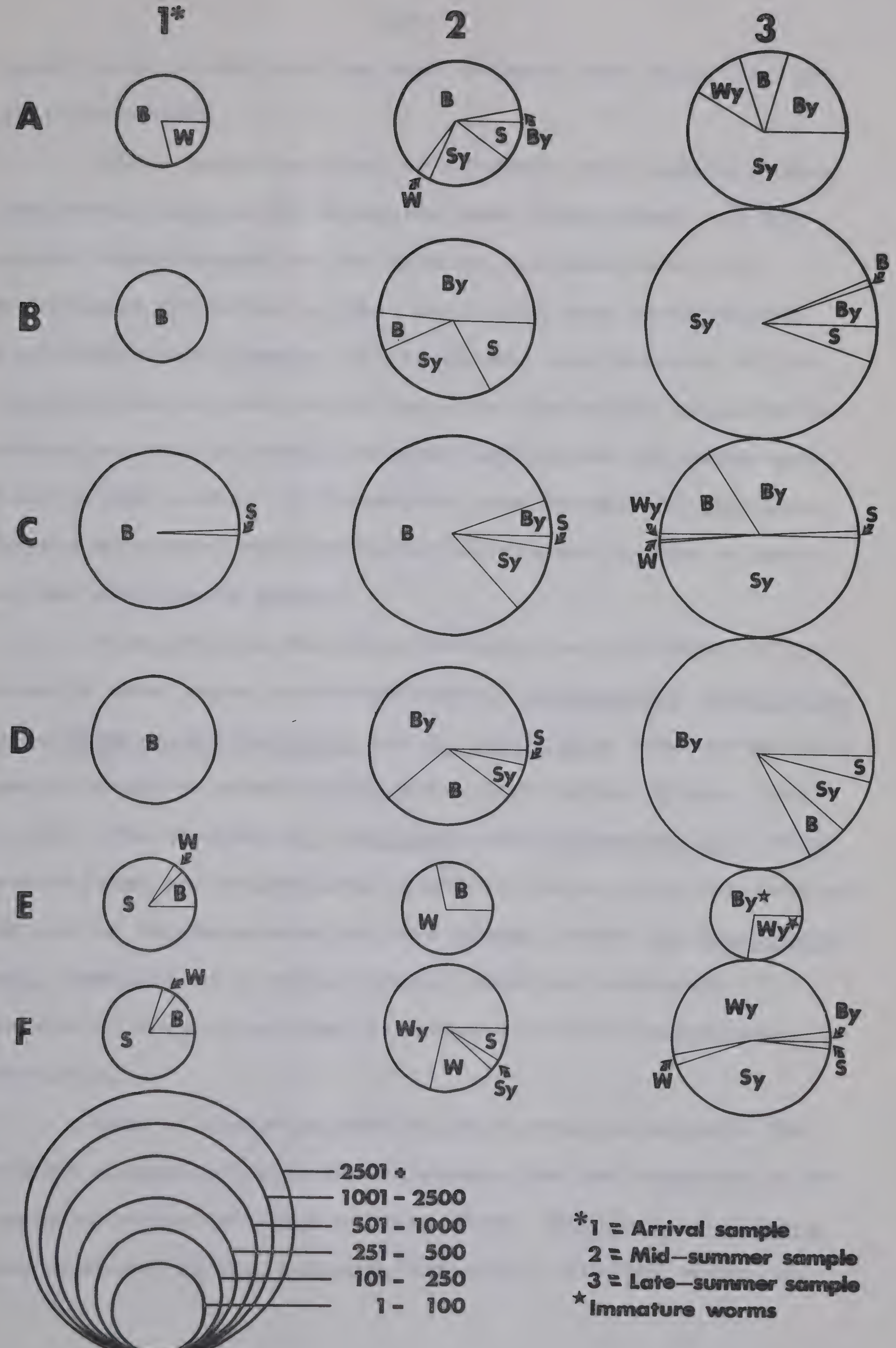
E. *Amidostomum anseris*

F. *Notocotylus attenuatus*

S = Snow adults, Sy = Snow young,

W = White-front adults, Wy = White-front young,

B = Brant adults, By = Brant young.


1*
2
3
A
B
C
D
E
F
B
W
By
S
Sy
Wy
By*
Wy*
2501 +
1001 - 2500
501 - 1000
251 - 500
101 - 250
1 - 100
*1 = Arrival sample
2 = Mid-summer sample
3 = Late-summer sample
*Immature worms

young geese contributed as much or more than their adults in late-summer.

Three basic patterns of exchange were apparent when individual species of helminths were considered. 1) Helminths were brought to the area by one main host and maintained primarily by that host with some contribution from other host groups. 2) Helminths were brought to the delta by one or more hosts and were thereafter acquired by others so that no one host group maintained the major portion of the pools. 3) Helminths were brought to the area by one main host but thereafter maintained by one or more of the other host groups.

Helminths in the first category were brought to the area by snow geese or white-fronts. Retinometra longivaginata, Epomidiostomum crami and A. spatulatum were established and maintained primarily by adult snow geese (Figure 18b, c, d). Two species (S. eurycerca and Tetrameres sp.) were established and maintained by white-fronts. The populations of all of the helminths in this group, except R. longivaginata, remained at a rather steady level or decreased markedly, suggesting that relatively little transmission occurred.

Some of the helminths in this group illustrate the effect of habitat on helminth faunas and how segregation of hosts affected exchange between them. Sarconema eurycerca was abundant in white-fronts but only a limited amount of

exchange occurred with snow geese and none with brant (Table 8). The infective pool for this filarid was probably present in black flies (Simuliidae) or other biting insects which were abundant in dense cover favoured by white-fronts. A close association of vector and definitive host was responsible for the prevalence of *Sarconema* in white-fronts. Other geese had little opportunity to become infected since neither biting insects nor white-fronts were abundant on areas of the delta used by them. Swans, on the other hand, are known to be hosts of *S. eurycerca* (McDonald, 1969b) and were generally more closely associated with white-fronts than were snows or brant. Swans may have been important in the circulation of this helminth.

An interesting aspect of the host-parasite relationship involving *S. eurycerca* was the apparent lack of pathology in white-fronts, even in infections of up to 18 worms. Gross pathology was always noted in snow geese and Kluge (1967) and Holden and Sladen (1968) reported pathology in swans. This is suggestive at least (along with the data presented above) that white-fronts serve as normal reservoir hosts and that pathological infections in swans and snow geese are the result of abnormal host-parasite relationships. This could be very important in terms of the competence of the latter hosts in maintaining infective pools.

Amidostomum spatulatum (Figure 18d) was very abundant

in snow geese but was apparently not transmitted to them on the breeding grounds. Transmission to white-fronts apparently did occur (prevalence and intensity increased over the summer, Table 8) but due to their upstream location, the pool of infective stages maintained by snow geese in the middle and outer delta was probably not the source of new infections in white-fronts. As pointed out earlier (p. 53), snow geese acquired the majority of their infections along the spring migration route in areas of similar ecology to those used by white-fronts throughout the summer but frequented by snow geese only on spring migration. White-fronts may have been exposed to the infective pool (which was the original source of infections in snow geese and the continuing source for infections of white-fronts) throughout the summer.

In view of the abundance of _A. spatulatum_ in snow geese in the spring, it is likely that they were responsible for the establishment of the pool of infective stages upstream to the Anderson River where ecological conditions were conducive to transmission. Thus infections in white-fronts were probably the result of an exchange with snow geese which occurred before the snows reached their nesting sites on the middle and outer delta. Snow geese carried their _A. spatulatum_ population with them to their breeding areas but for unknown reasons, a competent infective pool was apparently not established there. Proper conditions

for larval development may not have been present on the delta while they were apparently present further upstream in areas used by white-fronts. Some inhibiting factor on the delta, such as the high salinity of the soils (see Barry, 1967) or flooding of the area may have been responsible for these differences. At any rate, differences in the ecologies of their preferred habitats produced differences in the degree of exposure of white-fronts and snow geese to the pool of infective stages of A. spatulatum. Their segregation on the breeding grounds precluded any further exchange of the helminth between them.

Epomidiostomum crami (Figure 18c) was abundant in all three species of geese and was transmitted to the young of all three (Table 8). However, snow geese contributed the major portion of infective stages mainly because of their greater density. This helminth also appears to be somewhat better adapted to snow geese and white-fronts.

Infections in snows and white-fronts were most frequently encountered under the crushing plates with less frequent infections of the lining and muscularis. In brant, infections were encountered only in the muscularis. In any of the geese, infections in the latter location produced necrotic lesions surrounded by fibrous connective tissue and infiltrating leucocytes (Figure 20). Because of their more frequent occurrence in the muscularis of brant, infections in brant are probably more pathogenic than are

Figure 20. Section of gizzard muscularis infected with *Epomidiostmum crami* (Mallory's Triple Stain).

those in the other hosts. The shedding of eggs from lesions may also be difficult unless the worms migrate out (no evidence of this was seen except in the other hosts). Such infections could be a dead end as far as the worm is concerned, so that the contributions of brant to the infective pool (Figure 18c) may have been much less than indicated.

Tschertkovilepis krabbei and Trichostrongylus tenuis were the only helminths in group two. They were brought to the delta by all three species and were acquired by the young of all (Figure 18e, f). Transmission and exchange of these helminths was extensive with young and adult snow geese contributing most to the pools of infective stages because of their greater density.

The greatest number of species fell into the third category. Three of these species (Drepanidotaenia barrowensis, Drepanidotaenia lanceolata and Tschertkovilepis setigera), were brought to the delta by brant but were maintained primarily by young snow geese (Figure 19a, b, c). Adult snow geese and young brant were also relatively important contributors, particularly at mid-summer. Heterakis dispar was brought to the breeding grounds by brant but was maintained primarily by young brant (Figure 19d). In all cases, the populations of individual worms increased dramatically over the summer, indicating that transmission and exchange was extensive.

These helminths, along with those in the second category, are the best examples of the significant exchange which occurred between snow geese and brant and explain, in part, the great similarity of the faunas of young snows and adult brant.

The third category also contained *Amidostomum anseris* which was brought to the area primarily by snow geese (mostly because they were most abundant) and was thereafter maintained by other adult geese (Figure 19e). The population of the worm decreased to the extent that only a few immature worms were present in young brant and white-fronts at late-summer. Transmission of the worm at Anderson River was minimal.

The other species in the third category (*Notocotylus attenuatus* and *Parabisaccanthes philactes*) were brought to the area by snow geese and brant respectively, but were maintained primarily by young white-fronts (Figure 19f). However, young white-fronts were taken from upstream locations where they could have had little contact with the pools established by snow geese or brant. Infections in ducks may have been the major source of the pool of infective stages for *N. attenuatus* (a common helminth of ducks) while swans may have provided the major source of infection with *P. philactes* (one of four swans examined had 160 *P. philactes*). The upstream location of white-fronts would have made contact with these latter host groups more likely

than contact with other geese.

General Discussion

There was apparently little exchange of helminths between geese and other anseriformes. A relatively large proportion (9 of 33) of the species recovered could be traced to ducks or swans, but none of them was very abundant in the geese (in total, only 0.5% of the individual worms) so that the degree of exchange was small. In addition, only one helminth was present which could be traced to birds other than waterfowl. This is suggestive at least, that geese have helminth faunas rather characteristic of their ecological station.

The majority of the exchange occurred between geese and involved common species which may be considered typical of geese. The prominence of the common species in young geese and the relative scarcity of other forms provides strong support for this contention. It is also significant that few of these species were exchanged with other waterfowl. Those species that were possibly exchanged with ducks or swans were generally more important in the community of helminths of white-fronts, whose habitat preferences and low effective density limited exchange between them and other geese.

Snow geese and their young played central roles in the exchange of helminths, as was expected because of their abundance. Adult snows contributed the major portion of

the nucleus of infection for helminths which were relatively abundant in other hosts as well. They also played a major role in the maintenance of those pools. Young snows acquired relatively high populations of some of those helminths, complementing the role of the adults. In addition, young snows picked up large populations and were the major factor in the maintenance of other helminths introduced by brant. Most helminths which were transmitted extensively at Anderson River therefore, were circulated primarily through snow geese.

Despite their much lower density, brant were very important in the exchange of helminths because they brought helminths to the delta which were not present in other geese. Their coastal migration route apparently exposed them to infective pools (mostly of cestodes) which were unavailable to other geese on their inland routes. Their close association with snow geese on the breeding grounds and the resultant transfer of those helminths to snow geese (particularly the young) had a profound effect on the community of helminths in snow geese.

White-fronts played a minor role in the exchange of helminths because of their low density and lack of contact with other geese. Exchange between white-fronts and anseriformes other than geese was more common, but involved different helminths than those exchanged between brant and snow geese. In addition, the pools of infective stages

which maintained infections of the very common species in white-fronts probably constituted pools distinct from those which served as sources of infection of the same helminths in brant and snow geese. In view of the absence of significant exchange between snows and white-fronts on the breeding grounds, the relatively high similarity of their faunas suggests that more exchange between them occurred elsewhere. It seems likely that the overlapping portion of their spring migration route, where they were most closely associated, provided opportunities for exchange. Their similarities were probably hold-overs from that exchange.

In general, the degree of contact between host groups and their associated infective pools influenced the degree of exchange which occurred between them on the delta proper. Where there was little or no contact (e.g., between snows and white-fronts) there was limited exchange. Where contact was more frequent and prolonged, the exchange of helminths was enhanced.

Young geese were most closely associated with their parents and generally acquired helminth communities most like those of their parents. Although young white-fronts conformed to this generalization, their community was dominated by helminths probably acquired by virtue of close association with ducks and swans and showed little similarity to any of those present in other geese. Young snow geese were an exception which can be explained on the basis

of degree of association with other host groups.

The acquisition of a helminth community by young snow geese was strongly influenced by the two host groups with which they had closest contact, their parents and adult brant. Helminths such as *Tschertkovilepis krabbei*, *E. crami* and *T. tenuis* were acquired mainly from adult snow geese while other helminths (*D. barrowensis*, *D. lanceolata*, *Tschert. setigera* and *H. dispar*) originated from infections in brant. The greater similarity between the faunas of young snows and adult brant (relative to the young snow-snows similarity) was brought about by a complex of factors which favored transmission of cestodes (most prominent in young snows and brant) but did not favor transmission of the nematodes which were so prominent in adult snow geese. In effect, young snow geese acquired helminths from a number of infective pools regardless of their origin. They did not have a closer association with brant than with their adults, but helminths which dominated the fauna of adult snow geese were not as extensively transmitted on the Anderson River Delta as those brought in by brant.

The measures of exchange (species overlap and indexes of similarity) sometimes gave false impressions of the degree of exchange and had to be interpreted in the light of supporting data. For instance, a greater species overlap index between snow geese and white-fronts at

late-summer when both hosts had reduced numbers of species, suggested that there had been an exchange of helminths or a mutual acquisition of the same new species. In actual fact, the number and identity of their shared species remained constant so that the apparent exchange was not real. Similarly, the reduction of the population of a dominant helminth by one host group (e.g., A. spatulatum in snow geese), which was absent or less abundant in other groups, had the effect of increasing the proportions of other species in the fauna, resulting in greater similarity to other faunas without any exchange.

Although the helminths exchanged between geese in this study are apparently characteristic of geese, they were not equally abundant in all hosts (Appendices II and III), indicating, among other things, that some geese are better hosts for particular species of helminths than others. The exchange of such helminths among several species of geese presents the possibility that parasites which are more or less specific to one host will get into hosts which are unable to cope with infection. This could be the case with "pathogenic" infections of E. crami in brant and S. eurycerca in snow geese. In both cases, the finding of these helminths in those hosts constituted new host records and was the result of exchange with other hosts. The pathology noted could be the result of new, poorly adapted host-parasite relationships which might have

deleterious effects on both the parasite (in terms of completion of its life-cycle) and the host. Future studies concerned with helminth exchange among groups of ecologically associated hosts would gain much from a comparative study of host-parasite interactions as they affect the well being of both. In view of the slowly shrinking natural habitat available to breeding waterfowl, associations with each other and other host groups could become more prevalent, thereby increasing the probability of exchange among them. This could result in more frequent occurrences of pathology associated with abnormal host-parasite interactions which may prove significant in terms of management of waterfowl populations.

LITERATURE CITED

Barry, T.W. 1967. Geese of the Anderson River Delta, Northwest Territories. Ph.D. Thesis, University of Alberta.

Belopolskaya, M.M. 1956. The effects of migration on the parasite fauna of limicoline birds. Ezhegodn. Obshch. Estestvoisp. pri Akad. Nauk. Est. SSR, 49:95-103.

Bezubik, B. 1956. (Helminthofauna of wild ducks (Subfamily Anatinae)). Polish text. Acta Parasitol. Polonica, 4:407-510.

Busa, V. 1964. (Contribution on the knowledge of seasonal helminth-host relations of _Ganguleterakis dispar_ (Schrank, 1790) in the domestic goose in Slovakia (CSSR).) Studia Helminthol., I:287-292.

Buscher, H.N. 1965. Dynamics of the intestinal helminth fauna of three species of ducks. J. Wildlife Mangmt., 29:772-781.

__________. 1966. Intestinal helminths of the blue-winged teal, _Anas discors_ L., at Delta, Manitoba. Canad. J. Zool., 44:113-116.

Bykhovskaya-Pavlovskaya, I.E. 1962. (Trematodes of the bird fauna of USSR; ecologico-geographical survey.) Russian bext. Izdat. AN SSSR, Moskva, 407 p.

Campbell, R.C. 1967. Statistics for biologists. Cambridge University Press.

Colbo, M.H. 1965. Taxonomy and ecology of the helminths of the American coot in Alberta. M.Sc. Thesis, University of Alberta.

Cooch, F.G. 1964. Snow and blues. In J.P. Linduska (ed.) Waterfowl Tomorrow. U.S. Dept. Interior, Washington. p. 125-133.

Cornwell, G.W. & A.B. Cowan. 1963. Helminth populations of the canvasback (*Aythya valisineria*) and host-parasite-environmental interrelationships. Tr. 28. North Am. Wildlife and Natural Resources Conf., p. 173-198.

Cram, Eloise B. & Eugenia Cuvillier. 1934. Observations on *Trichostrongylus tenuis* infestation in domestic and game birds in the United States. Parasitology, 26:340-345.

Czaplinski, B. & L. Jarecka. 1967. Morphologie et cycle évolutif de *Tschertkovilepis krabbei* (Kowalewski, 1895) comb. n. - syn. *Drepanidotaenia prezwalskii* (Skrjabin, 1914), nec *Taenia tenuirostris* Rud., 1819 (Cestoda, Hymenolepididae). Acta Parasitol. Polonica, 15:289-304.

Dillon, O.W., Jr. 1959. Food habits of wild mallard ducks in three Louisiana parishes. Tr. 24. North Am. Wildlife Conf., p. 374-382.

Dogiel, V.A. 1964. General Parasitology (Translated by Z. Kabata from Russian, Third edition). Oliver and Boyd, Edinburgh and London.

Dubinina, M.N. 1953. (Cestodes of birds nesting in Western Siberia.) Parazit. Sborn. Zool. Inst. AN SSSR, 15:117-233.

Dzubin, Alex, Harvey W. Miller, & George V. Schildman. 1964. White-fronts. In J.P. Linduska (ed.) Waterfowl tomorrow. U.S. Dept. Interior, Washington, p. 135-143.

Fisher, R.A., A.S. Corbet, & C.B. Williams. 1943. The relation between the number of species and the number of individuals in a random sample of an animal population. J. Anim. Ecol., 12:42-58.

Gallimore, J.R. 1964. Taxonomy and ecology of helminths of grebes in Alberta. M.Sc. Thesis, University of Alberta.

Gower, W.C. 1938. Seasonal abundance of some parasites of wild ducks. J. Wildlife Mangmt., 2:223-232.

Graham, L.C. 1966. The ecology of helminths in breeding populations of lesser scaup (*Aythya affinis* Eyton) and ruddy ducks (*Oxyura jamaicensis* Gmelin). M.Sc. Thesis, University of Alberta.

Hansen, H.A., C.W. McNeil, & M.D. Priebe. 1957. Mortality of Canada geese with impacted gullets in eastern Washington, 1949-1954. J. Wildlife Mangmt., 21:96-98.

Hansen, H.A., & H.K. Nelson. 1964. Honkers large and small. In J.P. Linduska (ed.) Waterfowl tomorrow. U.S. Dept. Interior, Washington. p. 109-124.

Hanson, H.C. & J.H. Gilford. 1961. The prevalence of some helminth parasites in Canada geese wintering in southern Illinois. Tr. Illinois State Acad. Sc., 54:41-53.

Hanson, H.C., N.D. Levine, & S. Kantor. 1956. Filariae in a wintering flock of Canada geese. J. Wildlife mangmt., 20:89-92.

Herman, C.M., J.H. Steenis, & E.E. Wehr. 1955. Causes of winter losses among Canada geese. Tr. 20. North Am. Wildlife Conf., p. 161-165.

Herman, C.M., & E.E. Wehr. 1954. The occurrence of gizzard worms in Canada geese. J. Wildlife Mangmt., 18: 509-513.

Holden, B.L. and W.J.L. Sladen. 1968. Heartworm, Sarconema eurycerca infection in whistling swans, Cygnus columbianus, in Chesapeake Bay. Bull. Wildlife Disease Assoc., 4:126-128.

Holmes, J.C. & M. Colbo. 1970. Parasites of birds and mammals from Hazen Camp, Ellesmere Island, N.W.T. (in press).

Holmes, John C. & Ronald Podesta. 1968. The helminths of wolves and coyotes from the forested regions of Alberta. Canad. J. Zool., 46:1193-1204.

Joyeux, C., & J.G. Baer. 1936. Cestodes. Faune de France, Féd. Franç. Soc. Sc. Nat., (30), 613 p.

Kisielewska, K. 1957. Influence of some factors on the survival and invasity of eggs of the tapeworm Drepanidotaenia lanceolata (Bloch) and on the further development of larvae from such eggs. Acta. Parasitol. Polonica, 5:585-598.

Kluge, J. 1967. Avian parasitic (Sarconema eurycerca) pancarditis. Bull. Wildlife Disease Assoc. 3: 114-117.

Kotecki, N.R. 1964. Life cycle of Parabisaccanthes philactes (Schiller, 1951) Spassky et Reznik, 1963 in the intermediate host. Acta Parasitol. Polonica, 12:373-378.

Leiby, P.D., & O.W. Olsen. 1965. Life history studies on nematodes of the genera Amidostomum (Strongyloidea) and Epomidiostomum (Trichostrongyloidea) occurring in the gizzards of waterfowl. Proc. Helminth. Soc. Wash., 32:32-49.

McDonald, M.E. 1969a. Annotated bibliography of helminths of waterfowl (Anatidae). U.S. Dept. Interior Special Scientific Report--Wildlife No. 125. 333 p.

_____________. 1969b. Catalogue of helminths of waterfowl (Anatidae). U.S. Dept. Interior Special Scientific Report--Wildlife No. 126. 692 p.

MacArthur, R.H. 1957. On the relative abundance of bird species. Nat. Acad. Sci. Proc., 43:293-295.

Macfadyen, A. 1964. Animal ecology aims and methods. Sir Isaac Pitman & Sons Ltd., London. pp.174-202.

Margalef, R. 1957. La teoria de la informacion en ecologia. Memorias de la real academia de ciencias y artes (Barcelona), 33:373-449.

Okorokov, V.I. 1957. (Helminth fauna of wild aquatic birds of the Cheliabinsk oblast and seasonal dynamics of their most widespread diseases.) Russian text. Uchen. Zapiski Cheliabinsk. Gosudarstv. Pedagog. Inst., 3:177-185.

Oshmarin, P.G. 1950. Helminth fauna of birds of the Far East (Kamchatka, Zemlia Koriakov and Kurile Islands). Trudy Gel'mint. Lab. AN SSSR, 3:166-179.

Preston, F.W. 1948. The commonness and rarity of species. Ecology, 29:254-283.

Reichenow, E., H. Vogel & F. Weyer. 1952. Leitfaden zur Untersuchung der tierischen Parasiten des Menshchen und der Haustiere. Third ed., Leipzig.

Ryzhikov, K.M. 1956. (On the helminth fauna of Anatidae on their wintering grounds.) Trudy Gel'mint. Lab. AN SSSR, 8:131-139.

Sanders, Howard L. 1968. Marine benthic diversity: a comparative study. The American Naturalist, 102 (925):243-282.

Schiller, E.L. 1952. Studies on the helminth fauna of Alaska III. _Hymenolepis_ _kenaiensis_ n. sp., a cestode from the greater scaup (_Aythya_ _marila_ _nearactica_) with remarks on endemicity. Tr. Am. Micr. Soc., 71:146-149.

______________. 1954. Studies on the helminth fauna of Alaska. XVIII. Cestode parasites in young Anseriformes on the Yukon delta nesting grounds. Tr. Am. Micro. Soc., 73:194-201.

Shevtsov, A.A. 1964. (Seasonal and age dynamics of helminthiasis in ducks and geese in different zones of the Ukranian SSR.) Veterinariya, Kiev, (1):72-80.

Simpson, E.H. 1949. Measurement of diversity. Nature, 163:688.

Southwick, C. 1953. A system of age classification for field studies of waterfowl broods. J. Wildlife Mangmt., 17:1-8.

Spasskaya, L.P. 1966. (Cestodes of birds of the USSR. Hymenolepididae.) Russian text. Izdat. "Nauka", AN SSSR, AN Moldav. SSR, Inst. Zool., Moskva, 698 p.

Sugden, L.G. 1969. Foods, food selection and energy requirements of wild ducklings in southern Alberta. Ph.D. Thesis, Utah State University.

Sulgostowska, T. 1958. Flukes of birds of Druzno Lake. (Parasitofauna of the biocoenosis of Druzno Lake - Part III.) Acta Parasitol. Polonica, 6:111-142.

Sulgostowska, T. 1963. Trematodes of birds in the biocoenosis of the Lakes Druzno, Gołdapiwo, Mamry Potnocne and Swiecajty. Acta Parasitol. Polonica, 11:239-264.

Threlfall, William. 1967. Studies on the helminth parasites of the herring gull, Larus argentatus Pontopp., in Northern Caernarvonshire and Anglesey. Parasitology, 57:431-453.

Uemura, K. 1964. Statistical analysis of the data in Bilharziasis research. World Health Organization mimeographed note BILH/Exp. Com. 3/INF 8.64.

Ulmer, Martin J., & Frederick J. Vande Vusse. 1970. Morphology of Dendritobilharzia pulverulenta (Braun, 1901) Skrjabin, 1924 (Trematoda: Schistosomatidae) with notes on secondary hermaphroditism in males. J. Parasitol., 56:67-74.

Wehr, Everett E., & Carlton M. Herman. 1954. Age as a factor in the acquisition of parasites by Canada geese. J. Wildlife Mangmt., 18:239-247.

Wetzel, R. 1930. A new species of trematode of the genus Ornithobilharzia from the Canada goose. Proc. U.S. Nat. Mus., 78, Art. 3, 4 p.

Whittaker, R.H. 1965. Dominance and diversity in land plant communities. Science, 147:250-260.

Wisniewski, W.L. 1958. Characterization of the parasitofauna of an eutrophic lake. (Parasitofauna of the biocoenosis of Druzno Lake - Part I.) Acta Parasitol. Polonica, 6:1-64.

Zaskind, L.N. 1963. (Contribution to the helminth fauna of the *Anser anser* L. of the Kustanai region.) (Parazity Dikikh Zhivotnykh Kazakhstana), Russian text. Trudy Inst. Zool. AN Kazakh. SSR, 19:117-120.

Period	Spring	Arrival	1-15	16-30	1-15	16-31	1-15	Fall	Winter
Number examined	7	32	29	30	32	23	31	19	23
Helminth									
TREMATODA									
Echinoparyphium sp.								10-1.0 (1)	
Echinostoma revolutum	*14-1.0 (1)	19-1.0 (1-16)	14-1.0 (1-3)	7-4.0 (1-7)				5-2.0 (2)	
Notocotylus attenuatus	14-10.0 (10)	6-3.5 (1-6)	7-1.0 (1-2)	17-3.0 (1-5)	9-1.0 (1)	9-1.5 (1-2)	13-2.5 (1-8)		13-3.0 (3)
Zygocotyle lunata	14-1.0 (1)	3-1.0 (1)	10-1.0 (1-3)	10-1.0 (1-3)	13-1.0 (1-2)	4-1.0 (1)	6-1.5 (1-2)	16-1.0 (1)	
Apatemon anseris	14-8.0 (8)	6-9.5 (1-18)						10-4.0 (4)	30-1.0 (1-3)
CESTODA									
Anomotaenia ciliata			3-1.0 (1)	3-1.0 (1)	3-1.0 (1)				
Cloacotaenia megalops						4-2.0 (2)			
Dicranotaenia multistriata									44-1.0 (1-4)
Diorchis stefanskii				3-1.0 (1)					
Drepanidotaenia barrowensis					3-1.0 (1)	13-2.0 (1-5)			
D. lanceolata					16-2.0 (1-3)	30-3.0 (1-12)	37-1.5 (1-19)		
Fimbriaria fasciolaris						4-1.0 (1)			
Parabisaccanthes philactes						4-1.0 (1)			
Retinometra longivaginata		38-1.0 (1-15)	17-2.0 (1-5)	20-2.5 (1-10)	75-2.5 (1-16)	70-2.5 (1-9)	52-3.0 (1-10)		
Tschertkovilepis krabbei	57-3.0 (1-5)	50-2.0 (1-8)	17-1.0 (1-2)	27-1.0 (1-3)	78-2.0 (1-10)	65-2.0 (1-5)	58-2.0 (1-4)	10-1.5 (1-3)	4-1.0 (1)
Tschert. setigera		3-1.0 (1)			10-4.0 (1-9)	17-1.5 (1-2)	6-1.0 (1)		
Wardoides nyrocae		3-1.0 (1)							

Period	Spring		1-15	16-30	1-15	16-31	1-15	Fall	Winter
Number examined	7	32	29	30	32	23	31	19	23
Helminth									
NEMATODA									
Sarconema eurycerca	14-3.0 (3)				6-2.5 (1-4)		3-3.0 (3)	10-1.0 (1)	
Heterakis dispar	28-38.5 (6-71)		10-2.0 (1-3)	7-2.5 (1-4)	3-2.0 (2)	13-1.0 (1-7)	48-1.0 (1-9)	5-2.0 (2)	78-31.0 (1-306)
Tetrameres sp.	28-5.0 (4-6)	13-1.0 (1-3)	21-1.5 (1-13)	23-2.0 (1-6)	31-1.5 (1-6)	17-2.5 (1-7)	24-1.0 (1-2)	37-1.0 (1-3)	13-2.0 (1-18)
Amidostomum anseris	14-1.0 (1)	13-2.0 (1-3)	3-2.0 (2)					10-1.0 (1)	13-1.0 (1)
A. spatulatum	71-11.0 (2-35)	100-21.5 (1-100)	93-14.0 (1-32)	93-8.5 (1-35)	94-6.0 (1-36)	87-4.0 (1-27)	85-2.0 (1-14)	26-1.0 (1-2)	22-1.0 (1-2)
Epomidiostomum crami	100-4.0 (1-13)	100-8.0 (1-30)	97-5.0 (1-17)	84-5.0 (1-11)	100-8.0 (1-26)	96-6.0 (1-16)	82-5.0 (1-19)	100-7.0 (2-22)	100-9.0 (4-22)
Trichostrongylus tenuis	43-4.0 (3-7)	22-9.0 (2-66)	59-4.0 (1-33)	73-4.0 (1-20)	81-9.0 (1-52)	97-10.0 (1-52)	97-7.0 (1-85)	47-1.0 (1-12)	74-8.0 (1-42)
Capillaria obsignata	28-1.5 (1-2)	3-1.0 (1)							26-5.0 (2-21)
Capillaria sp.	14-1.0 (1)	6-1.0 (1)	10-1.0 (1)	3-1.0 (1)	7-1.0 (1)	4-1.0 (1-2)	19-1.0 (1-2)	10-1.0 (1)	4-1.0 (1)

* Prevalence (%) - Median Intensity / Range

Sample	Arrival			Mid-summer			Late-summer		
Host	Snows	White-fronts	Brant	Snows	White-fronts	Brant	Snows	White-fronts	Brant
No. examined	32	20	25	55	13	16	31	8	19
Helminth									
TREMATODA									
Echinostoma revolutum+	*19-1.0 (1-16)	40-2.0 (1-10)			31-2.0 (1-3)				
Catatropis pricei+			44-6.0 (1-50)						
Notocotylus attenuatus+	6-3.5 (1-6)	5-1.0 (1)	4-4.0 (4)	9-1.0 (1-2)	23-8.0 (2-15)		13-2.5 (1-8)	25-2.5 (1-4)	
Paramonostomum sp.			4-18.0 (18)						
Zygocotyle lunata	3-1.0 (1)			9-1.0 (1-2)			6-1.5 (1-2)		
Ornithobilharzia pricei						6-1.0 (1)			
Apatemon anseris	6-9.5 (1-18)								
CESTODA									
Anomotaenia ciliata				4-1.0 (1)		6-1.0 (1)			
Cloacotaenia megalops				2-2.0 (2)					
Diorchis stefanskii			4-1.0 (1)			13-1.0 (1)			11-1.5 (1-2)
Drepanidotaenia barrowensis+		35-4.0 (1-10)	32-6.5 (1-123)	7-1.5 (1-5)	38-1.0 (1-8)	38-7.0 (1-7)			42-2.5 (1-4)
Drepanidotaenia lanceolata+			24-2.5 (1-24)	24-2.0 (1-12)		44-2.0 (1-7)	37-1.5 (1-19)	25-2.5 (1-6)	
Fimbriaria fasciolaris				2-1.0 (1)					
Parabisaccanthes philactes+			8-2.0 (1-3)	2-1.0 (1)		6-3.0 (3)			11-5.0 (1-9)
Retinometra longivaginata+	38-1.0 (1-15)		44-1.0 (1-7)	73-2.5 (1-16)	8-1.0 (1)	38-4.0 (3-6)	52-3.0 (1-10)		32-4.0 (1-9)
Retinometra venusta+		5-2.0 (2)			31-2.0 (1-14)			25-4.5 (2-7)	

Host	Snows	White-fronts	Brant	Snows	White-fronts	Brant	Snows	White-fronts	Brant
No. examined	32	20	25	55	13	16	31	8	19
Sobolevicanthus gracilis						6-1.0 (1)			
Tschertkovilepis krabbei+	50-2.0 (1-8)	70-3.0 (1-12)	56-4.0 (1-10)	73-2.0 (1-10)	92-2.0 (1-10)	44-3.0 (1-5)	58-2.0 (1-4)	25-5.0 (1-8)	100-1.0 (1-2)
Tschertkovilepis setigera+	3-1.0 (1)		60-20.0 (1-156)	13-1.0 (1-9)		81-27.0 (3-75)	6-1.0 (1)	13-1.0 (1)	58-6.0 (2-53)
Wardium creplini					8-1.0 (1)				
Wardoides nyrocae	3-1.0 (1)		8-1.0 (1)						5-2.0 (2)
Hymenolepis sp.			20-2.0 (1-2)			6-1.0 (1)			
NEMATODA									
Sarconema eurycerca+		45-3.0 (1-13)		4-2.5 (1-4)	69-2.0 (1-18)		3-3.0 (3)	13-1.0 (1)	
Heterakis dispar+			28-20.0 (1-75)	7-1.5 (1-7)		75-6.0 (1-63)	48-1.0 (1-9)		63-5.0 (1-77)
Tetrameres fissispina+			36-2.0 (1-9)			25-5.0 (1-28)			37-2.0 (1-4)
Tetrameres sp.+	13-1.0 (1)	35-2.0 (1-10)		25-1.5 (1-7)	15-8.5 (1-16)		24-1.0 (1-2)	50-2.5 (1-4)	
Amidostomum anseris+	13-2.0 (1-3)	10-1.0 (1)	4-4.0 (4)		31-1.5 (1-3)	6-1.0 (1)			
Amidostomum spatulatum+	100-21.5 (1-100)	45-2.0 (1-4)	4-1.0 (1)	91-4.5 (1-36)	38-5.0 (3-14)		85-2.0 (1-14)	88-3.0 (1-5)	
Epomidiostomum crami+	100-8.0 (1-30)	100-14.0 (5-33)	68-7.0 (1-24)	98-6.5 (1-26)	100-16.0 (3-27)	86-5.0 (2-17)	82-5.0 (1-19)	100-8.0 (7-25)	58-4.0 (2-12)
Trichostrongylus tenuis+	22-9.0 (2-66)	10-12.0 (1-23)	48-11.5 (1-150)	87-10.0 (1-52)	15-6.0 (2-10)	81-18.0 (1-37)	97-7.0 (1-85)	38-13.0 (8-13)	95-22.5 (1-77)
Capillaria obsignata	3-1.0 (1)				8-1.0 (1)				
Capillaria sp.	6-1.0 (1)			9-1.0 (1)			19-1.0 (1-2)		

+ = "common" species

* = Prevalence(%)- Median Intensity / (Range)

APPENDIX III. Prevalence and intensity of infection with helminths recovered from young geese at the Anderson River Delta, N.W.T.

Sample	Mid-summer			Late-summer	
Host	Snows	White-fronts	Brant	Snows	White-fronts
Helminth					
TREMATODA					
Notocotylus attenuatus+	*2-1.0 (1)	44-9.0 (2-21)		32-1.5 (1-12)	100-8.0 (1-290)
CESTODA					
Dicranotaenia coronula				3-1.0 (1)	
Diorchis stefanskii	2-1.0 (1)		7-1.0 (1)	3-1.0 (1)	
Drepanidotaenia barrowensis+	12-1.0 (1-3)		7-1.0 (1)	42-2.0 (1-14)	33-5.0 (1-12)
Drepanidotaenia lanceolata+	12-3.0 (1-50)		44-6.0 (1-31)	48-10.0 (1-40)	
Fimbriaria fasciolaris	3-1.5 (1-2)		7-1.0 (1)		
Parabisaccanthes philactes+	6-1.0 (1)		4-1.0 (1)		62-2.0 (1-5)
Retinometra longivaginata+	5-1.0 (1)			16-1.0 (1)	
Retinometra venusta+					24-28.0 (12-47)
Sobolevicanthus gracilis	3-1.0 (1)		15-1.0 (1-2)	10-1.0 (1-2)	
Tschertkovilepis krabbei+	29-1.5 (1-7)		52-1.5 (1-6)	55-2.0 (1-5)	81-2.0 (1-5)
Tschertkovilepis setigera+	19-2.0 (1-11)		30-2.5 (1-7)	45-3.0 (1-41)	24-1.0 (1-33)
Wardoides nyrocae					
NEMATODA					
Heterakis dispar+	7-2.0 (1-15)		70-7.0 (1-54)	26-2.0 (1-14)	
Amidostomum anseris+					10-1.0 (1)
Amidostomum spatulatum+					5-1.0 (1)
Epomidiostomum crami+			4-2.0 (2)	16-1.0 (1)	29-2.5 (1-8)
Trichostrongylus tenuis+	21-3.5 (1-16)	11-2.0 (2)	30-3.0 (1-7)	55-5.0 (1-29)	29-1.5 (1-9)

+ = "common" species

* = Prevalence(%) - Median Intensity / (Range)