Helminths of Ross' and Greater White-fronted Geese Wintering in South Texas, U.S.A.

Alan M. Fedynich,[1] Richard S. Finger, Bart M. Ballard, Jason M. Garvon, and Michael J. Mayfield

Caesar Kleberg Wildlife Research Institute, Texas A&M University-Kingsville, 700 University Boulevard, MSC 218, Kingsville, Texas 78363-8202, U.S.A. (e-mail: alan.fedynich@tamuk.edu)

ABSTRACT: Helminth community structure and pattern were assessed in 16 Ross' geese, *Chen rossii*, and 46 greater white-fronted geese, *Anser albifrons*, collected during winter 1999–2000 in Kleberg County, Texas, U.S.A. Helminths found in individual Ross' geese ranged from 1 to 6 species and from 1 to 95 individuals; infracommunities averaged 3.5 ± 0.3 (SE) species and 42.5 ± 7.7 individuals. Ten species were found in the Ross' goose component community, in which *Amidostomum anseris, Epomidiostomum crami, Heterakis dispar*, and *Trichostrongylus tenuis* were the most prevalent and numerically dominant. Helminths found in individual white-fronted geese ranged from 4 to 117 individuals; infracommunities averaged 4.2 ± 0.2 species and 28.9 ± 4.0 individuals. Sixteen species were found in the white-fronted goose component community. *Epomidiostomum crami, Amidostomum spatulatum*, and *T. tenuis* were the most prevalent and numerically dominant. In white-fronted geese, chi-square and analysis of variance comparisons were possible for *A. anseris, A. spatulatum, E. crami, T. tenuis*, and *Drepanidotaenia* sp. Prevalence was significantly higher in the juvenile sample than the adult sample for *A. anseris* and *T. tenuis*, whereas *A. spatulatum* was significantly lower in the juvenile sample. Prevalence of *T. tenuis* was significantly higher in males than females. Mean abundance of *A. spatulatum* was significantly higher in the adult sample than the juvenile sample, whereas *T. tenuis* was significantly higher in the juvenile sample. No significant differences in mean abundance were observed because of host sex. On the basis of percentage similarity and Jaccard's indices, component communities between juvenile and adult white-fronted geese were most similar, followed by male and female white-fronted geese, and juvenile Ross' and white-fronted geese. Relatively low species richness, preponderance and numerical dominance of direct life cycle nematodes, and absence of helminths in a number of habitats suggests that the mainly herbivorous diet of Ross' and white-fronted geese dramatically influenced helminth community structure and pattern on the wintering grounds.

KEY WORDS: *Anser albifrons*, *Chen rossii*, community ecology, component community, greater white-fronted goose, helminths, infracommunity, Ross' goose, South Texas, U.S.A., wintering grounds.

Helminth studies in geese have generally focused on individual species (Schiller, 1951; 1952), guilds of species (Herman and Wehr, 1954; Tuggle and Crites, 1984), or surveys (Clinchy and Barker, 1994; Purvis et al., 1997). Only a few studies have used helminth community-based approaches. Neraasen and Holmes (1975) examined the dynamics of a cestode community within a 3-host system on the breeding grounds at Anderson River Delta, Canada, and Forbes et al. (1999) examined patterns of co-occurrence in helminth infracommunities of lesser snow geese (*Chen caerulescens caerulescens*) collected during winter and spring migration across 8 states in the United States.

Given the importance of the nonbreeding period to waterfowl (Anderson and Batt, 1983) and the lack of information on helminths in the Ross' goose (*Chen rossii*) and greater white-fronted goose (*Anser albifrons*; hereafter referred to as white-fronted goose) during winter, additional studies are warranted. This study examines helminth communities in Ross' and white-fronted geese wintering in south Texas by determining helminth infracommunities and component communities; comparing and contrasting helminth community structure and pattern between and within host groups; and relating these findings to host–parasite interactions.

MATERIALS AND METHODS

Sixteen Ross' geese (9 juvenile males, 2 adult males, 4 juvenile females, 1 adult female) and 46 white-fronted geese (13 juvenile males, 11 adult males, 8 juvenile females, 14 adult females) were shot during the hunting season in Kleberg County, Texas, U.S.A. (27°30′N; 97°57′W) from 3 November 1999 through 20 January 2000. For each bird, age was determined (juvenile or adult) by plumage coloration and sex determined by gonad examination. Viscera were removed in the field within 15 min of host death, placed in individual plastic bags, fast-frozen with a mixture of dry ice and alcohol (ca. −70°C), and placed on ice (Glass et al., 2002). Eviscerated carcasses were placed in individual plastic bags in coolers. Viscera and carcasses were stored in freezers at −10°C for subsequent necropsy. The following habitats were examined for helminths: eye surface and

---

nictating membrane, nasal cavity, nasal sinus, suborbital sinus, brain, trachea, gastrointestinal tract, body cavity, and all other internal organs.

Cestodes and trematodes were fixed in alcohol–formalin–acetic acid solution for 15–30 min and preserved in 70% ethanol. Nematodes were fixed in glacial acetic acid for 1–5 min and preserved in a mixture of 70% ethanol and 8% glycerin. The following helminth specimens were deposited in the United States National Parasite Collection (USNPC), Beltsville, Maryland, U.S.A.: *Dendritobilharzia pulverulenta* (USNPC 094563), *Echinostoma trivolvis* (USNPC 094561, 094564), *Zygocotyle lunata* (USNPC 094562, 094565), *Drepanidotaenia* sp. (USNPC 095000, 095001), *Microsomacanthus* sp. (USNPC 095002), *Amidostomum anseris* (USNPC 094552, 094556), *Amidostomum spatulatum* (USNPC 094557), *Epomidiostomum crami* (USNPC 094553, 094558), *Heterakis dispar* (USNPC 094554, 094559), *Trichostrongylus tenuis* (USNPC 094555, 094560). This study was approved by the Texas A&M University-Kingsville Animal Care and Use Committee, authorization number Y2K-6-3.

The terms prevalence, intensity, mean intensity, abundance, and mean abundance follow Bush et al. (1997). Common helminth species were defined as those with >75% prevalence across the collective host sample, intermediate species ≥25% and ≤75% prevalence, and uncommon species <25% prevalence. Infracommunity refers to all infrapopulations of parasite species that occur within a single host; component community refers to all infrapopulations of parasites occurring within a particular subset of a host species (Bush et al., 1997). The term habitat, in relation to helminths, refers to anatomical localities within the host.

Prevalence data for the intermediate and common species were analyzed with chi-square contingency tables (PROC FREQ; SAS Institute Inc., 1990) to determine if prevalence varied by the host main effects of age and sex. Continuity adjusted chi-square statistical procedure (SAS Institute Inc., 1990) was used when generated expected values were <5.

Abundance data for each of the intermediate and common species were tested for normality (PROC UNIVARIATE NORMAL; SAS Institute, Inc., 1990). Nonnormally distributed abundance data were rank transformed (PROC RANK; SAS Institute, Inc., 1990) before further statistical analyses. One-way analysis of variance (ANOVA) (PROC GLM; SAS Institute, Inc., 1990) was used to determine if abundance values of the intermediate and common helminth species varied by host main (age, sex) and interaction (age by sex) effects variables.

Because of the low numbers of adult Ross' geese ($n = 3$), chi-square, normality, and ANOVA analyses were not performed. In white-fronted geese, *A. anseris, A. spatulatum, E. crami, T. tenuis,* and *Drepanidotaenia* sp. met preplanned analysis criteria. Significance levels were set at $P \leq 0.05$. Descriptive statistics are presented as a mean value ± standard error.

Two similarity measures were used to assess differentiation (β) diversity. The percentage similarity index (PS$_I$; Krebs, 1989) was used to evaluate similarity of species' abundances, standardized as percentages, between component communities. Jaccard's coefficient of similarity index (J$_I$; Magurran, 1988) was used to measure numerical similarity of species shared between component communities. Helminths that occurred in both comparison groups, which could not be sufficiently separated (i.e., Hymenoli-

pidae spp., nematode spp.) were excluded before calculating the β diversity measures.

RESULTS

Helminths found in individual Ross' geese ranged from 1 to 6 species and from 1 to 95 individuals; infracommunities averaged 3.5 ± 0.3 species and 42.5 ± 7.7 individuals. The component community contained 10 species (7 nematodes, 2 trematodes, and 1 cestode), of which 5 (50%) were uncommon species (Table 1). *Amidostomum anseris, E. crami, H. dispar*, and *T. tenuis* had prevalences of 69, 88, 50, and 62%, respectively, and collectively accounted for 96% of the 680 total helminths. Trematodes occurred infrequently and numerically were minor components of the component community (Table 1).

Helminths found in individual white-fronted geese ranged from 1 to 7 species and from 4 to 117 individuals; infracommunities averaged 4.2 ± 0.2 species and 28.9 ± 4.0 individuals. The component community consisted of 16 species (8 nematodes, 4 trematodes, 3 cestodes, and 1 acanthocephalan). *Epomidiostomum crami, A. spatulatum*, and *T. tenuis* had prevalences of 96, 67, and 59%, respectively, and collectively accounted for 77% of the 1,330 total helminths (Table 2). All trematode and 2 cestode species occurred infrequently and numerically were minor components of the component community (Table 2).

Comparisons of PS$_I$ and J$_I$ between age classes of white-fronted geese found high similarity (Table 3). Component communities of juvenile and adult white-fronted geese had 12 and 13 species, respectively, and shared 11 species. Comparisons of white-fronted geese by sex also indicated a high level of similarity of species (Table 3). Component communities of male and female white-fronted geese had 12 and 14 species, respectively, and shared 11 species. However, relative percentages of individuals of each species (as measured by PS$_I$) was lower than that observed for the comparison by host age (Table 3). The J$_I$ comparison between juvenile Ross' and white-fronted geese had the highest degree of dissimilarity (Table 3). Juvenile Ross' geese had substantially fewer species than juvenile white-fronted geese (8 and 13 species, respectively) and shared only 7 species. Dissimilarity was also reflected in the PS$_I$ (Table 3).

Prevalence was significantly higher in the juvenile sample than the adult sample for *A. anseris* ($P = 0.046$) and *T. tenuis* ($P = 0.001$), but prevalence for *A. spatulatum* was significantly lower ($P = 0.009$) in the juvenile sample. Prevalence did not vary by host age for *E. crami* ($P = 0.394$) or *Drepanidotaenia* sp.

Table 1. Descriptive statistics for the helminth community collected from Ross' geese (*Chen rossii*) (N = 16) during winter 1999–2000 in Kleberg County, Texas, U.S.A.

Helminth taxon	Habitat*	Prevalence†	Intensity‡	Abundance§
Digena				
Echinostoma trivolvis	LI, SI	19% (3/16)	4.7 (±2.7, 2–10)	0.9 (±0.6, 14)
Zygocotyle lunata	C	12% (2/16)	1.0 (±0, 1)	0.1 (±0.1, 2)
Cestoda				
Drepanidotaenia sp.‖	C, LI, SI	31% (5/16)	2.0 (±0.4, 1–3)	0.6 (±0.3, 10)
Nematoda				
Amidostomum anseris	G	69% (11/16)	4.1 (±1.0, 1–11)	2.8 (±0.8, 45)
Capillaria sp.	C	6% (1/16)	1.0 (±0, 1)	0.1 (±0.1, 1)
Epomidiostomum crami	G	88% (14/16)	13.7 (±3.5, 1–47)	12.0 (±3.2, 192)
Heterakis dispar	C	50% (8/16)	6.9 (±1.7, 2–15)	3.4 (±1.2, 55)
Tetrameres sp.	P	6% (1/16)	1.0 (±0, 1)	0.1 (±0.1, 1)
Trichostrongylus tenuis	C	62% (10/16)	35.9 (±6.9, 2–63)	22.4 (±6.1, 359)
Nematode sp.¶	SI	6% (1/16)	1.0 (±0, 1)	0.1 (±0.1, 1)

* C = ceca; G = gizzard; LI = large intestine; SI = small intestine; P = proventriculus.
† Percent of individuals infected followed by the fraction of individuals infected.
‡ Mean value followed parenthetically by SE and range.
§ Mean value followed parenthetically by SE and total number of helminths collected.
‖ Identification based on strobila only (no scolices found).
¶ Unidentifiable partial nematode specimen.

($P = 0.447$). No significant differences were found in prevalence by host sex for *A. anseris* ($P = 0.958$), *A. spatulatum* ($P = 0.913$), *E. crami* ($P = 0.509$), and *Drepanidotaenia* sp. ($P = 0.489$), but prevalence of *T. tenuis* was significantly higher ($P = 0.019$) in the male sample than the female sample.

Abundance values were not normally distributed for any of the above 5 species ($P < 0.0001$ for each species). Mean abundance of *A. anseris* by host age was higher in the juvenile sample but not significantly so ($P = 0.079$). Mean abundance of *A. anseris* was similar for host sex ($P = 0.537$) and host age by sex interaction ($P = 0.632$). Mean abundance of *A. spatulatum* was significantly higher in the adult sample than the juvenile sample ($P = 0.012$) but was similar by host sex ($P = 0.671$) and the interaction of host age by sex ($P = 0.686$). Mean abundance of *E. crami* was not significantly different by host age ($P = 0.188$) or host sex ($P = 0.056$), despite higher abundances in the female sample, but a host age by sex interaction ($P = 0.029$) was observed. Mean abundance of *T. tenuis* was significantly higher in the juvenile sample than the adult sample ($P = 0.006$), and although higher in the male sample than the female sample, the difference was not significant ($P = 0.062$). No significant age by sex interaction was observed ($P = 0.257$). Mean abundance of *Drepanidotaenia* sp. was not significantly different by host

age ($P = 0.312$), sex ($P = 0.331$), or age by sex interaction ($P = 0.125$).

DISCUSSION

Infracommunities in Ross' geese were depauperate of helminth species. Low species richness at the infracommunity level affected the component community, which was also species poor, contained relatively few individuals, and was dominated numerically by 2 species (*E. crami* and *T. tenuis*). The white-fronted goose component community had nearly twice the species observed in the Ross' goose component community and twice as many species dominated numerically. However, infracommunities averaged about 1 species more than found in the Ross' goose (4.1 vs. 3.5), and averaged almost half the number of individuals (28.9 vs. 42.5). Our findings are consistent with those reported in wintering geese by Purvis et al. (1997) and Forbes et al. (1999) and contrasts dramatically with those in wintering *Anas* spp., in which both infracommunities and component communities tend to be species rich and complex (Wallace and Pence, 1986; Gray et al., 1989; Fedynich and Pence, 1994). Such differences are likely the result of variation in exposure probabilities to infective stages of helminths, which can be influenced by host diet (Glass et al., 2002), season, host

Table 2. Descriptive statistics for the helminth community collected from greater white-fronted geese (*Anser albifrons*) (*N* = 46) during winter 1999–2000 in Kleberg County, Texas, U.S.A.

Helminth taxon	Habitat*	Prevalence†	Intensity‡	Abundance§
Digena				
Dendritobilharzia pulverulenta	SI	2% (1/46)	1.0 (±0, 1)	<0.1 (±<0.1, 1)
Echinostoma trivolvis	LI, SI	17% (8/46)	2.1 (±0.5, 1–5)	0.4 (±0.1, 17)
Paramonostomum sp.	C	2% (1/46)	1.0 (±0, 1)	<0.1 (±<0.1, 1)
Zygocotyle lunata	C	20% (9/46)	1.8 (±0.2, 1–3)	0.3 (±0.1, 16)
Cestoda				
Drepanidotaenia sp.‖	LI, SI	37% (17/46)	2.8 (±0.6, 1–10)	1.0 (±0.3, 48)
Microsomacanthus sp.‖	LI, SI	15% (7/46)	1.1 (±0.1, 1–2)	0.2 (±0.1, 8)
Hymenolepidodae¶	C, LI, SI	13% (6/46)	1.3 (±0.3, 1–3)	0.2 (±0.1, 8)
Nematoda				
Amidostomum anseris	G	41% (19/46)	2.9 (±0.7, 1–11)	1.2 (±0.3, 56)
Amidostomum spatulatum	G	67% (31/46)	6.2 (±1.2, 1–25)	4.1 (±0.9, 191)
Capillaria sp.	SI	2% (1/46)	1.0 (±0, 1)	<0.1 (±<0.1, 1)
Epomidiostomum crami	G	96% (44/46)	14.0 (±2.7, 1–82)	13.4 (±2.6, 618)
Heterakis dispar	C	17% (8/46)	15.4 (±6.9, 1–52)	2.7 (±1.4, 123)
Tetramers sp.	P	20% (9/46)	1.1 (±0.1, 1–2)	0.2 (±0.1, 10)
Trichostrongylus tenuis	C	59% (27/46)	8.1 (±1.7, 1–33)	4.7 (±1.1, 218)
Nematode spp.#	C, CW	6% (3/46)	1.3 (±0.3, 1–2)	0.1 (±<0.1, 4)
Acanthocephala				
Polymorphus sp.	LI	9% (4/46)	2.5 (±0.9, 1–4)	0.2 (±0.1, 10)

* C = ceca; CW = carcass wash; G = gizzard; LI = large intestine; SI = small intestine; P = proventriculus.

† Percent of individuals infected followed by the fraction of individuals infected.

‡ Mean value followed parenthetically by SE and range.

§ Mean value followed parenthetically by SE and total number of helminths collected.

‖ Identification based on strobila only (no scolices found).

¶ Hymenolepididae strobila fragments that could not be further identified and found in host individuals where *Drepanidotaenia* sp. and *Microsomacanthus* sp. were not found.

Unidentifiable nematodes: partial specimen and larvae.

age, and host sex (Bush, 1990), co-occurrence among related host species (Neraasen and Holmes, 1975; Stock and Holmes, 1987), and biogeographic processes (Gregory, 1990; Poulin and Morand, 1999).

Our findings indicate a notable influence of host diet

Table 3. Percentage similarity (PS$_I$) and Jaccard's (J$_I$) indices for helminth communities from Ross' geese, *Chen rossii*, and greater white-fronted geese, *Anser albifrons*, collected during winter 1999–2000 in Kleberg County, Texas, U.S.A.

Comparison	PS$_I$*	J$_I$†
A. albifrons: Juveniles (21)‡ vs. adults (25)	71.9	0.85
A. albifrons: Males (24) vs. females (22)	67.1	0.73
Juveniles: *C. rossii* (13) vs. *A. albifrons* (21)	62.0	0.50

* Values for PS$_I$ range from 0 to 100, where 0 = completely dissimilar communities and 100 = completely similar communities.

† Values for J$_I$ range from 0 to 1, where 0 = completely dissimilar communities and 1 = completely similar communities.

‡ Sample sizes follow comparative group designations parenthetically.

on helminth communities. Both host species are herbivores (Ely and Dzubin, 1994; Ryder and Alisauskas, 1995), which dramatically reduces exposure to indirect life cycle helminths. This effect is indicated by the relative number of direct life cycle nematodes observed as well as their numerical dominance within the component communities of both hosts.

Forbes et al. (1999) observed a decline in prevalence and abundance of helminths in lesser snow geese and suggested that loss of helminths may be the result of limited or nonexistent recruitment during winter and spring migration. This likely had an effect on helminth assemblages in our study as well, particularly those infrapopulations of uncommon indirect life cycle species, which may have gone locally extinct within the host before the collection event. However, it should be noted that at least for Ross' geese, helminth assemblages with low species richness also can occur on the breeding grounds. Ryder (1967) reported 7 species, *Amidostomum* sp., *Epomidiostomum* sp., *Tropisurus* sp. (=*Tetrameres* sp.), *Echinostoma revolutum* (=*E. trivolvis*), *Notocotylus*

attenuatus, Z. lunata, and *Hymenolepis* sp., from a sample of 57 (40 adults, 17 young) Ross' geese collected in Canada during 1963 and 1964.

In white-fronted geese, host age did not play a significant role in the number of helminth species found. However, prevalence and abundance varied by host age in 3 of the 5 species examined statistically. Prevalence and abundance of *A. spatulatum* were higher in the adult sample whereas *A. anseris* and *T. tenuis* were higher in the juvenile sample. Forbes et al. (1999) compared mean abundance of 7 species and found 4 varied by host age or associated interaction effects. Of the 2 that varied by the host main effect of age, mean abundance of *T. tenuis* and *Drepanidotaenia lanceolata* were higher in the sub-adult sample (Forbes et al., 1999). In several species of ducks, juvenile host subpopulations tend to have more species of helminths, larger infrapopulations, higher prevalances, and higher abundances than the adult host subpopulations (Buscher, 1965; Wallace and Pence, 1986; Fedynich and Pence, 1994). Explanations for this pattern include age-specific differences in diet and immune system development, although these factors in wild geese have not been rigorously tested.

Influence of host sex on helminth community structure and pattern was evident for white-fronted geese. Species richness was somewhat higher in the female sample, with 2 additional species (*D. pulverulenta* and *Paramonostomum* sp.). Both J_I and PS_I indicated shared species, but proportions of species were more dissimilar between host sexes than that found between host age groups. Of the 5 species in which prevalence and abundance analyses could be performed, only prevalence of *T. tenuis* was significantly higher in the male sample, whereas abundance of *E. crami* was higher (although not significantly so) in the female sample and that of *T. tenuis* was higher in the male sample (although not significantly so). In lesser snow geese, Forbes et al. (1999) found slightly fewer differences in mean abundance by host sex than host age; 3 of 7 species varied by host sex or sex interaction effects (or both). Of those species, *T. tenuis* was significantly higher in the male sample. Variation in helminth communities by host sex could be attributable to differences in diet selection, time spent foraging, or differences in local habitat use. White-fronted geese are herbivores (Ely and Dzubin, 1994) so it seems unlikely that diet would account for sex-specific differences. However, Budeau et al. (1991) found snails were consumed only by prenesting females, presumably as a source of calcium for egg production. This could increase exposure of adult females to trematodes. Female white-fronted geese also spend significantly more time feeding than males during the prenesting period (Budeau et al., 1991), potentially increasing their exposure to helminth infective stages. Increased foraging time and selection for snails by prenesting females would not seem to account for the trend observed in our study of higher prevalence and abundance of *T. tenuis* in the male sample. Higher abundance of *E. crami* in the female sample could be attributable to increased foraging. Also, nonbreeding and failed breeders segregate from breeding pairs to undergo molt (Ely and Dzubin, 1994), providing at least some opportunity for differential exposure to helminths within various host subgroups and potentially influencing helminth community variation among host sexes on the breeding grounds.

Helminth species found in Ross' geese were those reported in white-fronted or lesser snow geese (or both) (Tuggle and Crites, 1984; Clinchy and Barker, 1994; Purvis et al., 1997). This supports the concept of the circulation or exchange of helminth species in closely related goose species (Neraasen and Holmes, 1975). However, on the basis of comparisons between juvenile Ross' and white-fronted goose component communities, it appears that there can be substantial differences between number of species found as well as species shared by these host species.

In conclusion, helminth communities in Ross' and white-fronted geese had relatively low species richness and were dominated numerically by nematodes with direct life cycles. Coupled with absence of helminths in a number of habitats, these findings suggest that the mainly herbivorous diet of Ross' and white-fronted geese, along with the likelihood of decreased transmission potential during winter, dramatically influenced helminth community structure and pattern in these hosts on the wintering grounds in south Texas.

ACKNOWLEDGMENTS

LITERATURE CITED

Anderson, M. G., and B. D. J. Batt. 1983. Workshop on the ecology of wintering waterfowl. Wildlife Society Bulletin 11:22–24.

Budeau, D. A., J. T. Ratti, and C. R. Ely. 1991. Energy dynamics, foraging ecology, and behavior of prenest-

ing greater white-fronted geese. Journal of Wildlife Management 55:556–563.

Buscher, H. N. 1965. Dynamics of the intestinal helminth fauna in three species of ducks. Journal of Wildlife Management 29:772–781.

Bush, A. O. 1990. Helminth communities in avian hosts: determinants of pattern. Pages 197–232 in G. W. Esch, A. O. Bush, and J. M. Aho, eds. Parasite Communities: Patterns and Processes. Chapman and Hall, New York.

Bush, A. O., K. D. Lafferty, J. M. Lotz, and A. W. Shostak. 1997. Parasitology meets ecology on its own terms: Margolis et al. revisited. Journal of Parasitology 83:575–583.

Clinchy, M., and I. K. Barker. 1994. Dynamics of parasitic infections at four sites within lesser snow geese (Chen caerulescens caerulescens) from the breeding colony at La Pérouse Bay, Manitoba, Canada. Journal of Parasitology 80:663–666.

Ely, C. R., and A. X. Dzubin. 1994. Greater white-fronted goose Anser albifrons. Pages 1–31 in A. Poole and F. Gill, eds. The Birds of North America, No. 131. The Birds of North America Inc., Philadelphia, Pennsylvania.

Fedynich, A. M., and D. B. Pence. 1994. Helminth community structure and pattern in a migratory host (Anas platyrhynchos). Canadian Journal of Zoology 72: 496–505.

Forbes, M. R., R. T. Alisauskas, J. D. McLaughlin, and K. M. Cuddington. 1999. Explaining co-occurrence among helminth species of lesser snow geese (Chen caerulescens) during their winter and spring migration. Oecologia 120:613–620.

Glass, J. W., A. M. Fedynich, M. F. Small, and S. J. Benn. 2002. Helminth community structure in an expanding white-winged dove (Zenaida asiatica asiatica) population. Journal of Wildlife Diseases 38: 68–74.

Gray, C. A., P. N. Gray, and D. B. Pence. 1989. Influence of social status on the helminth community of late-winter mallards. Canadian Journal of Zoology 67: 1937–1944.

Gregory, R. D. 1990. Parasites and host geographic range as illustrated by waterfowl. Functional Ecology 4: 645–654.

Herman, C. M., and E. E. Wehr. 1954. The occurrence of gizzard worms in Canada geese. Journal of Wildlife Management 18:509–513.

Krebs, C. J. 1989. Ecological Methodology. Harper Collins Publishers Inc., New York. 654 pp.

Magurran, A. E. 1988. Ecological Diversity and Its Measurement. Princeton University Press, Princeton, New Jersey. 179 pp.

Neraasen, T. G., and J. C. Holmes. 1975. The circulation of cestodes among three species of geese nesting on the Anderson River Delta, Canada. Acta Parasitologica Polonica 23:277–289.

Poulin, R., and S. Morand. 1999. Geographical distances and the similarity among parasite communities of conspecific host populations. Parasitology 119:369–374.

Purvis, J. R., D. E. Gawlik, N. O. Dronen, and N. J. Silvy. 1997. Helminths of wintering geese in Texas. Journal of Wildlife Diseases 33:660–663.

Ryder, J. P. 1967. The breeding biology of Ross' goose in the Perry River region, Northwest Territories. Canadian Wildlife Service Report Series 3:1–55.

Ryder, J. P., and R. T. Alisauskas. 1995. Ross' goose. Pages 1–27 in A. Poole and F. Gill, eds. The Birds of North America, No. 162. The Birds of North America Inc., Philadelphia, Pennsylvania.

SAS Institute Inc. 1990. SAS/STAT User's Guide: Vol. I, Version 6, 4th ed. SAS Institute Inc., Cary, North Carolina. 890 pp.

Schiller, E. L. 1951. Studies on the helminth fauna of Alaska. VI. The parasites of the emperor goose (Philacte canagica L.) with the description of Hymenolepis philactes, n. sp. Journal of Parasitology 37: 217–220.

Schiller, E. L. 1952. Studies on the helminth fauna of Alaska. IX—the cestode parasites of the white-fronted goose (Anser albifrons) with the description of Hymenolepis barrowensis, n. sp. Journal of Parasitology 38:32–34.

Stock, T. M., and J. C. Holmes. 1987. Host specificity and exchange of intestinal helminths among four species of grebes (Podicipedidae). Canadian Journal of Zoology 65:669–676.

Tuggle, B. N., and J. L. Crites. 1984. The prevalence and pathogenicity of gizzard nematodes of the genera Amidostomum and Epomidiostomum (Trichostrongylidae) in the lesser snow goose (Chen caerulescens caerulescens). Canadian Journal of Zoology 62:1849–1852.

Wallace, B. M., and D. B. Pence. 1986. Population dynamics of the helminth community from migrating blue-winged teal: loss of helminths without replacement on the wintering grounds. Canadian Journal of Zoology 64:1765–1773.